



Distribution widening of a ground-nesting social bee across Europe favored by climate change and urban setting

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Received 10 July 2023 – Revised 22 April 2024 – Accepted 3 May 2024

Abstract – Climate change and/or land use change were repeatedly reported as important for both range expansion of alien bee species and range shrinking for native bee species. However, environmental changes may also positively affect native species that may expand across contiguous areas to their native ones. Here, we focused on *Halictus scabiosae* (Rossi, 1790) (Hymenoptera: Halictidae), a ground-nesting, primitively eusocial wild bee that has its primary distribution in Western-Southern Europe but that was recently recorded in Eastern-Central Europe. In particular, we studied the range expansion patterns of *H. scabiosae*, and we hypothesized that previously unsuitable areas may be currently colonized because of environmental changes. In the last 5 years, *H. scabiosae* moved its densest record areas to North-Eastern Europe, but its ecological niche remained almost unchanged from 1970 to date, suggesting that this bee species is following its preferred conditions (high temperature, high temperature seasonality, and low precipitation seasonality). Potential distribution models revealed high suitability in still unoccupied North-Eastern areas, with urbanization increasingly important as potential stepping stones towards the expansion. The relevant role of urbanization is confirmed by the increase in the number of urban records through time and by the fact that cities with greater population density and greater fragmentation are more likely associated with this species' occurrence. *Halictus scabiosae* is thus expanding its range because climate change is producing—and urban environment is offering—suitable conditions in areas previously inadequate for its establishment.

Halictus scabiosae / Halictidae / climate / urbanization / species distribution models

1. INTRODUCTION

The distributions of species are limited by both physical barriers, such as mountain chains and large water bodies (Burrows et al. 2014; Warren et al. 2014), and the species' ecological niche (Pulliam 2000; Holt 2009). The ecological niche of a species encompasses different biological aspects such as inter-specific

competition, trophic associations, and physiological constraints (Soberón and Nakamura 2009). Indeed, a species can be defined by its Grinnellian niche, i.e., the habitat and environmental niche and its Eltonian niche, i.e., which emphasizes the functional attributes and the trophic position (Chase and Leibold 2003). Thus, it is consequently reflected by the favorable geographical space the species inhabits (Pulliam 2000). Furthermore, the ecological niche can be defined as *realized*, i.e., where the species actually lives, and as *fundamental*, i.e., representing all the environmental conditions

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Manuscript editor: Mathieu Lihoreau.

where the species is able to live (Peterson et al. 2011). Focusing on the physiological component of the ecological niche (i.e., Grinnellian niche) in ectothermic animals, such as insects, the climate plays certainly a key role in the distribution of many species (Pearson and Dawson 2003). Indeed, climate can affect species both directly and indirectly. First, the maximum temperature tolerance that the species can endure directly affects its distribution. Second, the thermal tolerance of the organisms used as food by a species (e.g., plants or other animals) can affect their persistence in a given area and thus consequently the persistence of the consumers (e.g., Gil-Tapetado et al. (2023)).

On the other hand, the distributions of species are not static and change through time (Lomolino et al. 2017; Huang et al. 2022). Species may expand, decrease, or shift their geographical distribution (Davis and Shaw 2001), leading either to biological colonization events (i.e., Gillespie and Roderick (2002)) or to local extinction events (i.e., Wiens (2016)).

Many species are known to have changed their geographical distributions because of the impacts of current climate change (Davis and Shaw 2001; Chen et al 2011; Huang et al. 2022). Many of these cases are relevant in terms of animal conservation, since changing environmental conditions lead many of the previously occupied areas to become unfavorable, in turn producing the reduction or the relocation of these species' distribution (Visconti et al. 2011). On the other hand, an increase of favorable climatic conditions into unoccupied areas may lead species to occupy these new areas. For example, of great conservation concern are also the numerous cases of distribution widening recorded for alien species, which under certain conditions easily become invasive and negatively impact the communities of their newly occupied areas. For example, through the well-known global warming, climate change is increasing the temperature of high-altitude and high-latitude areas, making them suitable for potentially invasive species (Boher et al. 2016; Padayachee et al. 2017), including bees (reviewed in Russo (2016), Russo et al. (2021)).

Other than climate change, land use change also plays an important role in shaping species distribution. Besides the conversion of natural areas into agricultural areas, urbanization seems to be especially relevant. The role of urbanization can have a negative or positive relationship with the distribution of many species, depending on how much the species can cope with urban conditions (Youngsteadt et al. 2017; Johnson et al. 2019; Frank and Backe 2022). Urbanization is also linked to climate change, since cities are known to present higher temperatures compared to the surrounding non-urban areas (Goward 1981; Han et al. 2014; Zhao et al. 2018), a phenomenon known as the urban heat island (UHI) effect. Such urban thermal regime can either serve as a barrier for many species or refugia for other species. Again, the beneficial effect of the UHI effect is documented for many alien and invasive species, including bees (e.g., Lanner et al. (2022)), which use cities as settlement areas and from which they could disperse to surrounding areas (Padayachee et al. 2017; Polidori et al. 2021).

Bees have an essential ecological role and provide the fundamental ecosystem service of pollination. However, there is increasing evidence for their decline (Potts et al. 2010) along with a possible reduction in their distribution (Gómez-Ruiz and Lacher 2019; González et al. 2021) because of global change. However, recent colonization of new areas by natural movements, leading to geographical expansion, was reported in several bee species (Dew et al. 2019; Rahimi et al. 2021; Sheffield and Palmier 2023).

Here, we focused on *Halictus scabiosae* (Rossi, 1790) (Hymenoptera: Halictidae) (Figure 1). This is a ground-nesting, widely polylectic wild bee species with a primitive level of eusociality and a flight season from mid-April to September (Knerer 1980; Ulrich et al. 2009; Brand and Chapuisat 2012). The species is distributed in the west of the Western Palearctic, especially in the Southern (Spain, Portugal, Italy) and Western (France, Austria, Switzerland, and southwest of Germany) Europe (Pauly et al. 2016). In 2016, this bee has been observed in areas of Eastern-Central Europe (Berlin, Germany), where it was previously never

