

Long-term changes in the composition and distribution of the Hungarian bumble bee fauna (Hymenoptera, Apidae, *Bombus*)

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Abstract

One of the most important pollinator taxa is *Bombus* (Hymenoptera, Apidae), the genus of bumble bees, since they are important, often specialized, pollinators of many plants. As a result of climate change, warming winters and changes in landscape structure, the distribution and frequency of *Bombus* species is constantly changing. To develop appropriate protection strategies, it is essential to monitor them and update the occurrence and threat status of the species.

The last review of the distribution of *Bombus* species in Hungary was completed 20 years ago. Here we present updated distribution maps based on published data from the last 20 years together with unpublished data collected in 2018–2021. Based on the new data, we examine changes in the last two decades. In the case of 9 species further studies should be carried out to confirm the presence of stable populations, while 3 species are recommended for protection by law in Hungary. Seven species showed increasing frequency, *B. argillaceus* and *B. haematurus*.

Keywords

bumble bee, climate change, distribution data, distribution map, pollination, threatened, UTM

Introduction

Due to the intensification of agriculture and spreading urbanization, landscape diversity is decreasing with a parallel increase of air, water and soil pollution throughout Europe (Luck et al. 2004; Gaston 2005; Firbank et al. 2008). The biodiversity of both natural and cultivated lands is becoming poorer and eurytopic, while invasive species are becoming more frequent (Stoate et al. 2002). Pollination is one of the most important ecosystem services (Williams 1994; Klein et al. 2007; Ricketts et al. 2008; Ollerton et al. 2011), but these effects and the intensive use of pesticides endanger it through decreasing the species richness and abundance of pollinators, such as bumble bees (Apidae: *Bombus* spp.) (Williams 1989; Kearns et al. 1998; Brittain et al. 2010). The bumble bees are one of the most important and specialized pollinators of both wild and cultivated flowering plants in the Northern Temperate Zone, especially where and/or when the temperature is too low for honey bees to do well (O'Toole and Raw 1991; Kearns and Inouye 1997; Steffan-Dewenter and Tscharrntke 1999; Kremen et al. 2002; Knight et al. 2005; Potts et al. 2010). Bumble bees are adapted to different nectar sources with their body size, morphology, and length of tongue (Inouye 1980; Williams 1986; Corbet 1996; Osborne and Williams 1996; Kearns and Thomson 2001; Raine and Chittka 2007). They are important pollinators of legumes, including cultivated alfalfa and clover (Anasiewicz and Warakomska 1969, 1977; Ruskowski and Bilinski 1969; Ruskowski 1971; Warakomska and Anasiewicz 1991; Tanács et al. 2009), rape seed, fruits such as apple, raspberry, blueberry and strawberry, vegetables such as tomato, green pepper, bean and cucurbits (pumpkin, melon, cucumber), and more than a thousand wildflowers (Goulson 2003). In a wider sense, they have an important role in maintaining natural- and agro-ecosystems and agricultural production (Senapathi et al. 2021).

The intensity and success of pollination are negatively affected by the decrease in the diversity and abundance of wild bees (Williams 1982; Donath 1985; Williams 1986; Rasmont 1988; Corbet et al. 1991; Buchmann and Nabhan 1996; Westrich 1996; Allen-Wardell et al. 1998; Goulson et al. 2005, 2008; Biesmeijer et al. 2006; Winfree et al. 2008; Williams and Osborne 2009; Potts et al. 2010; Szabó et al. 2012; Kerr et al. 2015). The survival probability of bumble bee populations has decreased by ca. 17% in Europe since the beginning of the 20th century (Soroye et al. 2020). Furthermore, due to the shift and loss of their area, the species composition of the bumble bee faunas of different regions is continuously changing (Novotny et al. 2021).

The last overview of the Hungarian bumble bee fauna was published in 2003 (Sároszpataki et al. 2003). In order to develop our knowledge and help to conserve and maintain the diversity of bumble bees, we summarize the published, unpublished and our newly collected distribution data and provide check-list and distribution maps of the Hungarian bumble bee fauna. The frequencies of species were calculated and compared with the values from 2003.

Materials and methods

The former distribution database of Hungarian bumble bee fauna used a 10×10 km UTM system (Sároszpataki et al. 2003). We built a new database combining the earlier data and the newly collected data. This new database contains partly published data of Jenő Papp collected between 1960 and 1970, Zsolt Józán collected between 1960 and 2019, Miklós Sároszpataki collected after 2000 and data of Dóra Arnóczkyné Jakab and Antal Nagy collected between 2018 and 2021. Data from the “izeltlabuak.hu” website (izeltlabuak.hu 2021, licence: CC BY 4.0) were also used after revision by the authors, as were the published data of Tanács et al. 2008, Szabó and Endes 2010, Kovács-Hajdu et al. 2014, Vaskor et al. 2015 and Tóth et al. 2017.

In the case of data collected after 2003, transect counts and direct search are used. Data collected in 2018–2021 with volatile traps designed for noctua pests were also added by Dóra Arnóczkyné Jakab and Antal Nagy. For identification of the collected materials, the keys of Móczár (1985) were used. Identification of two species pairs are problematic, so that data for *Bombus hortorum* / *B. ruderatus* (Figs 11, 12, 24) (Williams and Hernandez 2000), and *B. terrestris* / *B. lucorum* (Figs 17, 30, 31) (National Biodiversity Data Centre 2012; Bossert 2015) are presented on separate maps.

The database contains the following data by species: sampling site with GPS coordinates and/or locality name, sampling dates, and data source. In the original data set, Sároszpataki et al. (2003) used three periods to describe the chronology of data collections. Here, we add a fourth period for data collected after 2000. Data collected in different periods are marked with different signs in the distribution maps: +: before 1954, ×: between 1954–1970, ○ (empty circle): between 1971–2000 and ■ (grey square): after 2000. These signs differ from the original ones in order to clearly indicate the chronology of the data.

Bombus elegans is now recognized as a junior synonym of *B. distinguendus* (Williams 2011). As there were no new data for *B. bohemicus*, *B. consobrinus*, *B. distinguendus*, *B. fragrans*, *B. cullumanus serrisquama*, *B. subterraneus*, and *B. sylvestris*, as reflected in the maps (Figs 5, 8, 9, 27, 29, 33).

The relative frequencies of the species (*RF%*) were calculated based on the formula of Sároszpataki et al. (2003), which provide information about the spatial constancy of a given species:

$$RF\% = \frac{\text{number of cells occupied by species}}{\text{total number of UTM cells containing data}} \times 100$$

This index was used for comparison of former and newly calculated values. The frequency categories of species were recalculated also using this index and the original categories of Sároszpataki et al. (2003): I = rare (1–10%), II = moderately frequent (11–20%), III = frequent (21–40%), IV = common (>40%). In the case of species with relative frequency lower than 1%, Sároszpataki et al (2003) used the “data deficient” category. Here, we discuss the distribution, data source and age of the available data. If the presence of a species is in doubt “validation needed” category is used. This revision

Table 1. Checklist of the Hungarian bumble bee fauna with the relative frequency (*RF%*) and frequency category of the species published by Sárospataki et al. (2003) and calculated based on the actualized database built in 2021. * = protected in Hungary. E = locally extinct, cn = confirmation needed, I = rare (1–10%), II = moderately frequent (11–20%), III = frequent (21–40%), IV = common (> 41%).

	<i>RF%</i>		Frequency categories	
	2003	2021	2003	2021
<i>B. (Megabombus) argillaceus</i> * (Scopoli, 1763)	7.06	15.44	I	II
<i>B. (Psithyrus) barbutellus</i> (Kirby, 1802)	12.53	10.73	II	II
<i>B. (Psithyrus) bohemicus</i> (Seidl, 1838)	4.33	3.58	I	I-cn
<i>B. (Psithyrus) campestris</i> (Panzer, 1801)	4.78	6.21	I	I
<i>B. (Bombias) confusus</i> * (Schenck, 1861)	12.98	10.92	II	II-cn
<i>B. (Megabombus) consobrinus</i> (Dahlbom 1832)	0.23	0.19		cn
<i>B. (Bombus) cryptarum</i> (Fabricius, 1775)	-	0.19		cn
<i>B. (Subterraneobombus) distinguendus</i> (Morawitz 1869)	1.59	1.32		E
<i>B. (Subterraneobombus) fragrans</i> * (Pallas, 1771)	3.64	3.01	I	I-cn
<i>B. (Pyrobombus) haematurus</i> (Kriechbaumer, 1870)	3.87	10.92	I	II
<i>B. (Megabombus) hortorum</i> (Linnaeus, 1761)	37.13	42.94	III	IV
<i>B. (Thoracobombus) humilis</i> * (Illiger, 1806)	36.90	35.59	III	III
<i>B. (Pyrobombus) hypnorum</i> (Linnaeus, 1758)	6.38	9.42	I	I
<i>B. (Thoracobombus) laesus</i> * (Morawitz, 1875)	8.66	6.21	I	I-cn
<i>B. (Melanobombus) lapidarius</i> (Linnaeus, 1758)	57.63	59.13	IV	IV
<i>B. (Bombus) lucorum</i> (Linnaeus, 1761)	12.53	14.69	II	II
<i>B. (Thoracobombus) muscorum</i> * (Linnaeus, 1758)	19.59	18.46	II	II
<i>B. (Bombias) paradoxus</i> * (<i>Bombus confusus paradoxus</i> , Dalla Torre, 1882)	3.87	3.39	I	I-cn
<i>B. (Thoracobombus) pascuorum</i> (Scopoli, 1763)	47.38	51.79	IV	IV
<i>B. (Thoracobombus) pomorum</i> * (Panzer, 1805)	10.48	10.17	II	II
<i>B. (Pyrobombus) pratorum</i> (Linnaeus, 1761)	14.12	14.69	II	II
<i>B. (Thoracobombus) ruderarius</i> (Linnaeus, 1776)	37.13	39.74	III	III
<i>B. (Megabombus) ruderatus</i> * (Fabricius, 1775)	17.54	18.08	II	II
<i>B. (Psithyrus) rupestris</i> (Fabricius, 1793)	17.77	14.69	II	II
<i>B. (Cullumanobombus) cullumanus serrisquama</i> (Kirby, 1802)	0.46	0.38		E
<i>B. (Kallobombus) soroensis</i> * (Fabricius, 1776)	1.37	1.69	I	I
<i>B. (Subterraneobombus) subterraneus</i> * (Linnaeus, 1758)	9.11	7.53	I	II-cn
<i>B. (Thoracobombus) sylvarum</i> * (Linnaeus, 1761)	40.77	42.75	III	IV
<i>B. (Psithyrus) sylvestris</i> (Lepelletier, 1832)	1.14	0.94	I	cn
<i>B. (Bombus) terrestris</i> (Linnaeus, 1758)	68.34	77.21	IV	IV
<i>B. (Psithyrus) vestalis</i> (Fourcroy, 1785)	12.30	12.62	II	II

was also carried out in the case of rare species. In other cases, where the species could be seen as extinct, the “revised” category is used (Table 1).

