

Flora of the city of Brno, Czech Republic

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Abstract: Urban areas exert a significant influence on plant species assemblages. The mosaic of different urban land uses is reflected in the distribution patterns of different plant groups. Here we present the results of the first systematic and detailed floristic survey of the city of Brno, Czech Republic. We studied the flora of Brno from 2011 to 2021, and recorded all spontaneously occurring species in grid cells of 1.3 × 1.5 km. Our dataset includes 1,492 taxa found in the city, classified by their origin, residence time, invasion status, index of ecological specialization, and threat status in the Czech flora. Of these, 902 are native, 205 archaeophytes and 339 neophytes. The remaining 46 species with unknown status are probably remnants of cultivation or newly introduced species. Of the total list of species, 255 species are classified as threatened or near threatened in the Czech Republic. We analysed the effect of seven land-use categories on the proportions of these plant groups and found significant differences in the distribution of individual plant groups within the city. The proportions of plant groups except for threatened species reflected the proportions of individual land-use categories in the grid cells, although the strength and direction of these responses differed among plant groups. Native plant species richness was high in grid cells where forests predominate and the level of urbanization is low. In contrast, the proportion of archaeophytes and neophytes was much lower in the grid cells with a high proportion of forests. While archaeophytes predominated in the lowlands with agricultural land use, neophytes were more common in the central built-up areas of the city. To document the current distribution of all taxa found we supplement this study with a series of maps.

Keywords: alien species, biotic invasion, Czech Republic, land use, plant diversity, threatened species, urban ecology, urban flora, urbanization

Introduction

Urbanization is one of the most striking drivers of current biodiversity loss (Díaz et al. 2019). Urbanization leads to the loss of natural habitats and local species extinctions, but cities are also areas where the emergence of human-made habitats, accompanied by high species introduction rates, results in plant communities with novel combinations of species (Kowarik 2011, de Barros Ruas et al. 2022). However, our understanding of the patterns and mechanisms underlying the composition and distribution of these novel communities is far from complete.

Plant species in the urban environments are influenced by numerous factors, such as land-use types and their spatial structure, climatic, edaphic, and socioeconomic conditions, disturbances and other processes (Goddard et al. 2010, Shochat et al. 2010, Ramalho & Hobbs 2012). At the same time, humans plant selected species in cities and prevent them from being replaced by competitors or extirpated by natural enemies. Cities are also transportation hubs that facilitate the dispersal of species from one city to another, spreading urban-tolerant species across the globe (Aronson et al. 2014). Understanding the patterns and processes of urban biota is therefore fundamental to biodiversity conservation and ecosystem functioning. Although interest in the impact of urbanization on plant diversity is growing rapidly, especially in Europe, critical research gaps remain.

Floristic survey of urban areas has a long tradition in Central Europe. The history of this research is summarized in several articles (e.g. Sukopp et al. 1990, Wittig 1991, Pyšek 1995, 1998). In general, urban floras are studied with different methods and intensities (Pyšek 1995). Cumulative lists of plant species exist for several European cities. In the Czech Republic, such lists are available, for example, for Horažďovice (Mandák et al. 1993), Ostrava (Sobotková 1995), Prague (Špryňar & Münzbergová 1998), and Plzeň (Chocho-loušková & Pyšek 2003). However, species lists do not contain information on hotspots of plant diversity within a city, nor allow to determine the significance of individual elements within urban landscapes for the survival of specific plant species. It is also difficult to compare such lists due to the varying sizes of cities. In contrast, detailed floristic surveys, whether based on urban zones or grid mapping, are much less common. Typically, researchers divided the city into several urban patches and collected floristic data within each of them. Such an approach was used for Vienna (Adler & Mrkvicka 2003) and some other central-European cities. Although such data are very detailed and enable differentiation of the effect of landscape matrix on the occurrence of various plant groups, comparing them across different cities and landscapes is challenging.