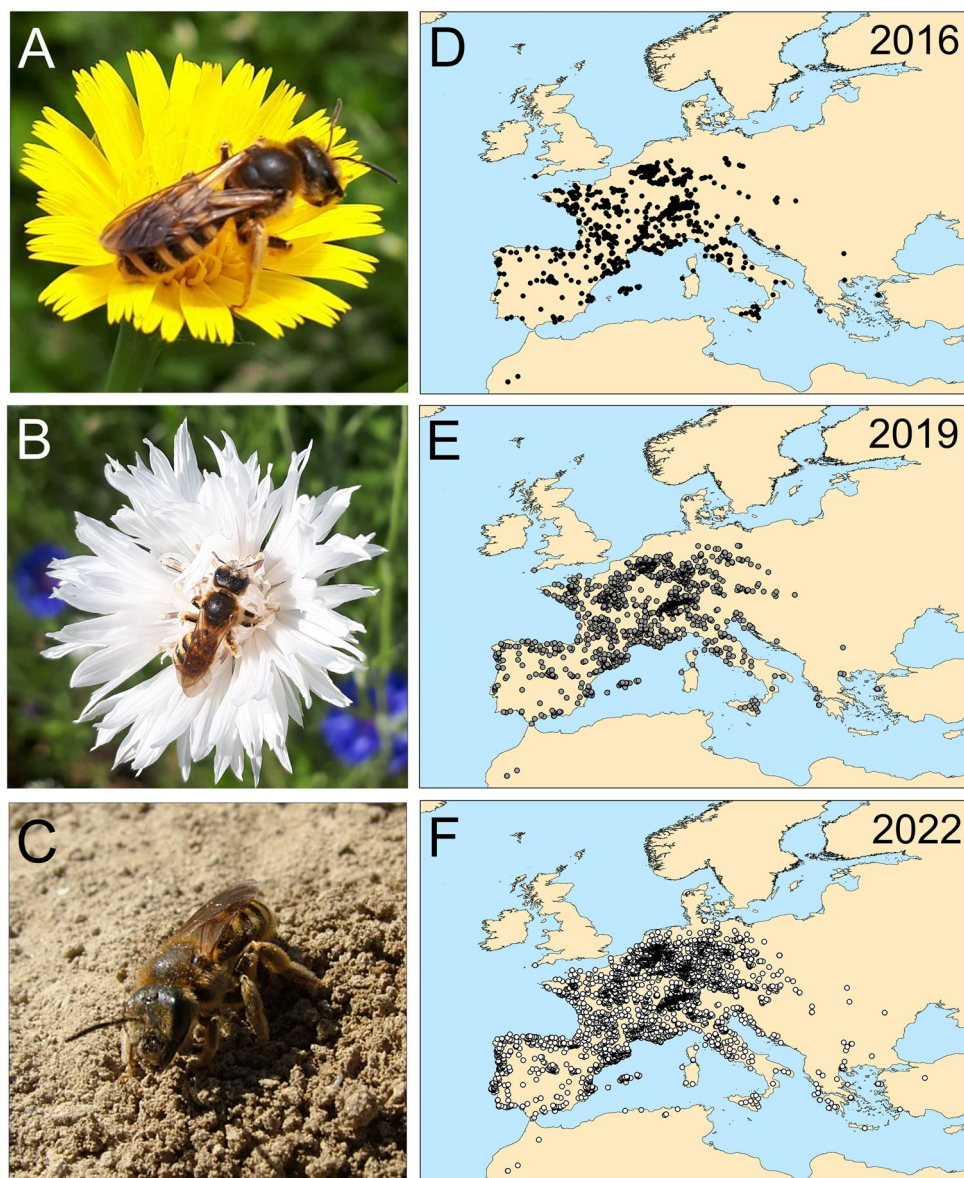


Figure 1. A–C Pictures showing females of *H. scabiosae* on flowers and on the nest. D–F Maps with all the available occurrence points of *H. scabiosae* available until 2016, until 2019, and until 2022.

recorded (Gathof et al. 2022). We hypothesized that the range expansion of *H. scabiosae* is being favored in recent years by climate change, allowing previously unsuitable areas to become suitable for establishment. Furthermore, we hypothesized that the urban environments are facilitating the colonization of these new areas, as already observed

for few other insects (e.g., Polidori et al. (2021)). To achieve our aims, we updated the distribution of the species, and we characterized its environmental (climate + land use) realized niche variation across the last years. Then, we performed species distribution models based on this niche, to determine new potential high suitability areas

for establishment and hence to roughly approximate its fundamental niche. Finally, we analyzed more in detail the role of urbanization in the range expansion process of this wild bee species by comparing traits of occupied *versus* unoccupied cities.

2. MATERIALS AND METHODS

2.1. Occurrence points

To obtain all the available geo-referenced records of *H. scabiosae* from Europe, we collected the data from the Global Biodiversity Information Facility (GBIF) (<http://www.GBIF.org>), the citizen science platforms Biodiversidad Virtual (www.biodiversidadvirtual.org), the Atlas of European Bees (Pauly et al. 2016), published works (Quaranta et al. 2004; Fortunato and Zandgiacomo 2013), and our own sampling data (uploaded in <https://observation.org/>). From this dataset, we deleted duplicate and incorrect records (i.e., records far out of range area or in water), as well as the pre-1970 occurrences. To avoid spatial bias and contagion in highly sampled areas (which occurs when the perceived suitability of neighboring habitat patches is not independent), we sieved all data on a 1 × 1 km grid, obtaining the centroids of the grids with presence points to be used in the species distribution models. We used this dataset in all the analyses except in the occurrence density point, in which all records were used (Supplementary Information DATASET.xlsx).

2.2. Environmental variables for realized niche construction

To analyze the climatic niche and the potential distribution of the species, we used the 19 bioclimatic variables of the current climate of WorldClim database version 2.1 (<http://www.worldclim.org>) (Figure S1) with 30-s cell sizes (i.e., grids of 1 × 1 km) and fitted into the western part of Western Palearctic (i.e., Europe). These bioclimatic variables present data over the period 1970–2000 and are commonly used to predict the potential distribution and

suitability of species, as indicated by temperature and precipitation patterns and their variation, which are variables overall ecologically meaningful for species, especially for ectotherms (Araújo and Guisan 2006; Peterson et al. 2011, 2015). We also used the human population density, a proxy for urbanization level, with higher human density reflecting a higher amount and density of urban-type human infrastructure and lower human density reflecting a lower amount of human influence and more rural or natural spaces. Population density was obtained from the Gridded Population of the World (GPW) (CIESIN-CIAT 2005, <https://sedac.ciesin.columbia.edu/data/collection/gpw-v3>).

To take into account the correlation among the environmental variables, a hierarchical cluster analysis based on the correlation matrix was performed, resulting in a dendrogram showing the similarity among them (Dormann et al. 2013). We used the Ward method (i.e., minimum variance clustering method), which is largely employed for this purpose (Harrell 2001). The chosen distance threshold separating different clusters was set at 0.3, i.e., 70% correlation among variables (e.g., Polidori et al. (2021), Rodrigo-Gómez et al. (2022)). To select the variables included in each cluster, we used the following criteria. First, we selected the variable that discriminates better between habitable and non-habitable areas in a previous simple environmental coverage model (see below). Second, we selected the most derived variable (or the one that is more precise to a specific period of the year) (Figure S1). Third, a variance inflation factor (VIF) was calculated (Lin et al. 2011), and those variables that overestimated the variance and contributed the most redundant information to the model (VIF > 5) were eliminated (Stine 1995; Miles 2014). Variable selection was carried out using the R v 3.5.0 program, through RStudio Software v 1.1.453 (RStudio Team 2023) using the *dismo* (Hijmans et al. 2017) and *HH* (Heiberger 2015) packages.