Since *RF%* considers the spatial distribution of the species based only on all occupied UTM cells, the other modified relative frequency value of species was calculated (*RF'%*) for all sampling periods. This modified value refers to both UTM-based distribution and sampling intensity as follows:

$$RF'\% = \frac{\text{number of occupied UTM cells by species from a given period}}{\text{total number of bee data from a given period}} \times 100$$

In this equation, only UTM-based distribution data could be used. Since we have numerous data without detailed locations, the fine-scale locality data cannot be

calculated. Using it the bias caused by the different sampling intensity of the different periods of the study can be decreased and the changes of relative frequencies of the species can be more correctly evaluated.

In the case of the morphologically similar *Bombus hortorum* / *B. ruderatus*, and *B. terrestris* / *B. lucorum* species pairs, the calculated *RF%* and *RF'%* values were adjusted. The ratio of the two species was calculated for each sampling period based on valid data, and its minimum was chosen for both species. During the calculations of *RF%* and *RF'%* values, valid data and the ratio (equal to this minimum value) of the dubious data were taken into consideration.

Results

Composition of the fauna

The national territory of Hungary is divided into by 1052 10×10 km UTM cells, of which 531 contain 3716 bumble bee records (species/UTM cell/period). The first data were collected in 1953 (Sároszpataki et al. 2003). The number of the studied UTM cells and data records have continuously increased since then. In the consecutive periods of sampling, nearly equal numbers of UTM cells were sampled (Fig. 1A), while the most data were collected in the third period, 1971–2000 (Fig. 1B). During the last, intensive period of data collection, more than 900 data records were collected, and the spatial coverage of the data set increased from 41.7% to 50.5%. From these new records, 829 were collected by the authors after 2000, with others from sources published after 2000.

The number of studied UTM cells, adjusted according to the length of the periods of data collection was nearly equal in all periods (Fig. 1A, B).

Data on 31 bumble bee species (6 of which are cuckoo bumble bees, subgenus *Psithyrus*) are presented. Two species (*B. distinguendus* and *B. cullumanus serrisquama*) have only archaic (at least 70 years old) data (Fig. 33), and we confirm Rakonczay's (1989) conclusion that they are locally extinct. Data formerly published on *B. elegans* included under *B. distinguendus*, so that our checklist comprises 29 species (Table 1). Most of the species (25/29) were already known before 1953 (Fig. 1C).

Among the listed species *B. fragrans* is strictly protected, while *B. argillaceus*, *B. confusus*, *B. humilis*, *B. laesus*, *B. muscorum*, *B. paradoxus*, *B. pomorum*, *B. ruderatus*, *B. sylvarum*, *B. soroeensis* and *B. subterraneus* are protected in Hungary (13/2001. (V. 9.) KöM decree) (Table 1).

As seen in Fig. 2, the number of records per species is very uneven, with seven having fewer than 10 records.

Changes in the relative frequencies of the species

In the last period of the studies, 835 data records of 21 species were collected from 259 UTM cells, while in the case of eight species we have no new data.

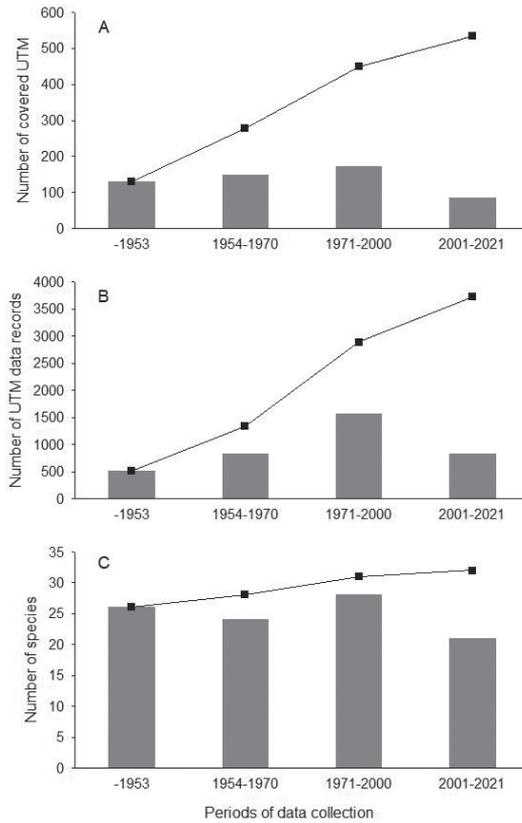


Figure 1. Number (bars) and cumulative number (line) of UTM cells with bumble bee data (A), number of data records (B) and number of species (C) in the consecutive periods of data collection in Hungary.

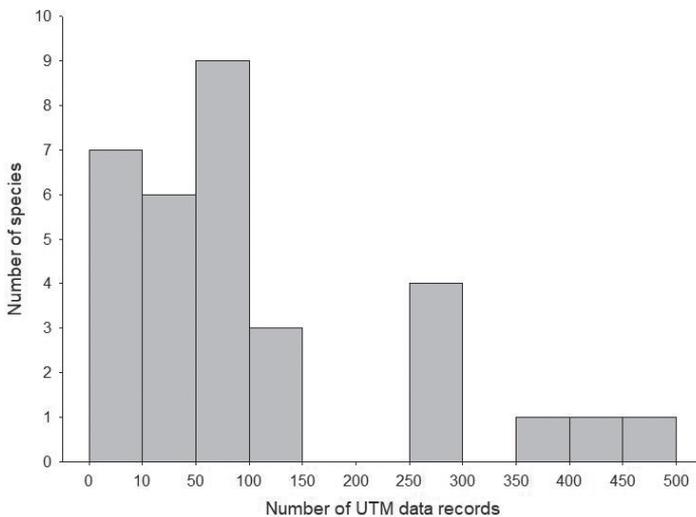


Figure 2. Distribution of data records among the bumble bee species of the Hungarian fauna.

The only valid Hungarian data on *B. consobrinus* were collected from the Gál-rét, in the Börzsöny Mountains (UTM cell: CU51) after 1970, the exact date unknown (Fig. 8). It has not been recorded in Hungary recently. *B. cryptarum*, belonging to the *B. lucorum* complex, also has only one record, thus its presence is dubious in Hungary (Fig. 17). *B. sylvestris* has only five records, collected in the 1971–2000 period, thus its relative frequency decreased to under 1% in the fauna (Fig. 29). The area of the rare *B. fragrans* had continuously decreased and it was not sampled after 2000 (Table 2, Fig. 9). Although *B. bohemicus* formerly was known both in the Bakony and the Bükk Mountains, it has not been reported in the last two decades (Fig. 5). Although *B. subterraneus* was once widely distributed but not abundant (Fig. 27), but it also has not been recorded after 2000, along with *B. confusus*, *B. laesus* and *B. paradoxus* (Figs 7, 15, 19).

Table 2. Bumble bees present in Hungary (29 species) with their modified relative frequency (*RF'*%) calculated for consecutive periods of samplings based on the revised database and the trend of frequency changes till 2005 (based on Sároszpatáki et al. 2005) and between 2005 and 2021. - = decreasing frequency, + = increasing frequency, u = unchanged, R = revised, ND = no data.

Species	Modified relative frequency (<i>RF'</i> %)				Trend	
	-1953	1954–1970	1971–2000	2001–2021	-2005	2005–2021
<i>B. argillaceus</i>	2.38	0.73	0.90	6.64	-	+
<i>B. barbutellus</i>	0.79	0.85	2.95	0.24		-
<i>B. bohemicus</i>	0.00	1.09	1.09	0.00		ND
<i>B. campestris</i>	0.00	1.09	1.22	1.42		+
<i>B. confusus</i>	2.97	2.67	2.37	0.00	-	-
<i>B. consobrinus</i>	0.00	0.00	0.06	0.00	ND	ND
<i>B. cryptarum</i>	ND	ND	ND	0.12	ND	ND
<i>B. fragrans</i>	2.97	0.12	0.06	0.00	-	-
<i>B. haematurus</i>	0.00	0.00	1.03	5.34	+	+
<i>B. hortorum</i>	4.75	8.13	8.34	8.19	u	u
<i>B. humilis</i>	9.31	9.59	6.35	3.68	-	-
<i>B. hypnorum</i>	0.20	0.12	1.67	2.85	+	+
<i>B. laesus</i>	5.94	0.24	0.45	0.00	-	-
<i>B. lapidarius</i>	10.10	9.10	13.09	11.39	u	u
<i>B. lucorum</i>	1.98	4.37	1.35	3.32	u	+
<i>B. muscorum</i>	6.34	3.64	2.82	1.78	-	-
<i>B. paradoxus</i>	1.78	0.12	0.58	0.00	-	-
<i>B. pascuorum</i>	9.90	11.29	9.37	11.86	u	+
<i>B. pomorum</i>	4.55	1.46	1.54	0.83	-	-
<i>B. pratorum</i>	2.18	1.94	3.08	2.02	u	u
<i>B. ruderarius</i>	4.75	6.92	8.28	6.64	u	u
<i>B. ruderatus</i>	5.94	3.76	1.86	2.14	-	-
<i>B. rupestris</i>	0.40	5.70	3.40	0.12		-
<i>B. soroensis</i>	0.20	0.00	0.32	0.36	+	+
<i>B. subterraneus</i>	1.98	0.97	1.67	0.00	u	-
<i>B. sylvarum</i>	8.51	10.19	6.74	7.59	-	u
<i>B. sylvestris</i>	0.00	0.00	0.32	0.00		ND
<i>B. terrestris</i>	9.90	13.11	15.92	15.30	u	u
<i>B. vestalis</i>	0.20	2.79	3.15	1.42		u

Relative frequencies of *B. humilis*, *B. muscorum* and *B. pomorum* have continuously decreased (Figs 13, 18, 21), while for *B. rupestris* this trend appeared between 1954–1970 (Fig. 25), and for *B. barbutellus* only after 2000 (Table 2). These changes in relative frequency do not alter rarity category in any of these cases (Table 1).

In contrast, the relative frequencies of 15 species have increased since the last review (Sárospataki 2003): *B. argillaceus*, *B. campestris*, *B. haematurus*, *B. hortorum*, *B. hypnorum*, *B. lapidarius*, *B. lucorum*, *B. pascuorum*, *B. pratorum*, *B. ruderarius*, *B. ruderatus*, *B. soroeensis*, *B. sylvarum*, *B. terrestris* and *B. vestalis* (Figs 3, 6, 10, 11, 14, 16, 17, 20, 22–24, 26, 28, 30, 32). In four species, the increased relative frequency leads to changes in the rarity category as well. The rarity category of *B. argillaceus* and *B. haematurus* is changed from I to II, and the changes in their relative frequencies were significant and rapid during the last 20 years. Rarity categories of *B. hortorum* and *B. sylvarum* changed from III to IV, showing smaller shifts in relative frequencies than in the two former species (Table 1 and 2).

Considering the long-term trends of the changes in the relative frequencies, seven of the 15 mentioned species showed stable values (*B. hortorum*, *B. lapidarius*, *B. pratorum*, *B. ruderarius*, *B. sylvarum*, *B. terrestris*, *B. vestalis*), while the frequency of *B. ruderatus* slightly decreased (Table 2).

Changes in the distribution of species

New data redraw the area of many *Bombus* species. In the case of the East-Mediterranean *B. argillaceus*, the first protected *Bombus* species in Hungary, both the northern (Tiszatelek; cell EU64) and the eastern (Túrístvándi; cell FU22) occurrences in Hungary were recorded after 2000. The relative frequency of the species had decreased between the 1950s and 2000, however, it has spread since 2000 and become widely distributed in the whole country (Table 2, Fig. 3).