Floristic grid maps exist for several cities in Europe, e.g. Rome (Celesti-Grappo 1995), Brussels (Godefroid & Koedam 2007), Zurich (Landolt 2001), Pécs (Wirth et al. 2020), and Ljubljana (Jogan et al. 2022). Despite variation in grid-cell sizes among these studies, the grid data allow to link floristic and environmental information, enabling comparisons of patterns between cities. All of the above-mentioned studies have shown that urban floras are generally extremely species-rich. While native species represent a large proportion of urban floras, cities also serve as hotspots for alien species introduced

both unintentionally and intentionally. The latter are mostly ornamental plants that have escaped from cultivation. The above-mentioned studies also showed that floras of cities respond very dynamically to disturbances and other environmental changes. At the same time, each city has its own peculiarities related to its unique landscape structure and history.

The Czech Republic has a long tradition of detailed floristic surveys. However, grid mapping has mainly been used for surveys of flora within several protected areas, e.g. the Podyjí/Thayatal National Park (Grulich 1997, Němec 2021), Protected Landscape Area Křivoklátsko (Kolbek et al. 1999), Protected Landscape Area Bílé Karpaty/White Carpathians (Jongepier & Pechanec 2006), and the Soutok area at the confluence of the Morava and Dyje rivers (Vicherek et al. 2000). As far as we know, grid-cell floristic data from Czech cities do not exist.

Here we present the results of a comprehensive survey of the current vascular flora of the city of Brno. With a population of nearly 400,000 inhabitants (<https://www.czso.cz>), it is the second-largest city in the Czech Republic after the capital, Prague. Brno is the administrative centre of the South Moravian Region. The city is situated in a topographically heterogeneous landscape with a mosaic of various land-use types. The area of today's city has been settled continuously since the Palaeolithic. The town was founded in the 13th century, and since then it has gradually developed into the largest city in Moravia, the eastern part of the Czech Republic. The city has an important industrial legacy dating back to the late 18th century and experienced significant development in the 20th century. This development led to the expansion of residential and commercial areas, especially on the periphery and in suburban municipalities, alongside the construction of highways and other infrastructure development. Due to the economic transformation since 1989, numerous brownfields have emerged.

The aims of this study are (i) to map and characterize the current urban flora of the city of Brno, (ii) to identify urban areas with high plant diversity or a high proportion of certain plant groups, and (iii) to explore how land use affects the distribution patterns of urban flora.

Materials and methods

Study area

The study area comprises the present-day administrative district of Brno-City (Brno-město in Czech; Fig. 1A). The total area of the district is 230.18 km². The population is 396,101 with a population density of 1,721 inhabitants per km² (<https://www.czso.cz>). The city is located in the south-eastern part of the Czech Republic, on the geographical border between the Carpathian Foredeep Basin and the Bohemian Massif, and on the border between the phytogeographical regions of Mesophyticum and Pannonian Thermophyticum (Skalický 1988). The elevation of the city ranges from 187 m a.s.l. at the confluence of the Svatka and Svitava rivers to 479 m a.s.l. at the summit of Kopeček hill. There are extensive floodplains in the south and south-east, isolated hills, deep river valleys and a hilly landscape, especially in the northern and western parts of the city. Brno has a mosaic of different bedrocks, with granodiorites and loess being the most prominent (Hanžl et al. 1999). Two rivers, a dam lake, several fishponds and other small water bodies, as well as periodic wetlands on arable land form potential habitat for aquatic and