The final set of selected climatic variables that were used to perform all the analyses was temperature seasonality (Bio4), minimum

temperature of the coldest month (Bio6), mean temperature of the wettest quarter (Bio8), precipitation of the driest month (Bio14), precipitation seasonality (Bio15), precipitation of wettest quarter (Bio16), and precipitation of warmest quarter (Bio18), plus the human population density (Dens) (Figure S1, Supplementary Information DATAset.xlsx).

2.3. Distribution and realized niche

We analyzed the changes in the distribution of *H. scabiosae* across time considering three different years as breaks: 2016 (the first record of *H. scabiosae* in Berlin), 2019 (a mid-term period between 2016 and the current period), and 2022 (the whole current distribution). Hence, we had three periods: 1970–2016 (until 2016), 1970–2019 (until 2019), and 1970–2022 (until 2022). We performed, for each period, a point density exploration to obtain the spatial accumulation of all the collected records in Europe, hence highlighting the areas with higher density. This analysis was carried out in ArcGIS for Desktop v 10.8 (ESRI 2019) with the *Point Density* tool.

To study the relationships between the possible effect of climate change and the distribution of *H. scabiosae*, we estimated the thermal anomaly of each year from 2011 to 2022 by comparing the mean annual temperatures in those years with the mean annual temperature between 1880 and 1920 period (used as a basis) (NASA 2023, <https://data.giss.nasa.gov/gistemp/>). Then, we associated those anomaly values with the mean latitude of all the occurrences by year, as well as with the annual increase of latitude by year.

To study the possible niche changes across periods, we used the seven selected variables to calculate the niche overlap, niche equivalency, and niche similarity of *H. scabiosae* across the three periods, and we compared these values between pairs of periods (Wiens and Graham 2005; Broennimann et al. 2012; Guisan et al. 2014). We also calculated the niche expansion (% of increasing niche), niche stability (% of niche which remains stable), and niche unfilling (% of niche still to be occupied). The niche overlap between periods was calculated using

Schoener's *D* index (Schoener 1970), which varies from 0 (no overlap between niches) to 1 (whole overlap). We followed Broennimann et al. (2012) to calculate the niche equivalency (i.e., whether the niche overlap is constant when randomly reallocating the occurrences of both entities among the native and colonized areas) and the niche similarity (i.e., whether the overlap between observed niches in native and colonized areas is different from the overlap between the observed niche in one area and niches selected at random from the other area). The null hypothesis for niche equivalency cannot be rejected if the observed value of *D* falls within the density of 95% of 1000 simulated values, while the species occupies environments in both of its ranges that are more similar to each other than expected if the observed overlap is greater than 95% of 1000 simulated values. These statistical analyses were performed using the *ecospat* package (Di Cola et al. 2017) in RStudio.

Finally, to test for differences in the selected variables across the three periods, we carried out an ANOVA based on the occurrences in 1970–2016, 2017–2019, and 2020–2022. The significant ANOVAs were followed by pairwise comparisons (Student's *t*-test).

2.4. Potential distribution models and fundamental niche

We estimated the potential distribution of *H. scabiosae* in the “until 2016,” “until 2019,” and “until 2022” periods through ensemble species distribution modelling. We used six different algorithms through the *biomod2* library (Thuiller et al. 2003, 2019): generalized linear model (GLM), generalized additive model (GAM), artificial neural network (ANN), classification tree analysis (CTA), random forest (RF), and maximum entropy (MaxEnt). The ensemble models are based on the average of 60 individual models (i.e., 10 iterations \times 6 algorithms) and were used to predict the potential distribution of the studied bee species.

The construction of background and pseudoabsences was based on the simple

environmental coverage model, following previous similar studies (Gil-Tapetado et al. 2018; Rodrigo-Gómez et al. 2022). This simple model is based on those areas that had all their values within the maximum and minimum range of each selected variable, and such areas were then used to establish the background points. Those areas that did not fulfil at least two of these variables were instead used to establish the pseudoabsences points.

Presence and pseudoabsence data were split in 75/25% to generate an external AUC (area under the receiver operating characteristic curve) evaluation for the ensemble model, independently of the internal AUC evaluations (80/20%) of each individual model generated by *biomod2*. A total of 60 individual models were tested with their individual AUC evaluation, choosing only the models with AUC > 0.7 (i.e., good to excellent performance of the model following the scale of Swets (1988)). The models which fulfilled this condition were used to calculate each ensemble average model.

Finally, ensemble models were evaluated through the external AUC test with 25% of the data. The *cut-off* values for each final ensemble model were calculated with the total sum of squares (TSS) of the ensemble model (until 2016 = 0.61; until 2019 = 0.72; until 2022 = 0.74) to establish the areas of the presence of *H. scabiosae* by each period. We also obtained the significance of each studied variable and performed ANOVAs for each variable comparing 10,000 random points within the areas of presence defined by the *cut-off* value for each period. Species distribution models were carried out using the R v 3.5.0 program, through RStudio Software v 1.1.453. Maps were built in ArcGIS for Desktop v 10.8.

2.5. Land use and the effect of urban traits

We compared the accumulation of occurrences along time (2011–2022) slotted in three different categories: urban, forest, and pasture. These categories were associated with occurrence points by joining the original CORINE Land Cover categories as follows: urban, 1–11; forest, 15–17,

22–25, and 29; and pasture, 12–14, 18–21, and 26–28. The remaining categories (e.g., beaches, dunes, sands or glaciers, and perpetual snow) were ignored because they were irrelevant. With these three major categories, we then calculated the average cumulative number of records and fitted these values to simple exponential models.

To explore how urbanization traits can affect the presence or absence of *H. scabiosae* in cities (i.e., regardless of climatic variables), we obtained the variables retrieved from cities where this bee species has or has not been found in published works based on intensive and standardized urban samplings. The considered city traits follow those selected in the global analysis of Ferrari and Polidori (2022), i.e., surface (city size), human population size and density, the ratio between green areas and impervious surfaces (green/impervious), and normalized edge density green (ED green, a measure of fragmentation). We consulted the compiled data of Ferrari and Polidori (2022) to obtain European cities with the presence or absences of *H. scabiosae* (i.e., where the species has not been reported in any inventory study and is not known to occur), adding three more cities (Madrid, Milan, and Rome), where the presence of this species was confirmed. The city borders were downloaded from Eurostat <https://ec.europa.eu/eurostat/web/main/home>; the land use information for the analyses was based on CORINE Land Cover and was downloaded from Copernicus Global Land Service (Buchhorn et al. 2020), and the green/impervious and ED green have been calculated in QGIS 3.16 with LecoS–Landscape Ecology Statistics 3.0.1 (Jung 2022) plugin, following the methodology described on Ferrari and Polidori (2022). We retrieved surface, population size, and population density for each city from <https://www.wikipedia.en>. Finally, to verify which urban variables influence *H. scabiosae* occurrence in a city, we compared the median values of the urban variables with a Mann–Whitney test between cities with or without bee presence.