The intensive spread of *B. haematurus* was also detected. The first data on the species were collected in the 1980s, but till 2003 it was only known from the central and southern parts of Transdanubia in western Hungary. After that, it appeared east from the Danube and the Tisza Rivers as well (Fig. 10).

We had no data on *B. hypnorum* from Hungary after the 1990s. Before that it was known from the hilly areas of Transdanubia and northern Hungary. It newly appeared in Transdanubia in 2015 and has been collected several times since 2018 also in eastern Hungary (Fig. 14).

Discussion

The last review of the Hungarian bumble bee fauna was published in 2003 (Sárospataki et al. 2003) and the vulnerability status of the species was assessed in 2005 (Sárospataki et al. 2005). Since 2000, more than 900 data records have been collected. After that 531 of the 1052 10×10 km UTM cells covering Hungary contained 3716 bumble bee data records (species/UTM cell/date), providing the possibility to recalculate the relative frequency and threatened status of the species and redraw their known distributions.

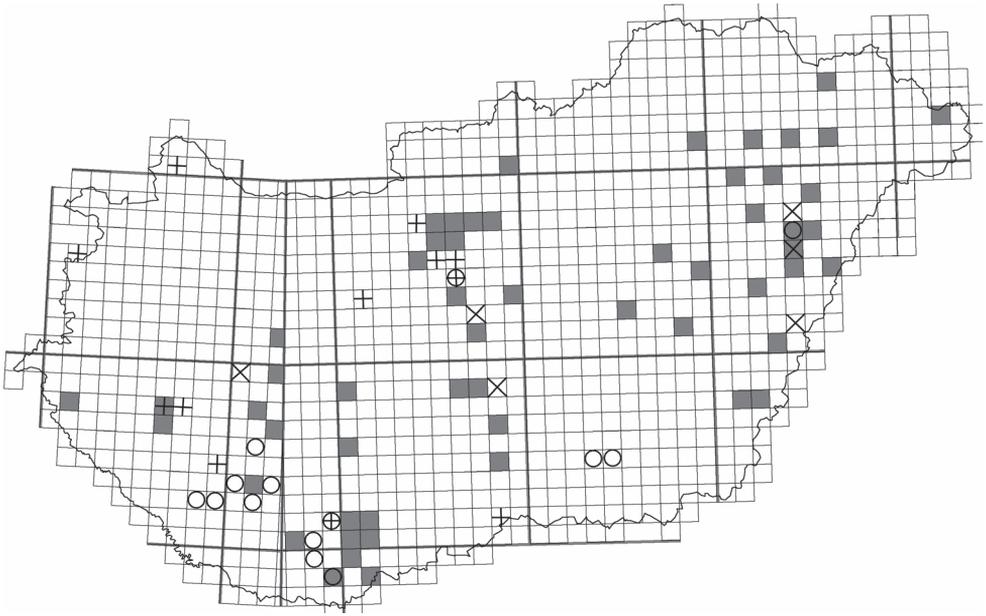


Figure 3. *Bombus argillaceus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

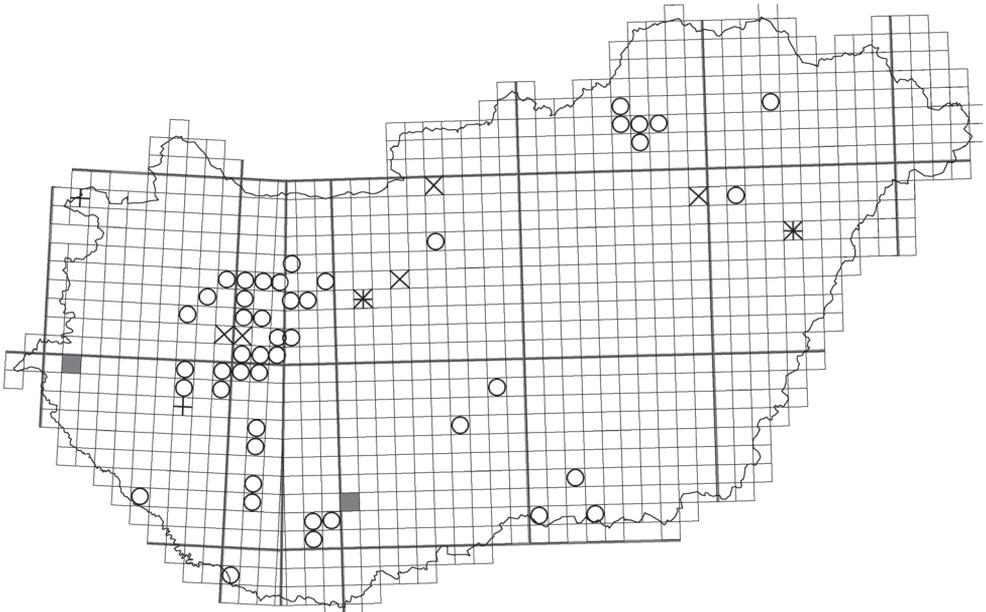


Figure 4. *Bombus barbutellus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

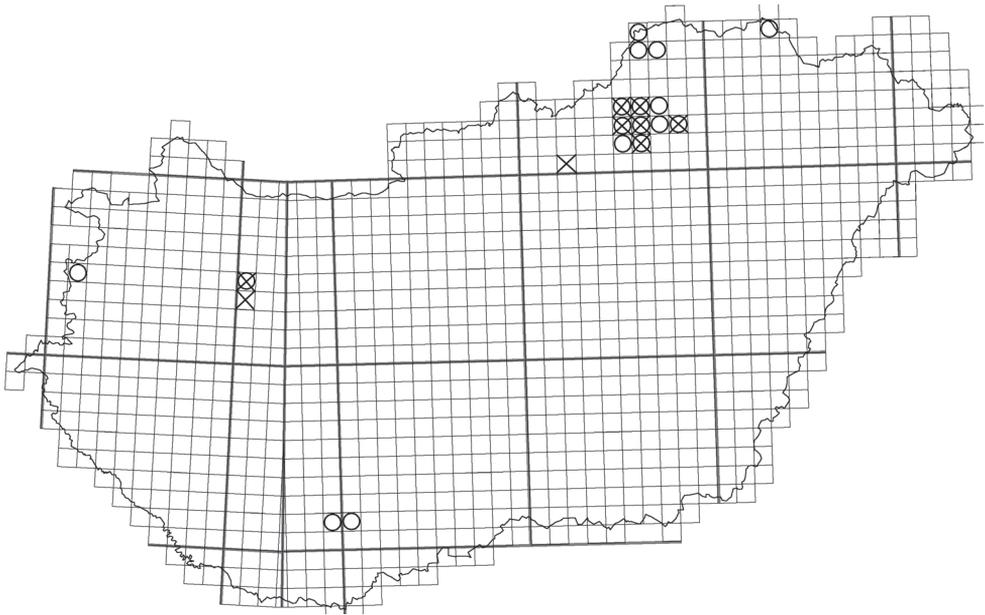


Figure 5. *Bombus bohemicus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

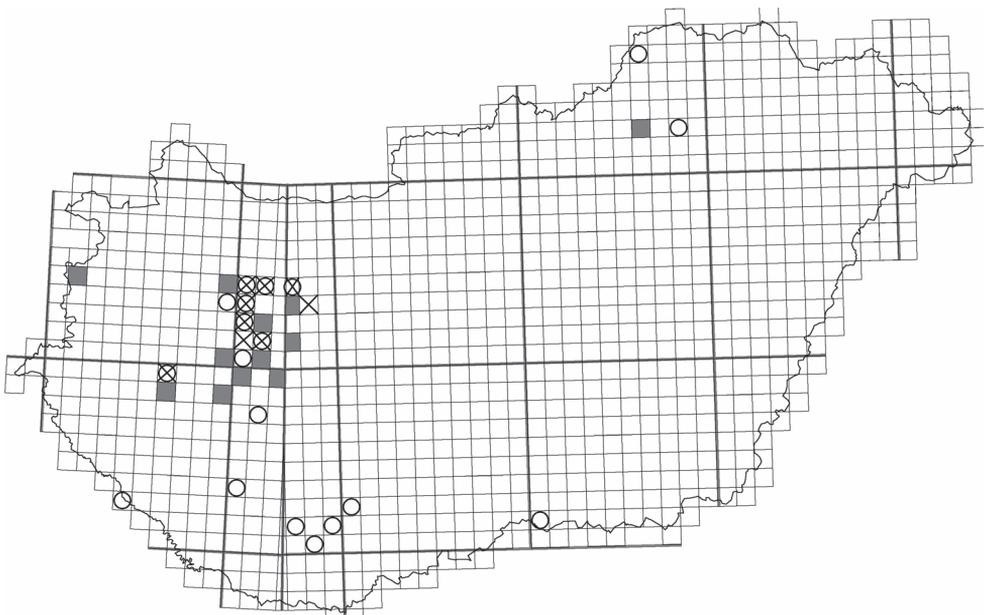


Figure 6. *Bombus campestris* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

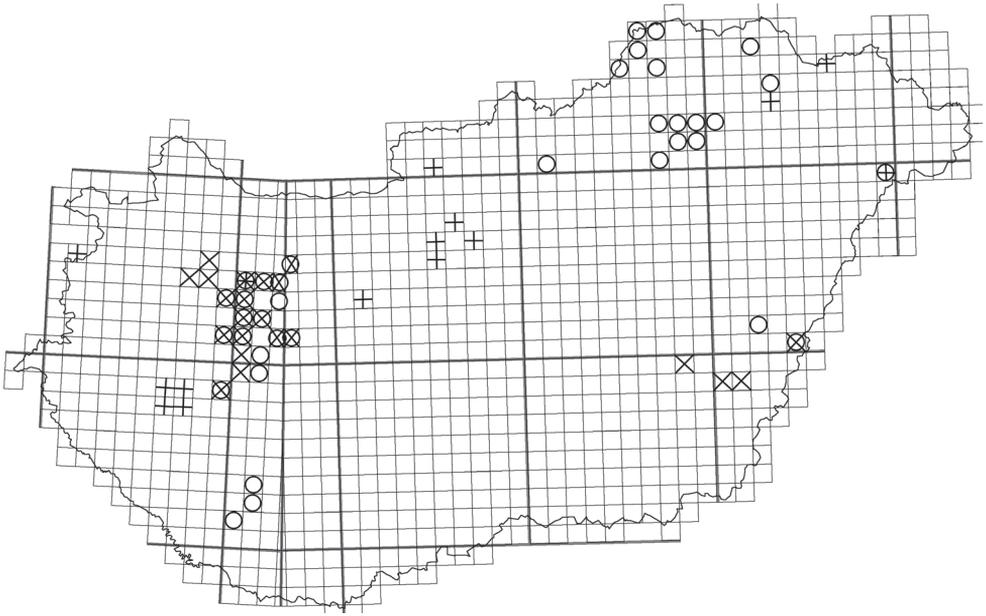


Figure 7. *Bombus confusus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

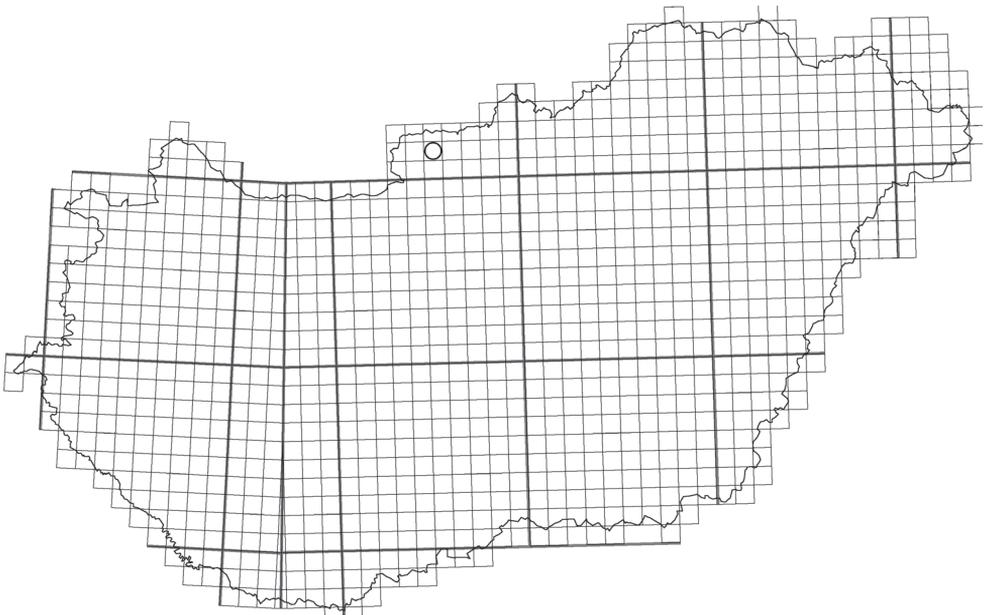


Figure 8. *Bombus consobrinus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