3. RESULTS

Overall, we retrieved 5460 georeferenced records of *H. scabiosae* (Figure 1). The comparison of occurrence density across periods (until

2016, until 2019, and until 2022) indicates that the densest areas have changed their location, appearing in the last years in more Northern and more Eastern areas in Europe. In particular, the bee species has recently colonized parts

of Germany, Netherlands, and Czech Republic, all countries with null to few records until 2016 (Figure 2A). A further increase of colonization of these areas can be also appreciated from 2018 to 2022 (Figure 2B–C). However, the

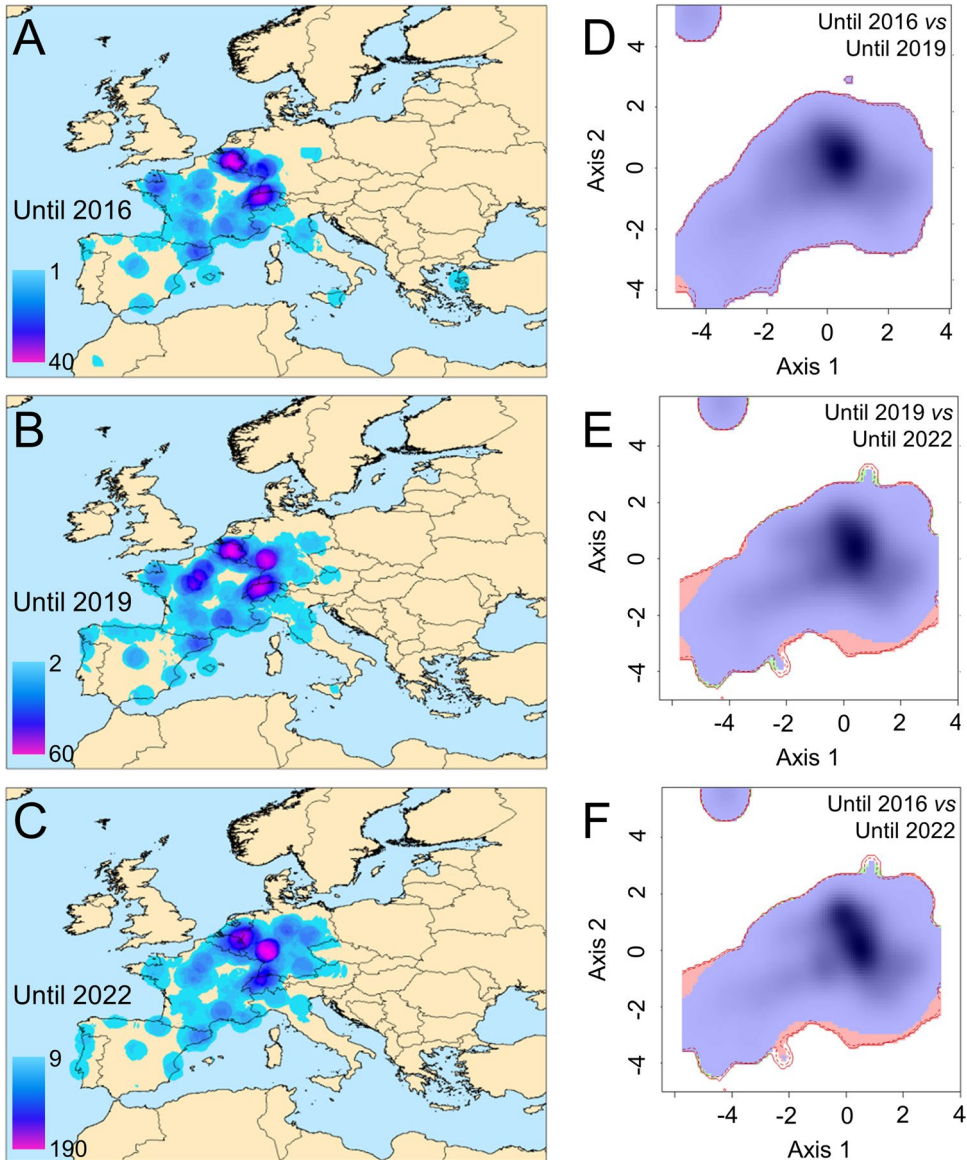


Figure 2. A–C Occurrence density of *H. scabiosae*. Magenta-colored areas indicate areas of high density, and light blue-colored areas indicate areas of lower occurrence density. D–F Comparison of climatic niches of *H. scabiosae* across periods. Colors indicate niche expansion (red), stability (blue), and unfilling (green). Darker shading indicates a higher density of species occurrences in each period.

climatic niche of *H. scabiosae* remained almost unchanged in across the three periods (Figure 2D–F). The comparison among the periods showed that the niche of *H. scabiosae* remained essentially stable (99.82% on average across the three periods), similar though not equivalent (Table I). The highest niche overlap (Schoener's *D* index) was found between the first two periods (until 2016 and until 2019), while the lowest value was found between the first (until 2016) and the last (until 2022) periods. Niche expansion was overall low with a little increase in 2022 (Table I). Hence, the ecological niche of *H. scabiosae* effectively remained largely unchanged between 1970 and 2022, despite the important expansion of its geographical range.

While the niche of *H. scabiosae* seemed to be stable, we detected subtle but significant changes in the climate and urbanization variables associated with the occurrences across the periods (1970–2016, 2017–2019, and 2020–2023). In particular, there has been an increase in temperature seasonality ($F = 18.75$, $p < 0.0001$), in minimum temperature of the coldest month ($F = 29.13$, $p < 0.0001$), in mean temperature of the wettest quarter ($F = 29.61$, $p < 0.0001$), in precipitation of the wettest quarter ($F = 6.142$, $p = 0.0022$), and in population density (i.e., urbanization) ($F = 10.84$, $p < 0.0001$) (Figure 3). Some of these changes can be appreciated

already from 2016 to 2019 and then from 2016 to 2022, while others appeared from 2019 to 2022. Precipitation of the driest quarter did not change ($F = 2.986$, $p = 0.0506$), while lower precipitation seasonality appeared between 2016 and 2019, compared with the other periods ($F = 6.998$, $p = 0.00092$) (Figure 3).