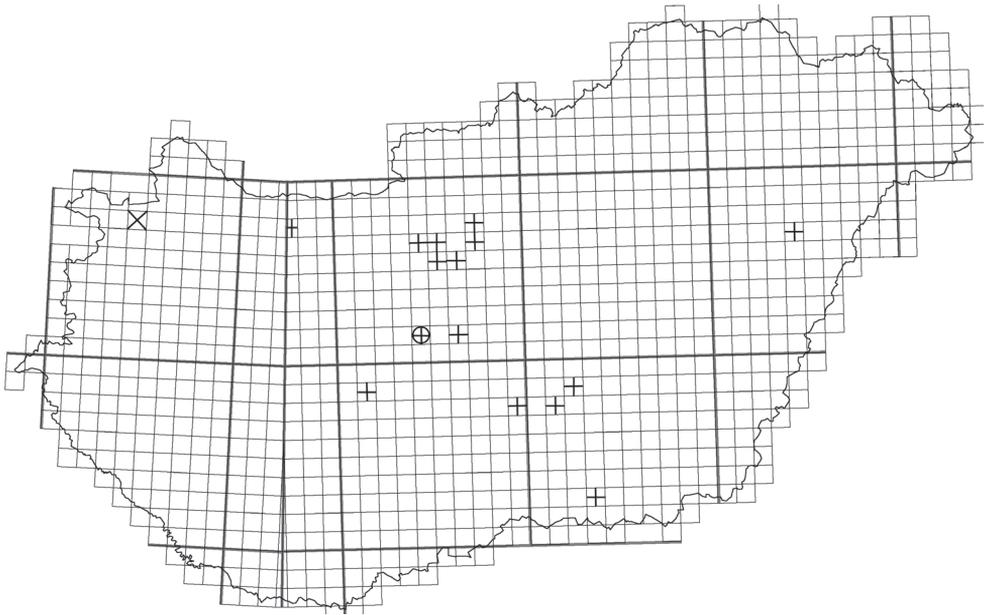


Figure 9. *Bombus fragrans* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

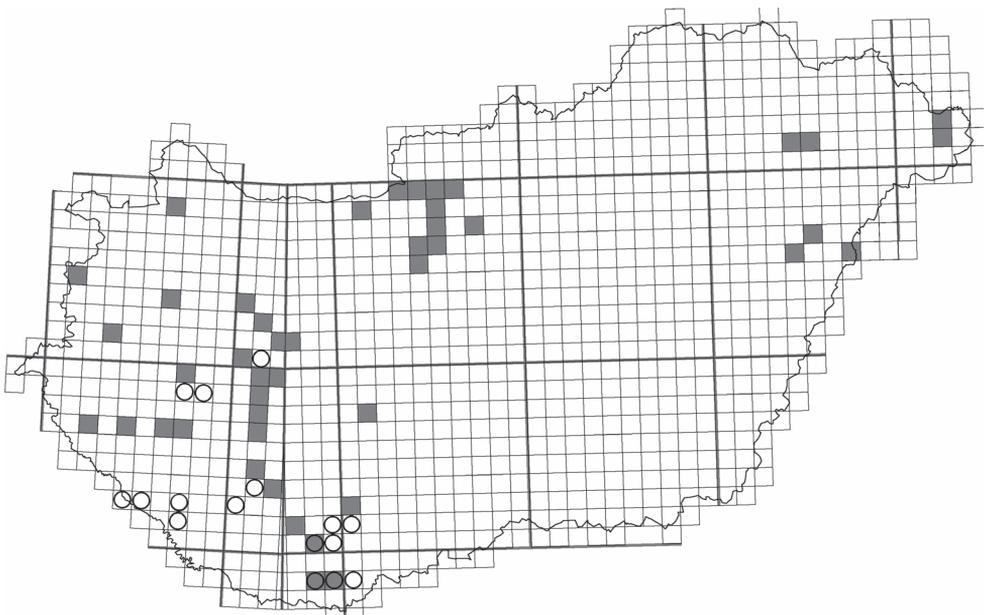


Figure 10. *Bombus haematurus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

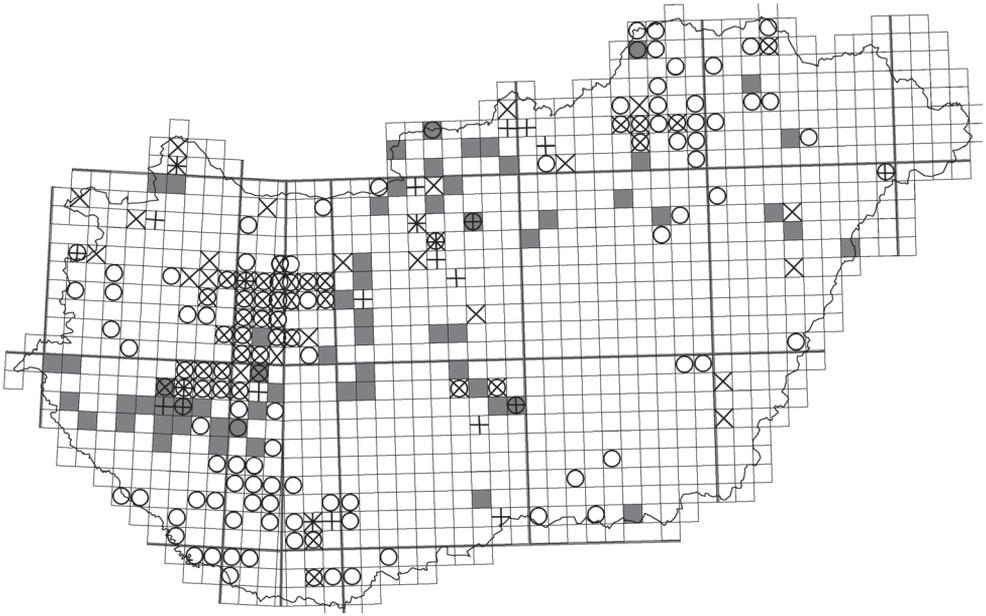


Figure 11. *Bombus hortorum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

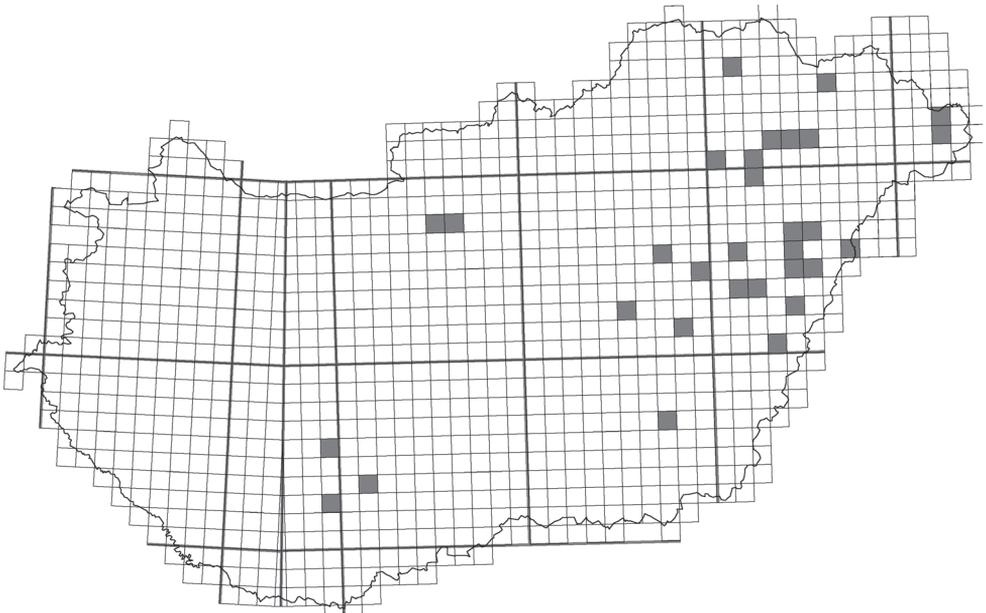


Figure 12. *Bombus hortorum/ruderatus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