The species distribution models (Figure 4) showed an increase of high suitability areas towards Northern and Eastern Europe in each of the three considered periods, as well as an increase across the periods. For example, in the model based on the records until 2016, the bee species was predicted to expand to North and colonize the UK, Denmark, and Southern coasts of Scandinavia (Figure 4A). Such suitability in the Scandinavian territories has even increased in more recent times, as shown by models based on the records until 2018 and until 2022. Interestingly, some areas in Southern Europe, and in particular the Iberian Peninsula (and to a lesser extent also Southern Italy), would suffer a weak but appreciable reduction of suitability from 2016 to 2022. The most important variables that define the potential distribution of *H. scabiosae* (Table II) were the minimum temperature of the coldest month, the temperature seasonality, and the precipitation of the wettest quarter. The former variable decreased in importance from the

Table I Niche expansion, niche stability, niche unfilling and niche overlap (Schoener's *D*) of *H. scabiosae* in the three periods (1970–2016, 1970–2019, 1970–2022) and results of niche equivalency test and niche similarity test among periods. Measures of niche expansion and unfilling are based on the 90th percentiles of the common environment between ranges. Niche overlap (Schoener's *D*) values are compared with 1000 simulated data sets for the three periods. p = probability value

Parameter	Until 2016 vs until 2019	Until 2016 vs until 2022	Until 2019 vs until 2022
Niche expansion (%)	0.031	0.300	0.214
Niche stability (%)	99.969	99.700	99.786
Niche unfilling (%)	0.000	0.085	0.033
Niche overlap (<i>D</i>)	0.894	0.699	0.777
Niche equivalency (p)	0.109	1.000	0.970
Niche similarity (p)	0.010	0.069	0.050

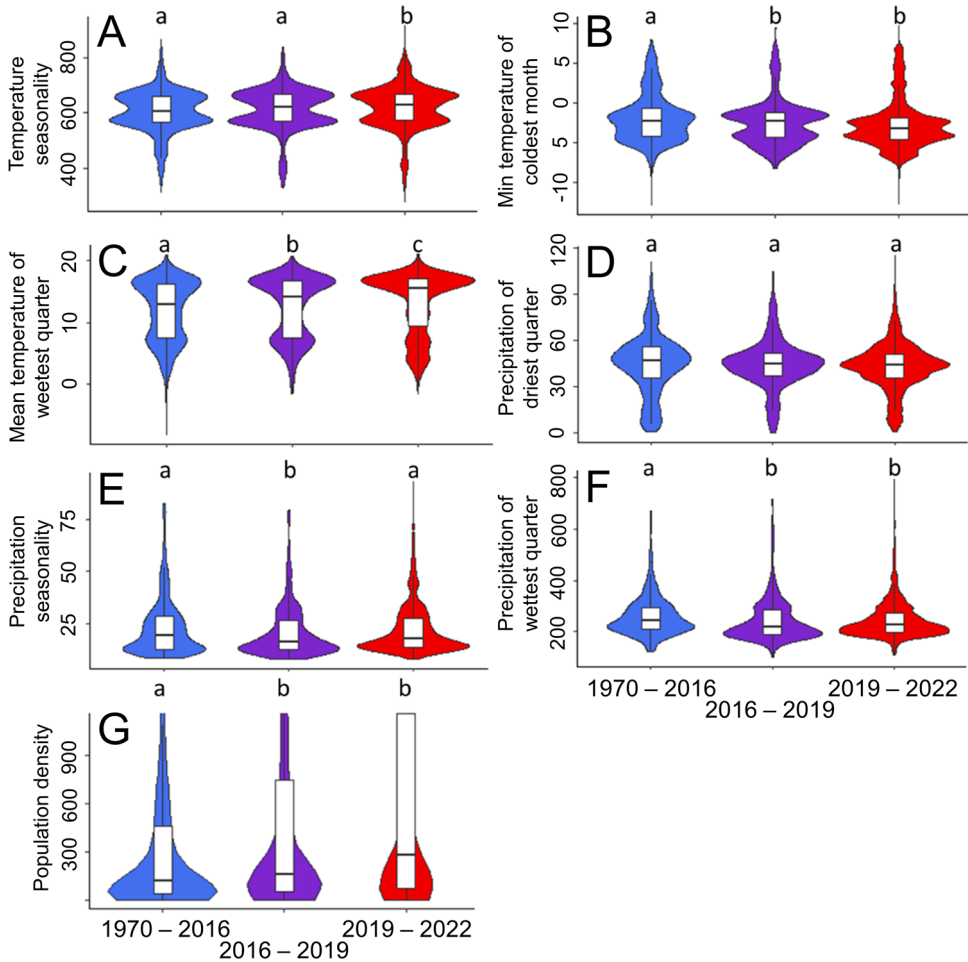


Figure 3. Violin and Box and Whisker plots showing the value distribution of the environmental variables (A–G), associated with the occurrence records in the three periods. Significantly different groups are denoted by a and b for each variable following ANOVA.

2016 model to the 2022 model, while urbanization increased in importance across periods (Table II). Other variables were less important (Table II, Figure S2). As in the comparisons based on the occurrences across periods, also using the models' output data, there were significant differences in some variables among periods, such as an increase of temperature seasonality ($F=29.08$, $p<0.0001$), precipitation seasonality ($F=61.41$, $p<0.0001$), and urbanization ($F=16.71$, $p<0.0001$) (Figure 4B). Mean temperatures and precipitation values also varied across periods (Figure S2).

Variation in the latitude of records, as well as the mean latitude of records, was positively associated with thermal anomaly through the years (Figure 5A) (mean latitude: estimate = 2.0282, t value = 2.366, $p=0.0396$; variation in latitude: estimate = 0.4913, t value = 2.445, $p=0.0345$). That is, global warming is constantly adding species' records towards Northern areas. The accumulation of occurrences of *H. scabiosae* through time, separated by habitat type (Figure 5B), showed an exponential increase of records in the last years for all habitats, indicating an ongoing important increase in geo-referenced information