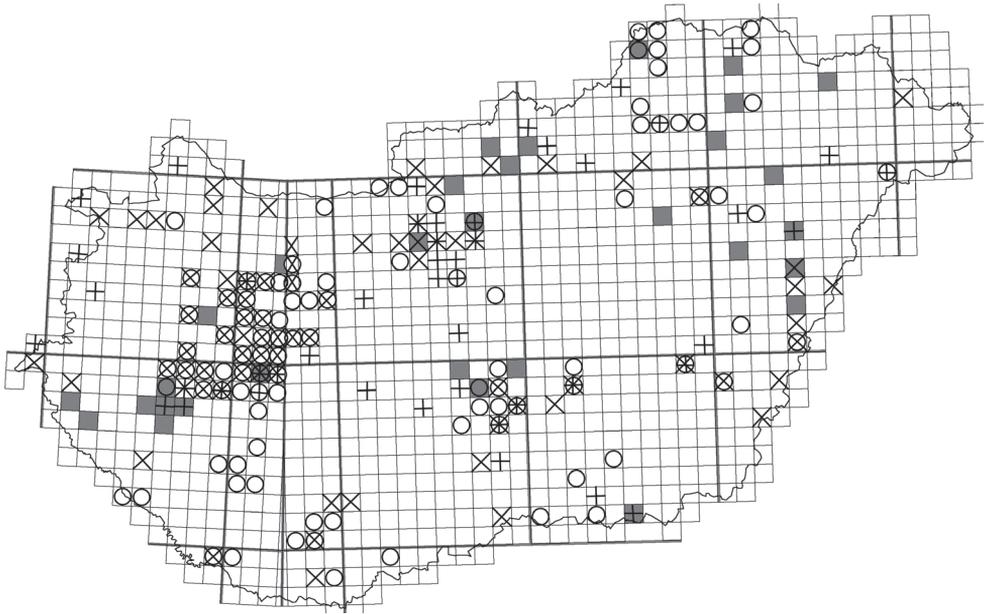


Figure 13. *Bombus humilis* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

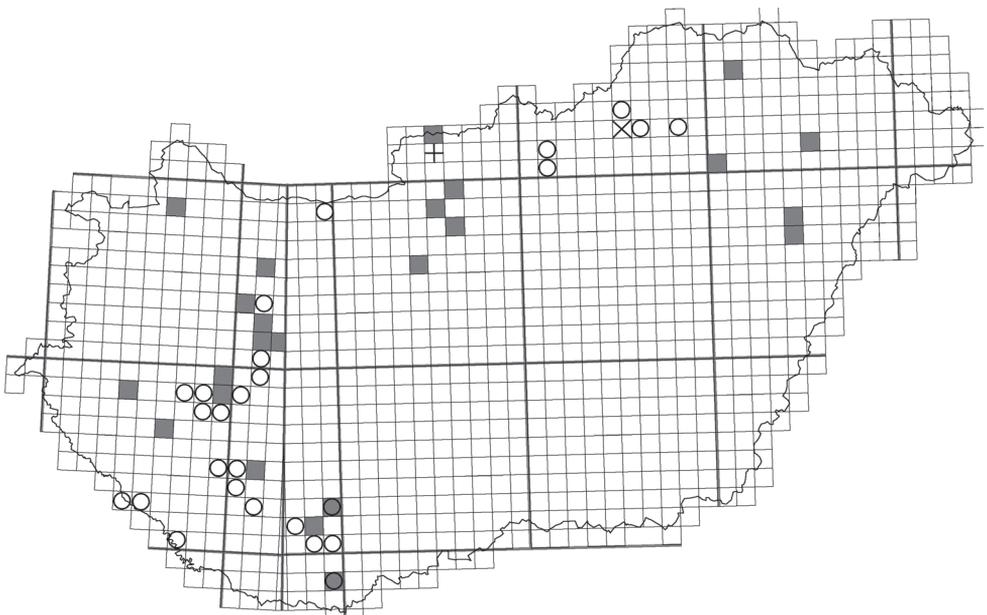


Figure 14. *Bombus hypnorum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

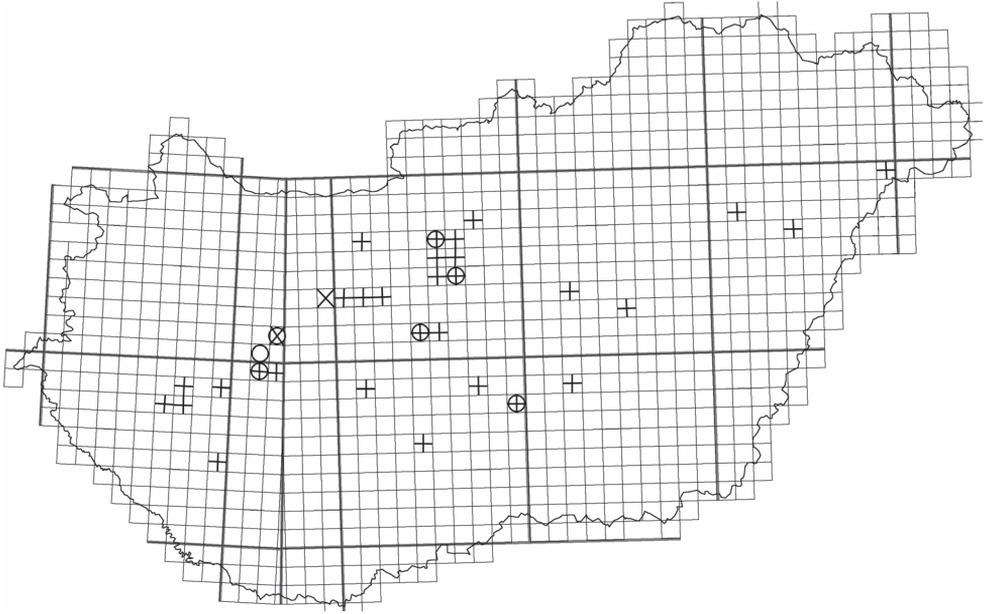


Figure 15. *Bombus laesus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

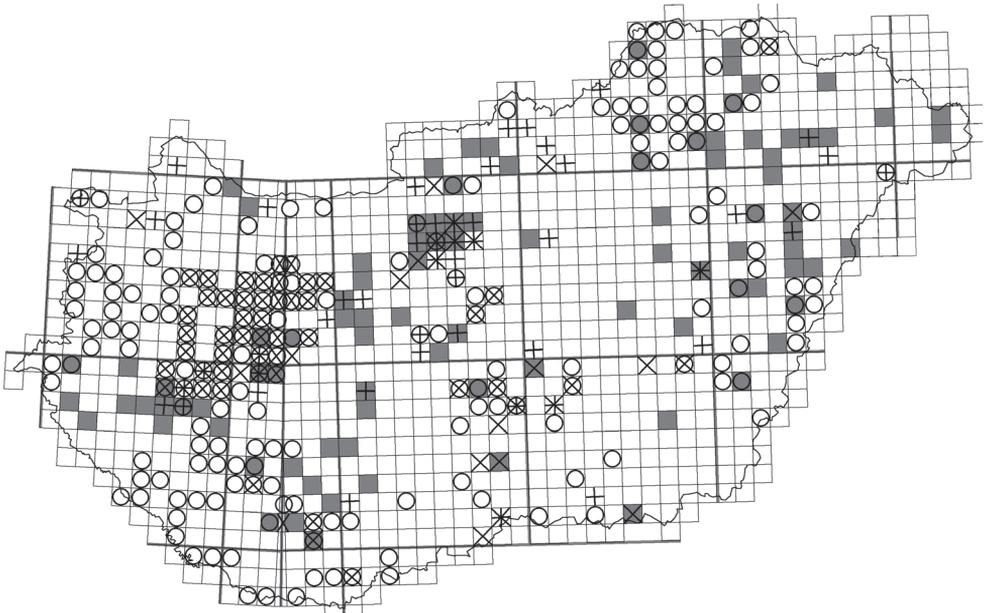


Figure 16. *Bombus lapidarius* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

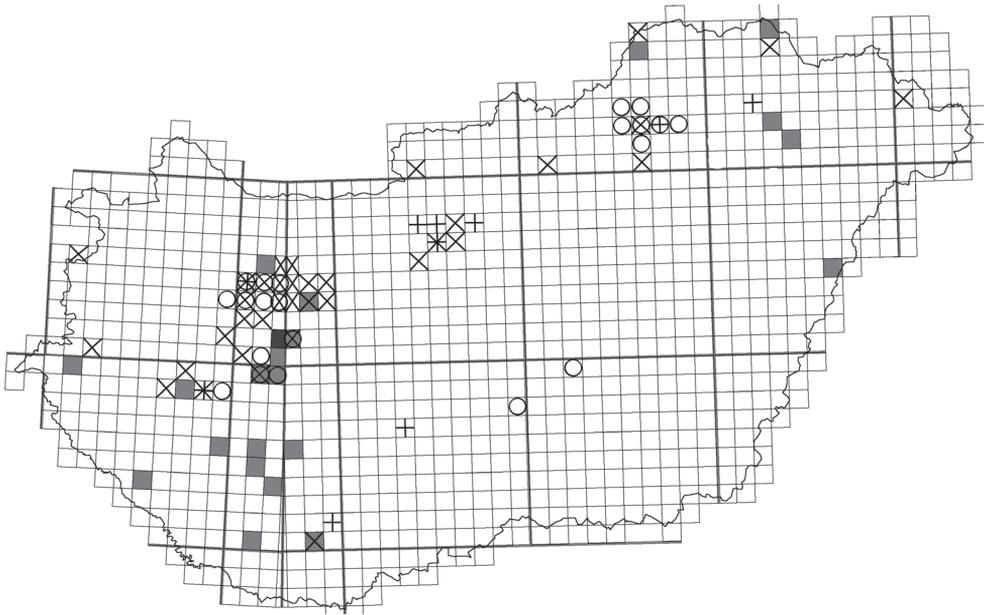


Figure 17. *Bombus lucorum* and *Bombus cryptarum*. *B. cryptarum* belongs to the *B. lucorum* species complex, with only one Hungarian data from YN21 UTM cell where *B. lucorum* have been not reported yet. Distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

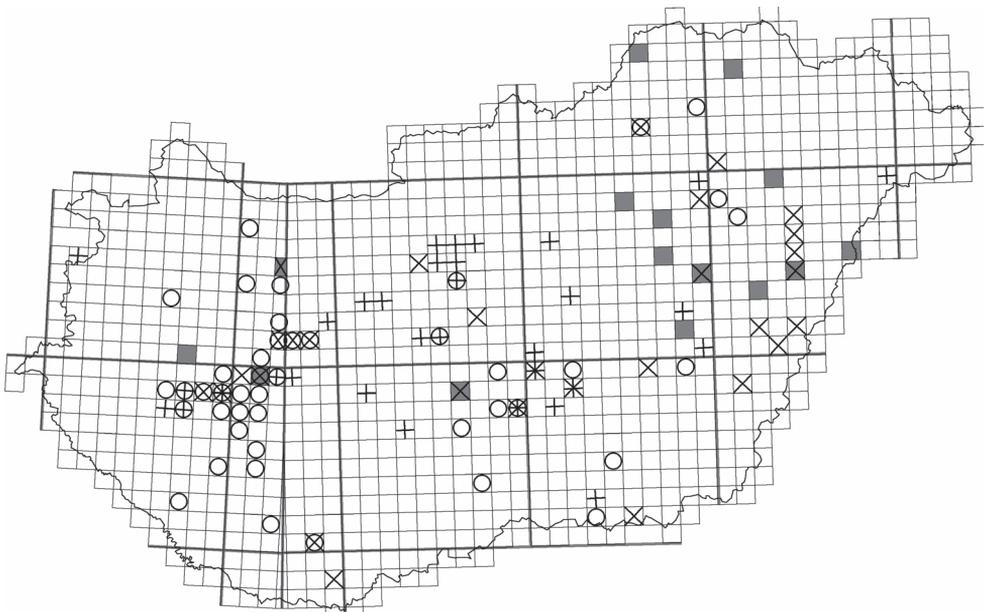


Figure 18. *Bombus muscorum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

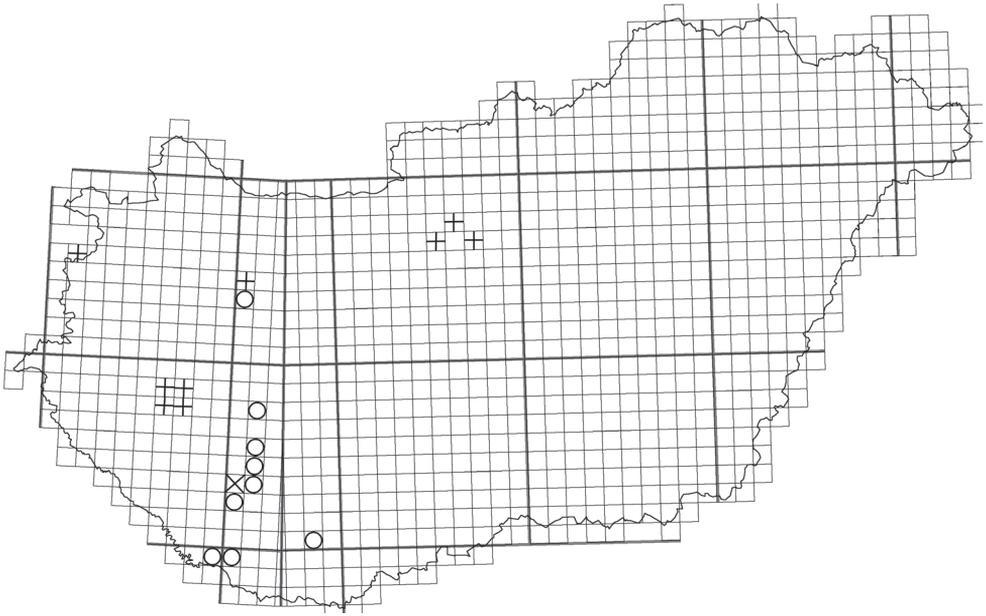


Figure 19. *Bombus paradoxus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