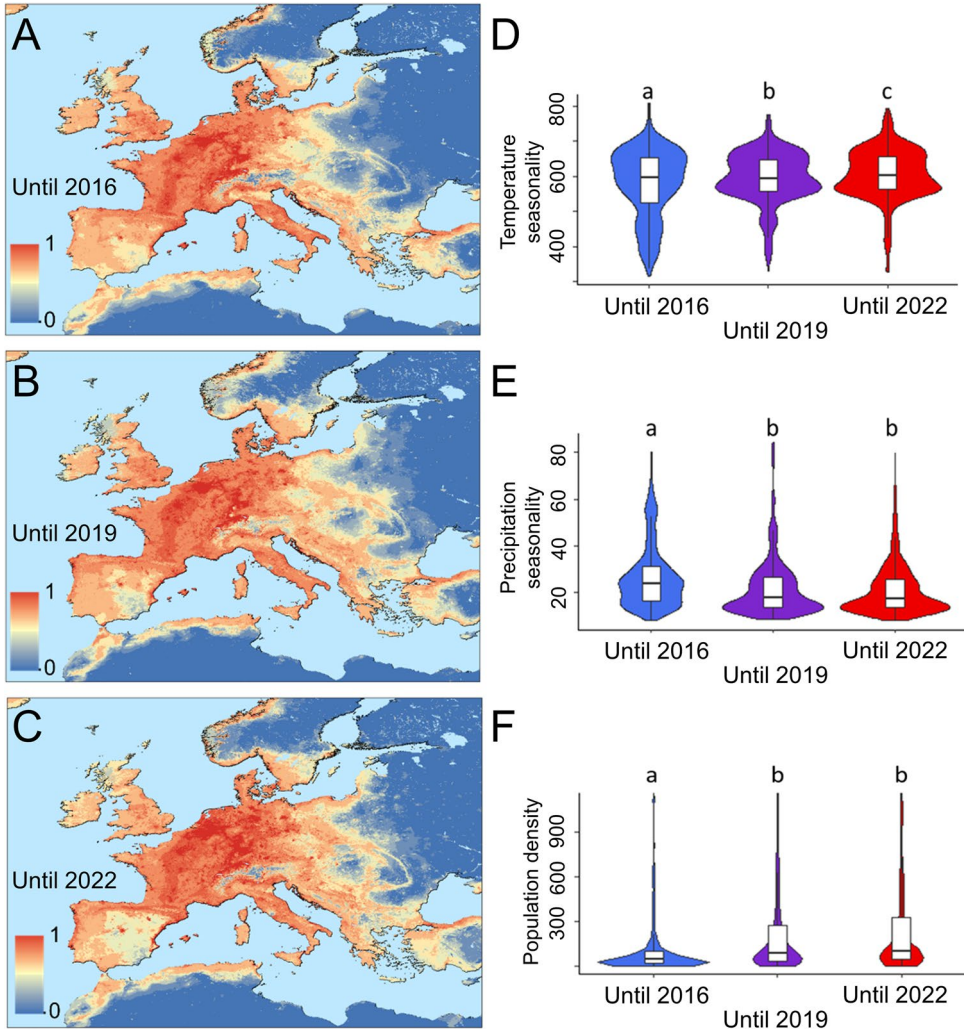


Figure 4. A–C Maps of species distribution models considering the three different periods (1970–2016, 1970–2019, and 1970–2022). D–F Violin and Box and Whisker plots showing the value distribution of three relevant environmental variables associated with 10,000 random points in high suitability areas from each model across the three periods. Significantly different groups are denoted by a and b for each variable following ANOVA.

on this wild bee. However, the accumulation of occurrences also showed different patterns depending on the habitat type. In fact, while pasture records remained the most abundant across years, the urban records abruptly increased since 2019, surpassing in number the forest records (and the overall average number of records) until 2022

(Figure 5B). Hence, urbanization is increasingly becoming important for this species' settlement in new areas. Furthermore, *H. scabiosae* is more likely to be found in more heavily urban environments, i.e., in European cities with greater population density and greater green areas fragmentation (ED green) (Table III, Figure 6).

Table II Variable importance for each used algorithm for the models of the three periods (1970–2026, 1970–2019, and 1970–2022). Mean and standard deviation are also included. *ANN* artificial neural network, *CTA* classification tree analysis, *GAM* generalized additive model, *GLM* generalized linear models, *MAXENT* maximum entropy, *RF* random forest, *Bio4* temperature seasonality, *Bio6* minimum temperature of the coldest month, *Bio8* mean temperature of the wettest quarter, *Bio14* precipitation of the driest month, *Bio15* precipitation seasonality, *Bio16* precipitation of the wettest quarter, *Dens* human population density

	Bio4	Bio6	Bio8	Bio14	Bio15	Bio16	Population density
2016							
ANN	13.37	29.43	12.86	11.61	32.00	65.73	10.82
CTA	44.56	38.79	0.04	10.72	4.72	6.64	3.44
GAM	24.12	49.85	0.27	8.78	13.12	18.37	1.50
GLM	21.71	51.19	0.00	0.68	7.62	18.35	0.54
MAXENT	13.89	32.21	8.79	3.80	18.86	4.33	13.51
RF	20.72	22.64	20.54	14.70	22.53	8.43	23.33
Mean	23.06	37.35	7.08	8.38	16.47	20.31	8.86
SD	11.39	11.45	8.53	5.22	10.11	23.04	8.81
2019							
ANN	10.23	46.39	1.84	13.59	23.69	52.91	4.45
CTA	44.71	14.97	0.00	35.77	3.11	10.80	15.59
GAM	38.05	22.77	0.25	26.88	36.97	44.72	1.85
GLM	39.68	25.50	0.00	5.89	11.75	29.97	0.00
MAXENT	24.89	22.12	11.01	2.16	32.87	13.05	21.41
RF	22.22	14.44	15.45	12.67	19.46	6.85	21.80
Mean	29.96	24.37	4.76	16.16	21.31	26.38	10.85
SD	13.06	11.67	6.74	12.80	12.73	19.26	9.93
2022							
ANN	20.10	20.96	3.58	10.94	28.76	55.00	25.90
CTA	33.14	29.30	0.00	12.63	6.72	21.09	11.67
GAM	24.20	34.84	0.10	12.78	23.98	37.32	0.17
GLM	22.92	35.55	1.11	1.68	14.06	33.86	0.19
MAXENT	21.40	18.85	8.17	0.97	17.47	9.78	22.79
RF	19.31	10.34	10.71	10.84	12.52	4.90	20.59
Mean	23.51	24.97	3.95	8.31	17.25	26.99	13.55
SD	5.05	9.96	4.52	5.47	8.02	18.75	11.39

4. DISCUSSION

The distribution of *H. scabiosae* has experienced a clear expansion in the last years towards North-Eastern Europe, and this seems to be driven by climate change and an increasing use of urban habitats. Our collected data, as well as previous publications, indicate that there were no records of *H. scabiosae* in Eastern-Central Europe

until the observation in Berlin in 2016 (Pauly et al. 2016; Dew et al. 2019; Gathof et al. 2022). The potential distribution model further predicted such range expansion, up to Northern countries (e.g., in Scandinavia) that are still not occupied.

Most of the previous studies on bee geographical range variation in recent times revealed a reduction, rather than an expansion, of occupied areas. Many North American and European