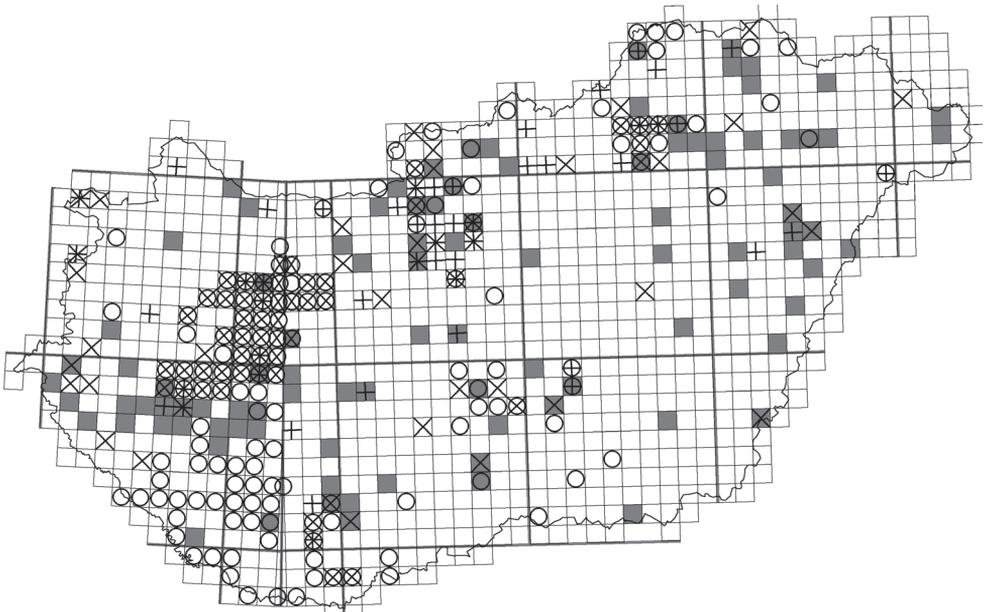


Figure 20. *Bombus pascuorum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

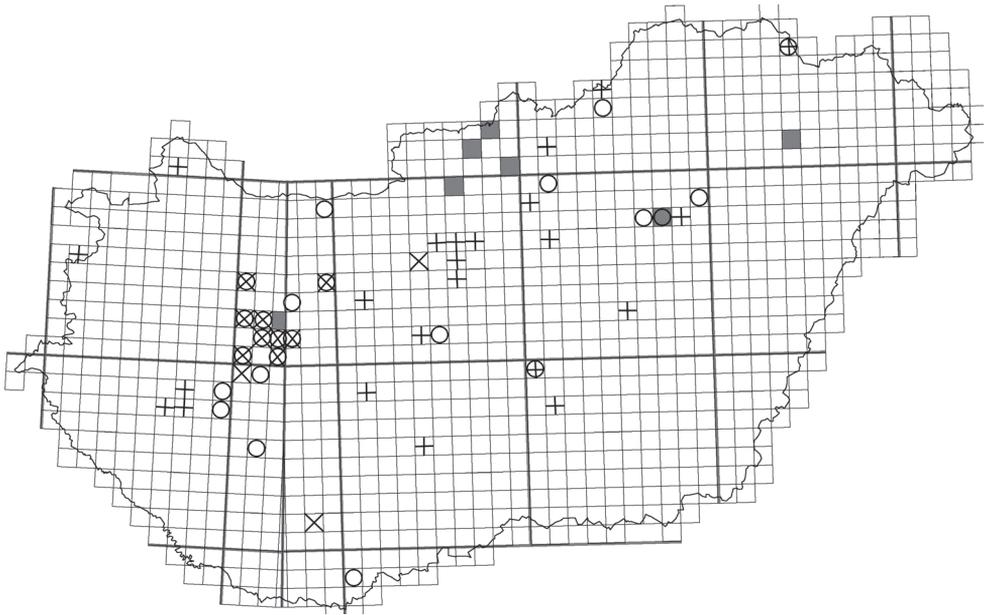


Figure 21. *Bombus pomorum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

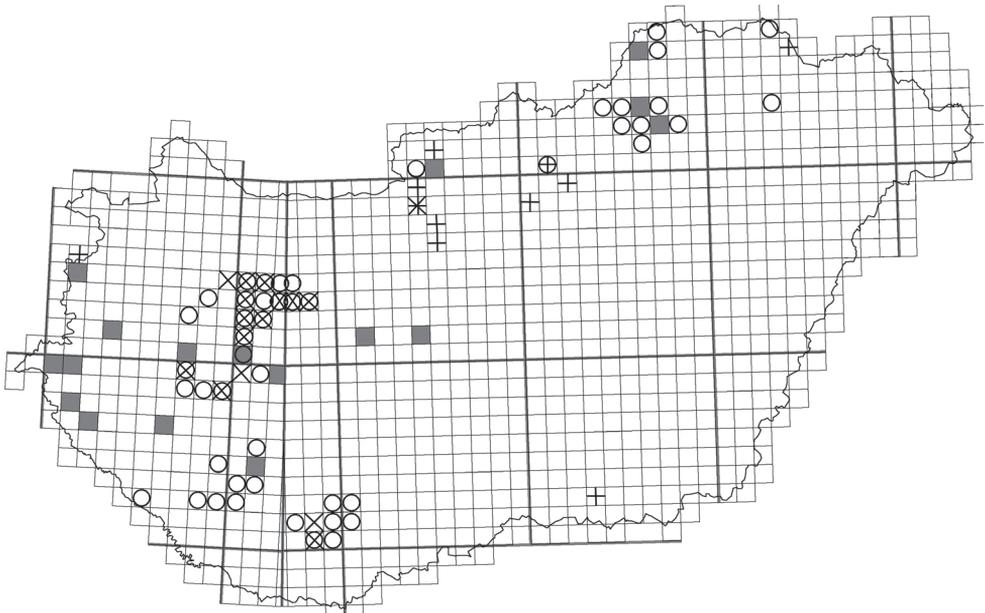


Figure 22. *Bombus pratorum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

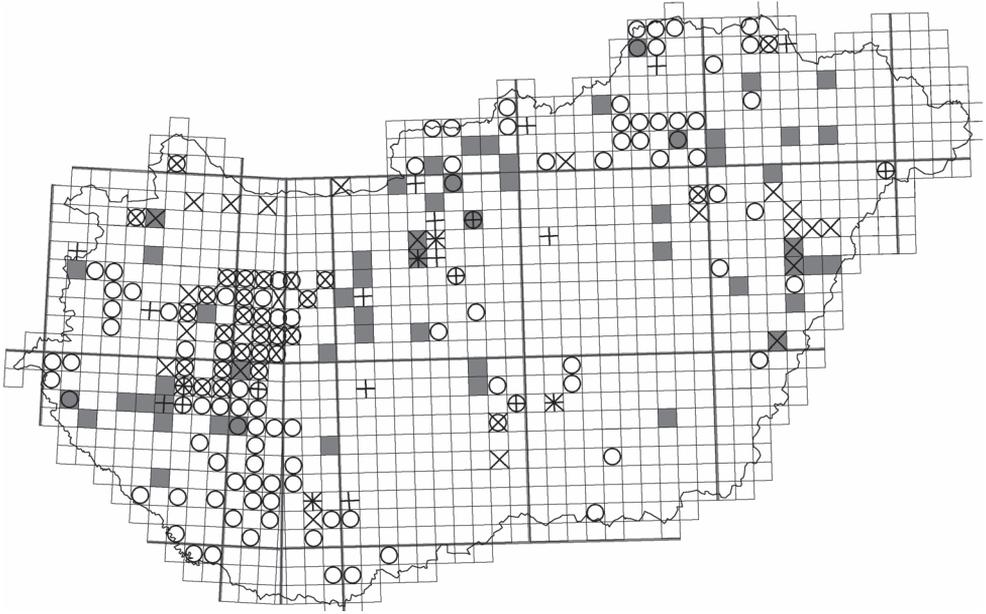


Figure 23. *Bombus ruderarius* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

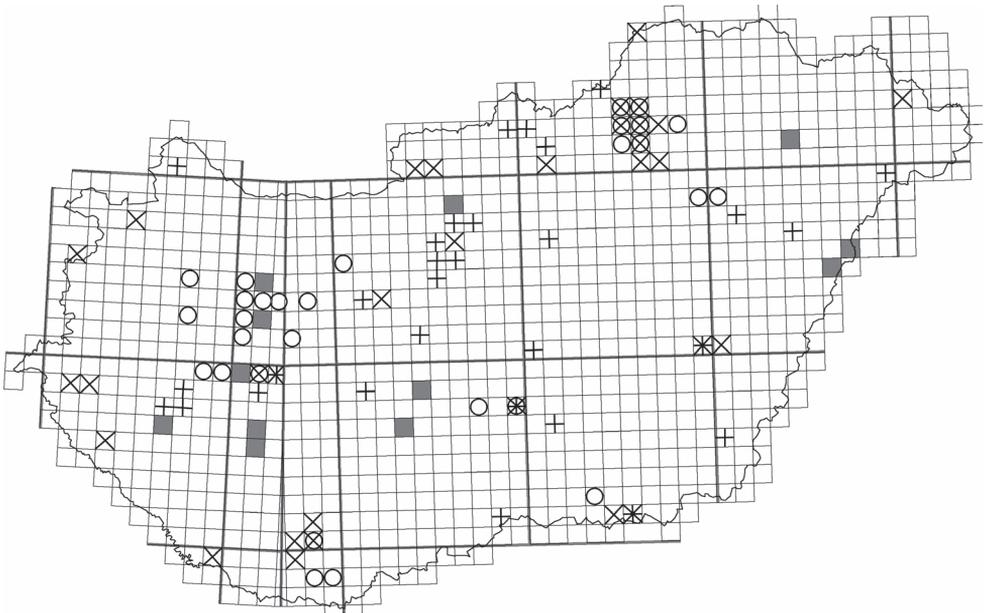


Figure 24. *Bombus ruderatus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

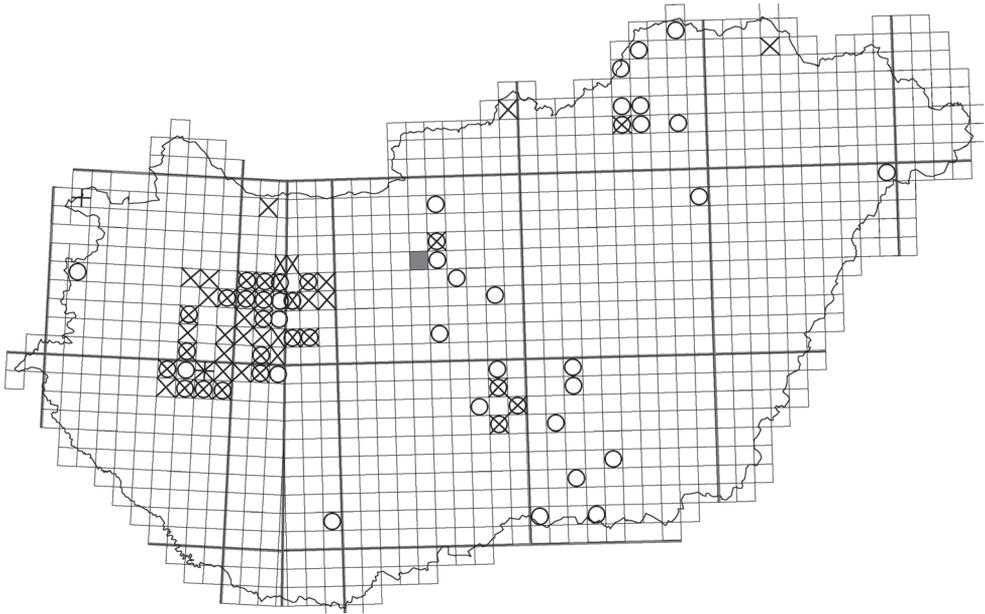


Figure 25. *Bombus rupestris* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

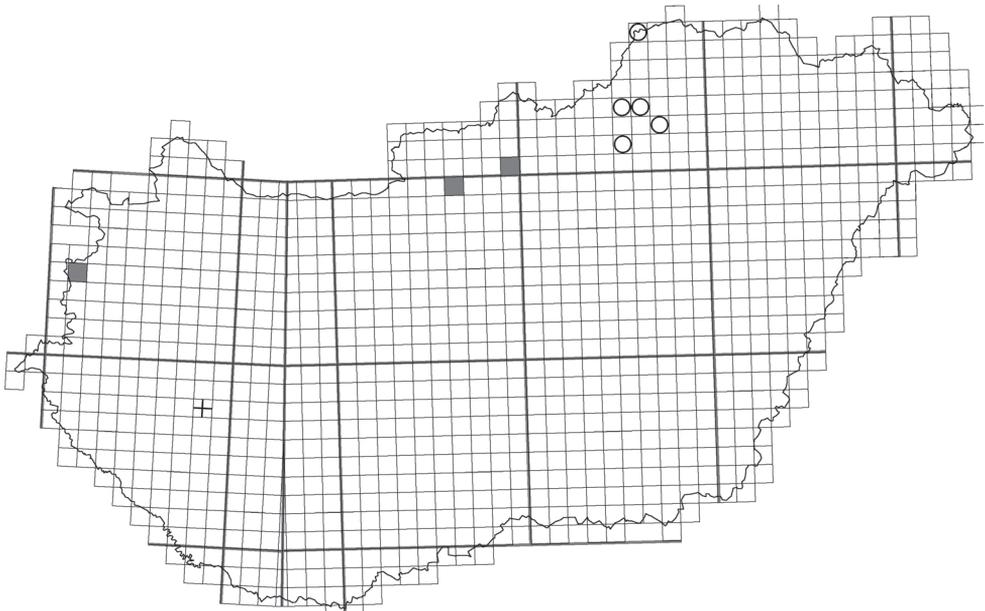


Figure 26. *Bombus soroensis* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

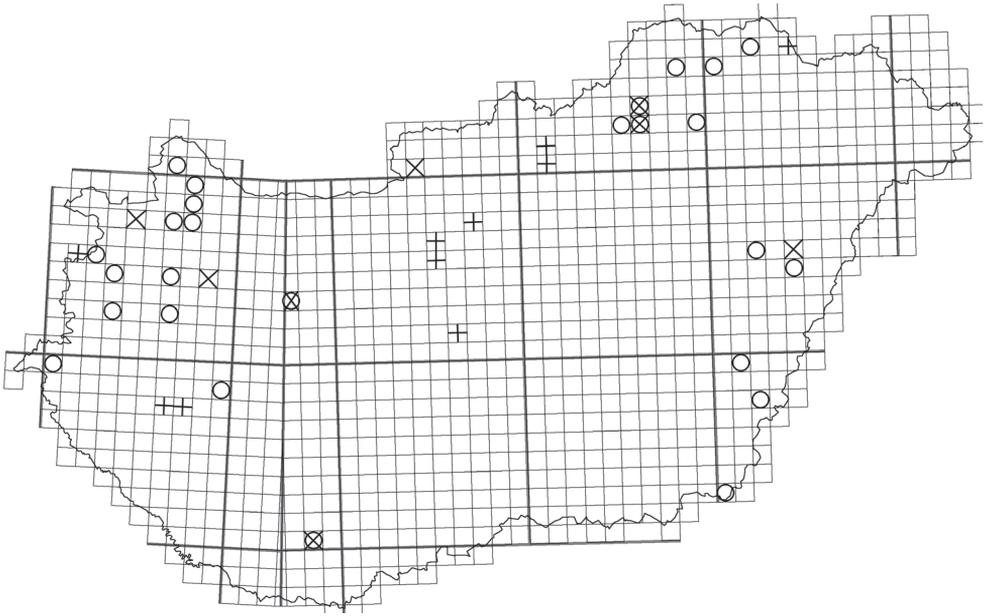


Figure 27. *Bombus subterraneus* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

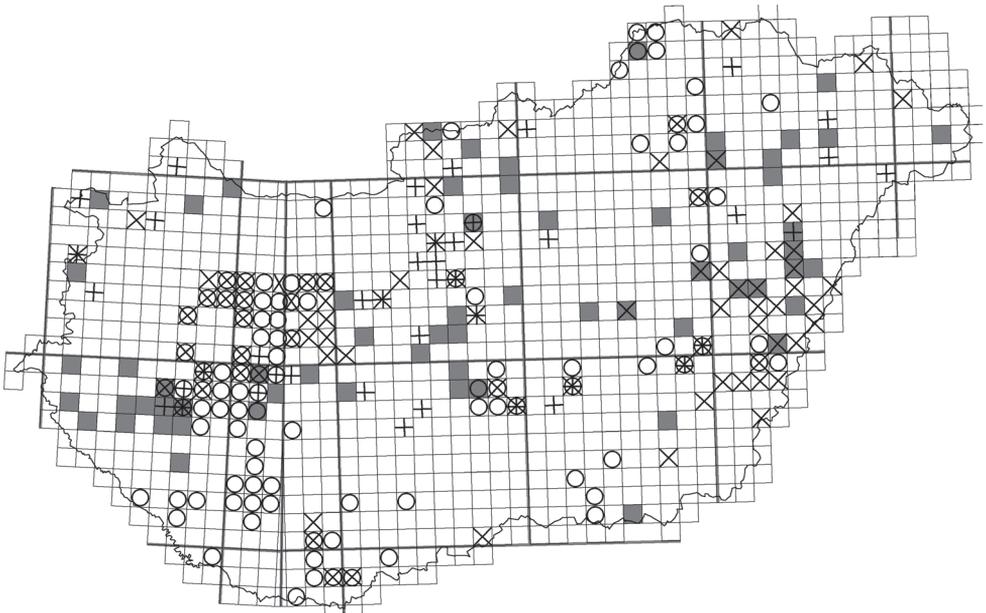


Figure 28. *Bombus sylvarum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, x: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

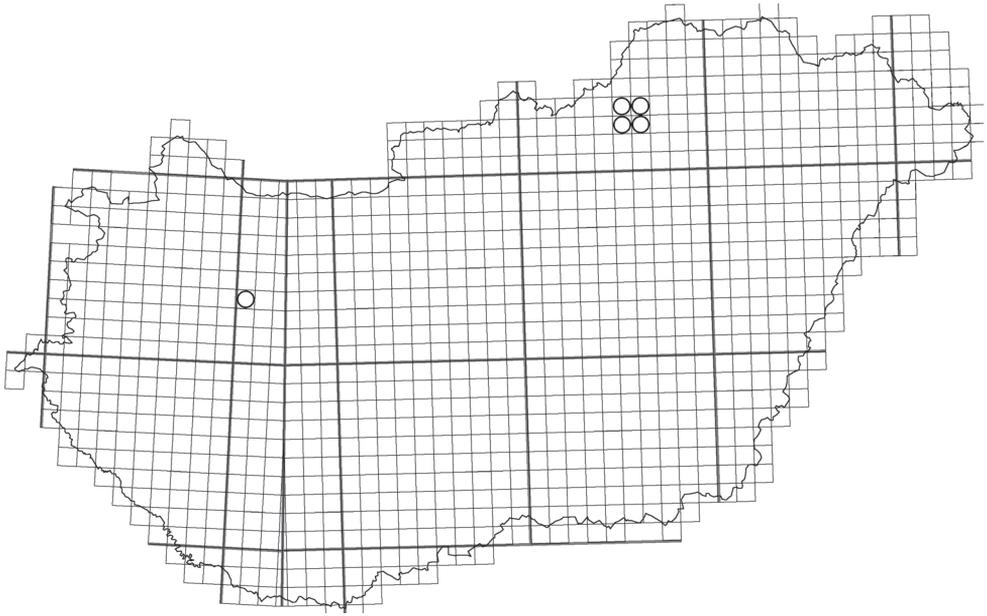


Figure 29. *Bombus sylvestris* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

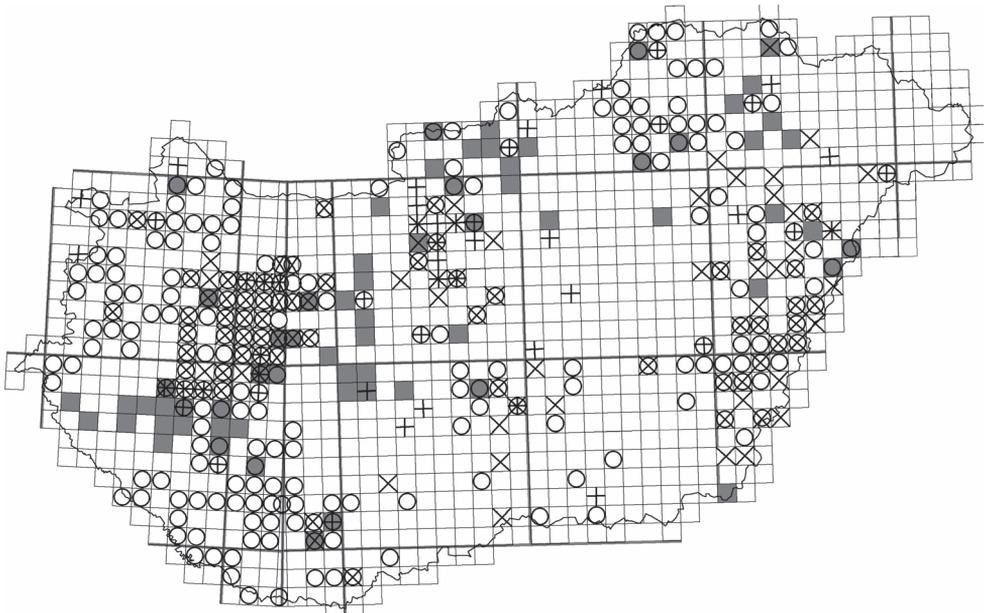


Figure 30. *Bombus terrestris* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