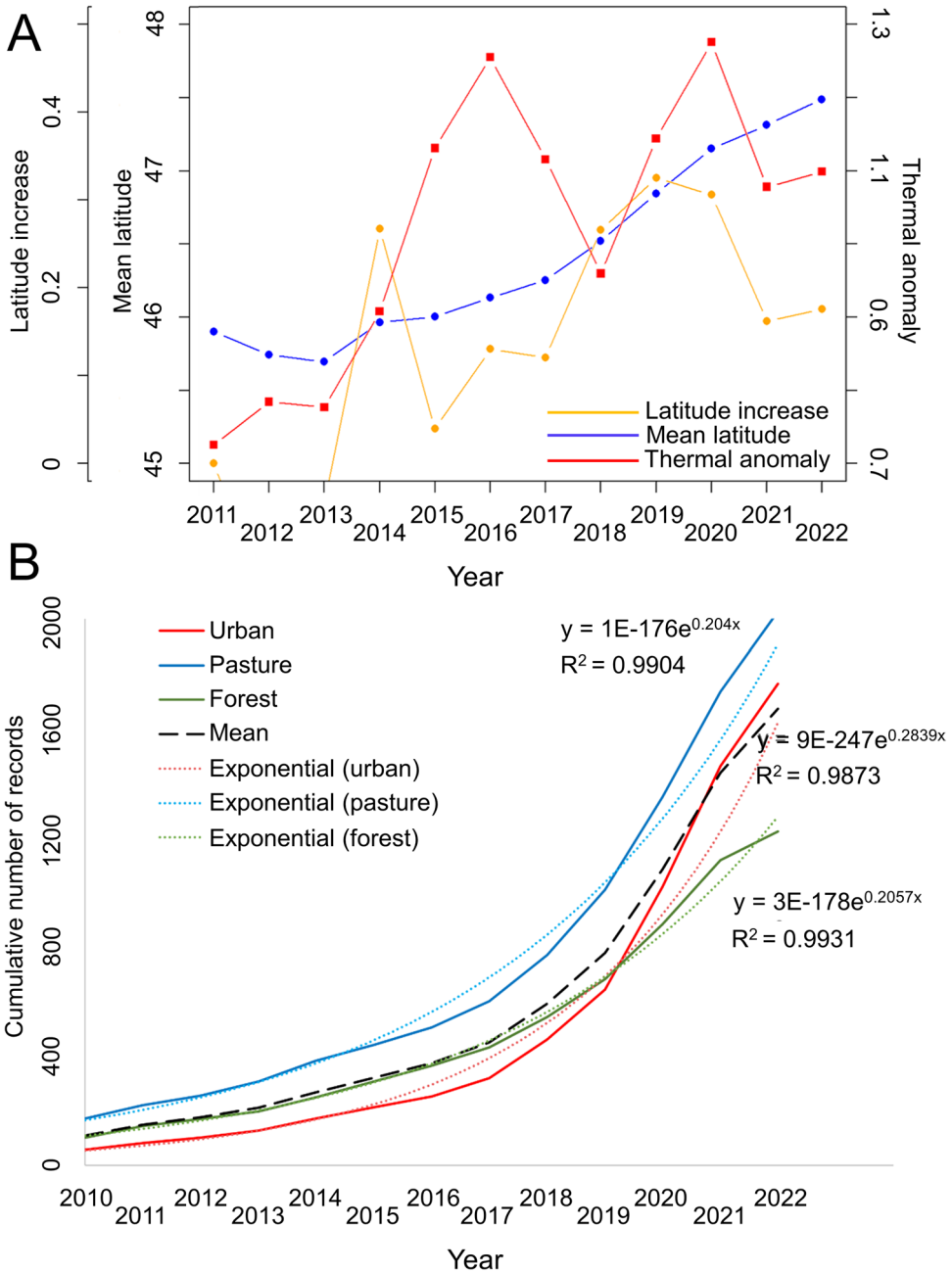


Figure 5. **A** Relationship between the annual mean latitude of the occurrences of *H. scabiosae* (blue), the annual increase of latitude (orange), and the annual thermal anomaly (red). **B** Annual cumulative occurrence records for *H. scabiosae* considering the type of land cover: urban (red), pasture (blue), and forest (green). Mean, tendency curves, and the corresponding R^2 values and equations were included.

Table III Results of *U* Mann–Whitney analyses of presence and collated absences of *H. scabiosae* in European cities and different urban variables: surface (city size), population size and density, green/impervious (the ratio between green areas and impervious surfaces), and ED green (normalized edge density green)

Parameter	<i>U</i> (value)	<i>z</i> (value)	<i>p</i>
Surface	32	0.050	0.956
Population size	22	1.055	0.291
Green/impervious	25	0.754	0.451
Population density	13	1.960	0.050
ED green	11	2.162	0.030

studies on the genus *Bombus* highlighted a decline in populations due to climate change (Cameron et al. 2011; Jacobson et al. 2018; Kerr et al. 2015), with consequent range reduction especially in the Southern areas (e.g., Rasmont et al. (2015) and Sirois-Delisle and Kerr (2018)). While Northern areas may become more suitable, as predicted by potential distribution models, it is likely that not all species may shift into

such new areas to escape from the increasingly hotter Southern sites (Kerr et al. 2015; Pyke et al. 2016; Imbach et al. 2017; Sirois-Delisle and Kerr 2018; Martínez-López et al. 2021). Similarly, the distribution of several bee species in the Neotropics seems to shrink due to climate change (Faleiro et al. 2018; Giannini et al. 2020). In general, the most threatened bee species would be those with a specialized resource use and those with limited dispersal capabilities (Casey et al. 2015; Rasmont et al. 2015; Nemésio et al. 2016; Buckner and Danforth 2022).

However, climate change may also convert harsh areas to more suitable ones, possibly leading to colonization events (Kerr et al. 2015), as shown by recent evidence of bee species shifting their range without disappearing from their historical one. These evidences include colonization events increasingly observed for alien/invasive bee species (Russo 2016; Polidori and Sánchez-Fernández 2020; Lanner et al. 2021; Russo et al. 2021; Gutierrez et al. 2023), but also expansion by naturally adding new areas which are contiguous with their historical ones (Martins et al. 2015; Silva et al. 2015; de Oliveira et al. 2018; Dew et al. 2019; Rahimi et al. 2021; Sheffield and Palmier

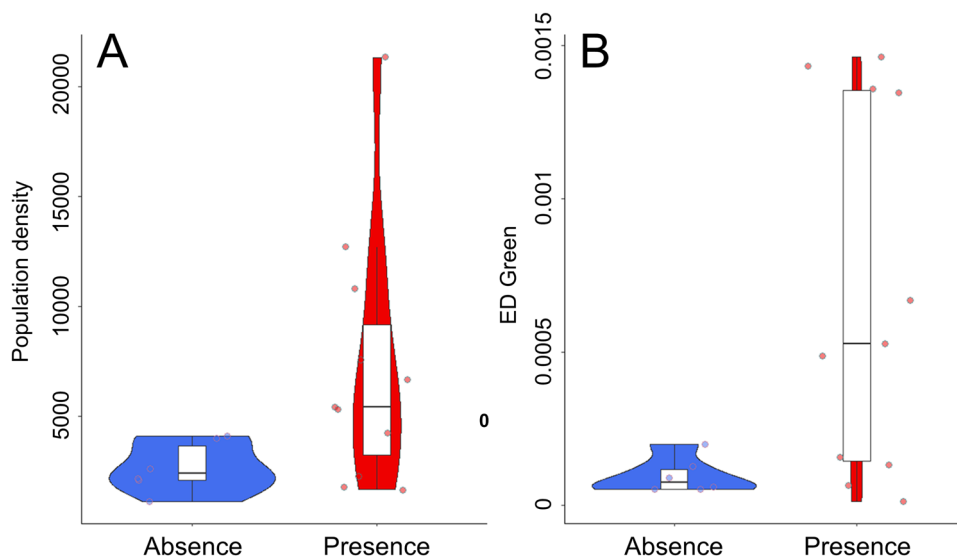


Figure 6. Violin and Box and Whisker plots showing the value distribution of the two most relevant environmental variables in European cities with either presence or absence of *H. scabiosae* (see Table III).

2023). *Halictus scabiosae* seems a further example of the latter phenomenon, though our models open to the possibility that in the future Southern European areas—currently greatly occupied—may become progressively more unsuitable due to global warming.