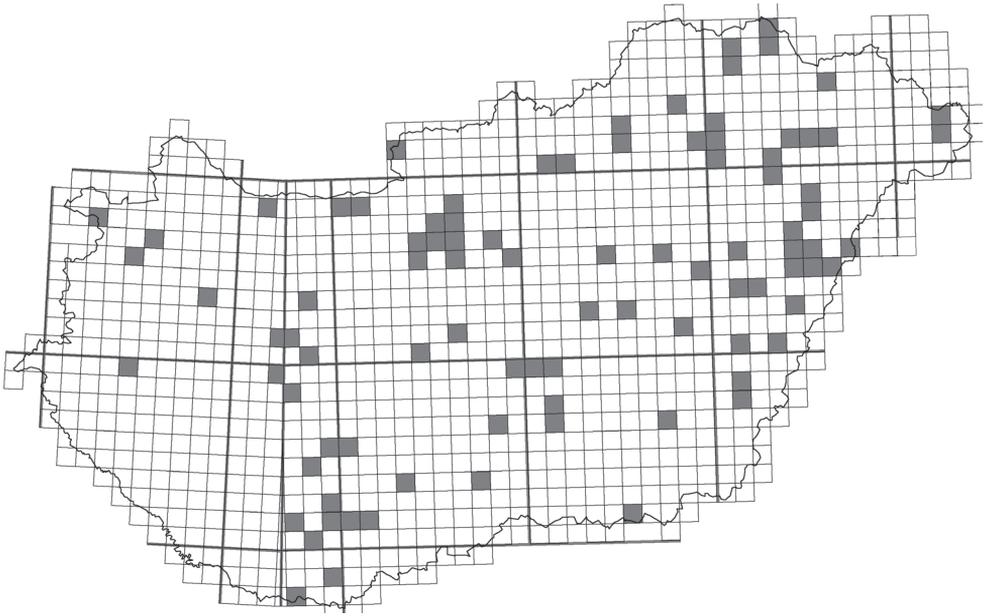


Figure 31. *Bombus terrestris/lucorum* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

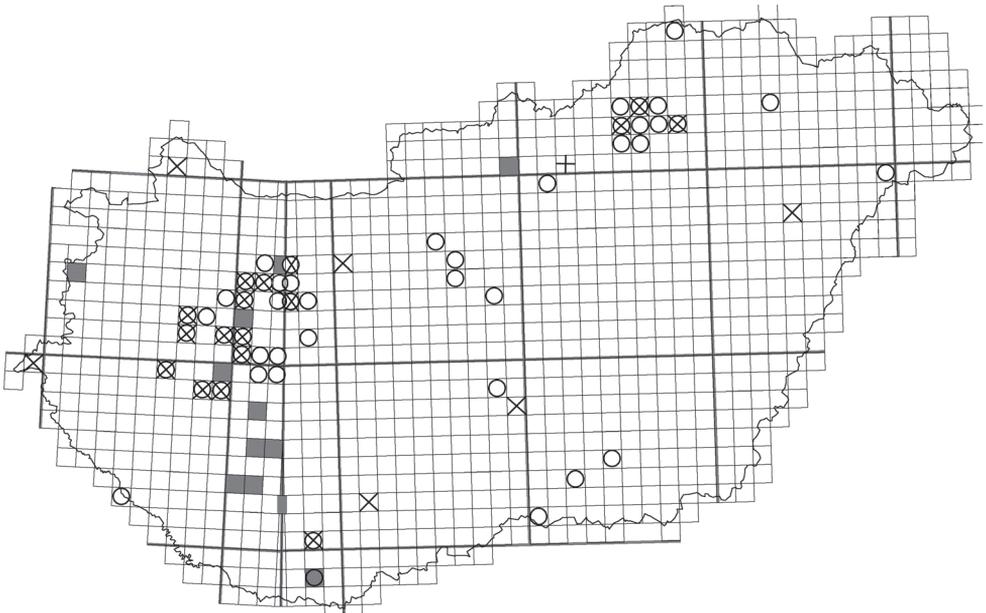


Figure 32. *Bombus vestalis* distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

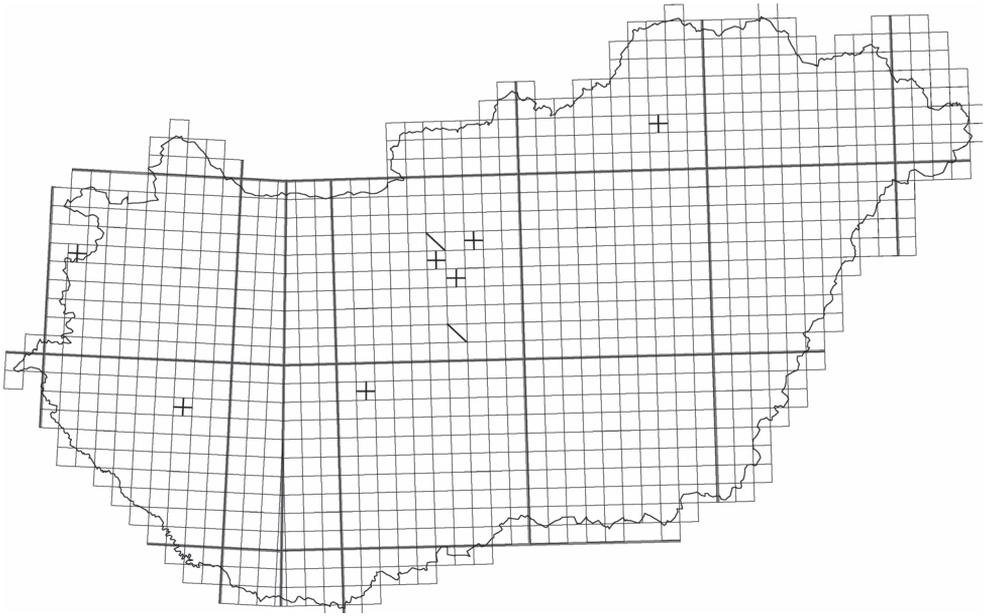


Figure 33. Local extinct species: *Bombus distinguendus* (+), *Bombus cullumanus serrisquama* (∅), distribution maps of bumble bee species present in Hungary according to periods of data collection and/or publication. +: before 1954, ×: 1954–1970, empty circle: 1971–2000 and grey square: after 2000.

Confirming the result of Rakonczay (1989), of the 31 species previously recorded in Hungary, *B. cullumanus serrisquama* and *B. distinguendus* can be considered extinct in Hungary, due to the lack of recent records.

Most species have only a few and in many cases even only archaic records, that accounted for the reevaluation of their status and need of further targeted investigations. The occurrence of 9 species (*B. bohemicus*, *B. confusus*, *B. consobrinus*, *B. cryptarum*, *B. fragrans*, *B. laesus*, *B. paradoxus* (synonym *B. confusus paradoxus*), *B. subterraneus*, *B. sylvestris*) in Hungary needs verification. On the other hand, distribution of other seven species have become well known with more than 250 UTM data records that allow us to draw a more realistic picture on their distribution, vulnerability status and their role in ecosystem services.

The relative frequencies of the species were recalculated and decreasing of the relative frequency of 11 species were detected and four of them has no data from the last two decades.

Seven species showed constant distribution, while seven others had increasing relative frequencies. In the case of five species, the trend of relative frequency changed during the latest period of studies: the trend of *B. sylvarum* changed from decreasing to stable, while the trend of *B. pascuorum* and *B. lucorum* changed from stable to increasing, and the trend of *B. argillaceus* changed from decreasing to increasing.

Although members of subgenus *Psithyrus* were not studied previously (Sároszpatáki et al. 2005), relative frequency trends of their four representatives could also be revealed

based on our data: the relative frequency of *B. campestris* was increasing through all the studied periods, while the trend of *B. barbutellus* and *B. rupestris* changed from increasing to decreasing, and the trend of *B. vestalis* changed from increasing to stable. Due to their rarity and decreasing relative frequencies, their protected status can be recommended. The area of the species formerly classified as *Psithyrus* are within the area of their host species. The relative frequencies of *B. lapidarius* and *B. terrestris*, which are the hosts of *B. rupestris* and *B. vestalis* were not changed during the studied periods. Contrarily, among the hosts of *B. barbutellus*, the frequency of *B. hortorum* was stable, while frequency of *B. argillaceus* increased and *B. ruderatus* showed an opposite trend.

The previously observed increasing relative frequency of *B. hypnorum* and *B. soroensis* remain increasing also after 2000. The intensive increase of relative frequencies of *B. haematurus* and *B. argillaceus* showed continuous spread of these species in Hungary during the last two decades. It can be explained rather with natural expansion, than artificial spreading of managed colonies, since their use is not common in Hungary, however the greening programs and promotion of sustainable agricultural methods can also help their spread. Although the expansion of the area of *B. haematurus* to northwest in Central Europe was already known (Biella et al. 2020), their spread to the northeast is first published here. Considering the direction of its spread it will be worth to study its appearance northeast of Hungary, e.g. in Ukraine and East Slovakia and later in Belarus.

Twenty years ago, *Bombus argillaceus* was a rare species with a decreasing distribution and was classified as critically endangered according to the IUCN (Sároszpataki et al. 2005; Kosior et al. 2007). In the last 20 years, its relative frequency has increased significantly, and now it is a moderately frequent species in Hungary. As with *Bombus haematurus*, it will be worthwhile studying the northern limits of its range.

Conclusion

Climate change, warming winters and changes in landscape structure can significantly affect the distribution of bumble bee species in Hungary (Biella et al. 2020; Novotny et al. 2021). Beyond the effects of the climate change, the distribution of bumble bees is strongly affected by their heat-stress resistance. Since, the Mediterranean and temperate zone widely distributed eurytopic species are less sensitive to heat stress and warming, than the rare stenotopic species adapted to cold climate, thus further expansion of their area can be expected in the near future (Rasmont et al. 2015; Martinet et al. 2020). This ongoing process was clearly showed by our results on the intensive expansion of *B. argillaceus* and *B. haematurus*, which can resist to heat stress, and the high relative frequency of the widely distributed *B. terrestris*. Findings of Rasmont et al. (2015) were also confirmed by the decreasing relative frequency of eight species (*B. barbutellus*, *B. confusus*, *B. humilis*, *B. muscorum*, *B. pomorum*, *B. ruderatus*, *B. rupestris*, *B. subterraneus*) of the Hungarian fauna, that also proved the significant and even dramatic effect of climate change on *Bombus* assemblages.

Regular monitoring of *Bombus* assemblages is recommended. The actualized distribution maps provide basis for both gap analysis and prioritization. The investigation of previously unexplored areas (white patches) and UTM cells containing only archaic data, as well as confirmation of the data of species with dubious data should be prioritized.

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