Because of the great niche stability observed across periods, it appears that *H. scabiosae* is colonizing areas having a priori the same conditions of its historical range, perhaps suggesting that this species cannot adapt easily to new conditions. Our results differ from other studies of insects after introducing them to new areas which are not contingent to their native ones. Indeed, while introductions to non-native areas are often accompanied by niche shift (i.e., a shift of density of occurrence within the niche space, or expansion or retraction of the niche limits) (e.g., Bates et al. 2020; Polidori and Sánchez-Fernández 2020; Zhou et al. 2023), a simple expansion of the native range generally is not expected to come with such a shift, exactly as observed here. More studies analyzing natural expansions rather than introductions outside the native range could help assess the generality of this pattern. Until recent years (mid-2010), probably North-Eastern Europe was overall unfavorable for this wild bee species. Our results indicate that there is a significant and positive relationship between the thermal anomaly and the increase in mean annual latitude, suggesting indeed an effect of climate change on the distribution change of *H. scabiosae*. Certainly, the predictions based on the ecological niche inferred from distribution records do not always reflect the actual physiological tolerances, but they can still be an important starting point to evaluate potential distributions (Kerr et al. 2015).

In addition to climate change, our results showed that *H. scabiosae* is increasingly using urban sites for establishing, while expanding its range, and that it is especially settling in strongly urbanized locations. This could be due to the fact that in Europe, at higher latitudes, characterized by lower temperatures, cities show a higher temperature through the UHI effect. The range expansion of this bee species in North-Eastern Europe seems to be thus facilitated by

urban areas through the UHI effect. This use of warmer urban sites as “checkpoints” in the colonization of overall colder areas was also documented in another hymenopteran species, the mud-nesting wasp *Sceliphron curvatum* (Smith, 1870) (Sphecidae) (Polidori et al. 2021), which is finding very suitable (hotter) areas in European Northern cities surrounded by less-suitable (colder) areas.

While we cannot exclude that cities may be attractive for *H. scabiosae* also because of higher flora diversity from ornamental plants (Baldock et al. 2015; Beninde et al. 2015; Hall et al. 2017; Theodorou et al. 2020), we may exclude that cities are offering further abundant fundamental resources, such as nesting sites, to this bee species. In fact, while aerial-nesting species (i.e., bees nesting in wood tunnels) seem to be favored in urban habitats, which offer rich man-made structures that can be exploited for nesting (Ayers and Rehan 2021), large amounts of impervious surfaces seem to limit nesting opportunities for ground-nesting species (Threlfall et al. 2015; Quistberg et al. 2016). Indeed, not surprisingly, invasive bee species heavily using urban habitats while expanding their range are aerial nesters (Fitch et al. 2019; Geslin et al. 2020). However, *H. scabiosae* can still settle in urban parks and green areas within the cities, and it is likely exploiting such areas very efficiently while expanding its range. *Halictus scabiosae*, as most eusocial Halictidae, often nest at high density. Thus, they preferentially nest in hard and compact soils that can support the subterranean structure of multi-tunnel, aggregated nests (Cane 1991; Potts and Willmer 1997; Polidori et al. 2010; Antoine and Forrest 2021). Urban parks rarely have very sandy soils, and thus, urban park soil may be suitable for this species. The strong use of urban habitats by *H. scabiosae* also matches with the general trend, at global scale, that cities with highly fragmented green areas present a higher proportion of both eusocial species and large-bodied bees (Ferrari and Polidori 2022).

Though we do not know if *H. scabiosae* is representing or will represent a disturbing

component in the new European colonized areas, we can highlight some points that may preliminarily suggest limited negative impacts. First, the geographical expansion of this species is occurring through new continental regions which are contiguous with the ancestrally occupied ones. This does not match with the typical scenario of alien bee species, which usually move to disjunct areas, often negatively impacting the newly exploited habitats (e.g., Graham et al. (2019)). Second, *H. scabiosae* is known to possess a highly tolerant behavior (González et al. 2018), making it unlikely to engage in heavy inter-specific competition with other bees through aggression (in opposition to what found for invasive bee species (Roulston and Malfi 2012)). Being a ground-nesting species, *H. scabiosae* would also compete with few local bee species for nesting sites in cities, since ground-nesting bees seem generally poorly represented in urban habitats (see above). However, it is true that in the case of a high abundance of *H. scabiosae*, competition for nesting areas may increase up to a level that may lead to the displacement of the other ground-nesting bee species in cities. Third, unlike what often happens for invasive bee species (e.g., Arbetman et al. 2013), the expansion across Europe makes highly unlikely the introduction of new pathogens by this species and thus pathogen spillover with other bees in the new areas. Furthermore, a recent study revealed microparasite infections to be rare in a French population of *H. scabiosae* (Tuerlings et al. 2023). Hence, the range expansion of *H. scabiosae* may effectively contribute to pollination services in the new territories without negatively impacting the local bee fauna (Wenzel et al. 2020; Ghisbain et al. 2021). However, precise data on the ecological interactions of this bee species with other native ones are necessary to confirm this suggestion.

Finally, our study highlights the potential of citizen science to study changes in bee species' distribution. Indeed, the occurrence data of *H. scabiosae* used in our study mainly comes from citizen science photo-sharing platforms, based on the georeferenced photographs of many amateur collaborators. This type of data for insects has increased in recent years

and can be used to study biological colonization (Pusceddu et al. 2019; Gil-Tapetado et al. 2023), especially for easily recognizable species (McGeoch 1998; Chowdhury et al. 2023) such as *H. scabiosae*. There are some clear obstacles to the recognition of many wild bee species from photographic sources, but a citizen science approach may in the future be used to monitor certain iconic and easily recognizable species. Importantly, these data can introduce biases into ecological studies if carried out without proper methodologies (e.g., Geldmann et al. (2016)). For example, without proper data filtering, the number of records from locations with potentially more photographable individuals can disproportionately increase. Furthermore, areas that are simply easier to access may allocate a greater abundance of records. In our study, by sieving all records to one per 1×1 km grid, we likely avoid such type of biases. At last, citizen science approaches may engage the public in dissemination activities, raising awareness of the risks wild bees face in disturbed environments.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1007/s13592-024-01077-5>.

ACKNOWLEDGEMENTS

We thank Anita Grossmann for the stimulating discussion about the expansion of *Halictus scabiosae* in Europe.

AUTHOR CONTRIBUTION

Carlo Polidori and Diego Gil-Tapetado conceived the study; Diego Gil-Tapetado, Carlo Polidori, Federico Ronchetti, and Andrea Ferrari collected the data; Diego Gil-Tapetado, Carlo Polidori, and Andrea Ferrari analyzed the data; Diego Gil-Tapetado and Carlo Polidori wrote the manuscript; all authors read, revise, and approved the final version of the manuscript.

FUNDING OPEN ACCESS FUNDING PROVIDED BY UNIVERSITÀ DEGLI STUDI DI MILANO WITHIN THE CRUI-CARE AGREEMENT.

DATA AVAILABILITY

All data analyzed during this study are included in this published article (and its supplementary information file DATASET.xlsx).

CODE AVAILABILITY

Not applicable.

DECLARATIONS

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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