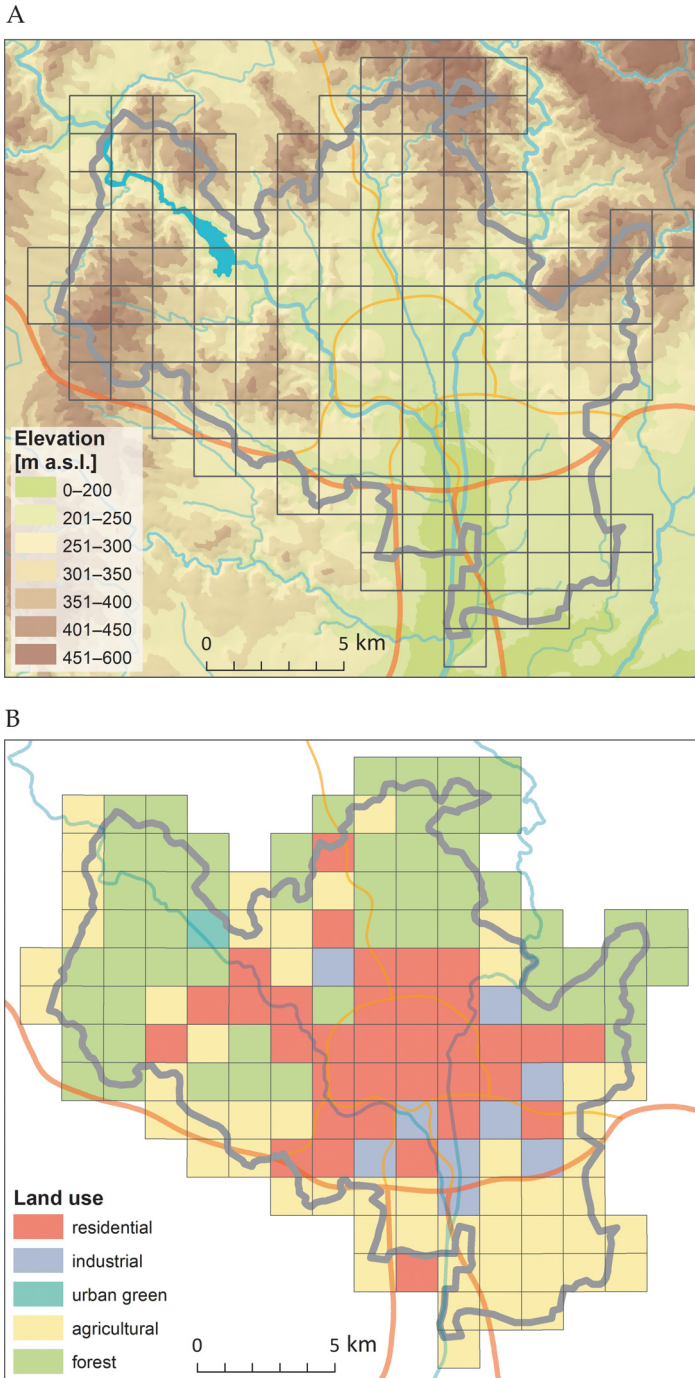


Fig. 1. The study area of the city of Brno divided into 152 grid cells sized approximately 1.5 km × 1.3 km with (A) elevations and (B) prevailing land-use type (the type with the largest area in a given cell). The city boundary is in grey, rivers and water bodies in blue and major highways and roads in orange.

wetland species. Brno is situated in an area characterized by a subcontinental climate, which is one of the warmest and driest regions in the Czech Republic. The mean annual temperature reaches 10.0 °C, a minimum monthly mean temperature of –0.9 °C is in January and a maximum of 20.6 °C is in July. The total annual precipitation is 511 mm with a minimum monthly total of 22 mm in February and a maximum of 71 mm in July. These values refer to the warm south-eastern part of the city (Brno-Tuřany weather station, 241 m a.s.l.) and the reference period of 1991–2020 (<https://www.chmi.cz>). The territory of Brno includes a small part of the Protected Landscape Area Moravian Karst and numerous small-scale, specially protected areas (Šmiták 1992, <https://www.mapy.cz>).

History of the botanical research

Botanical research into the flora of the city and the entire province of Moravia was started by C. F. Hochstetter in the late 1810s. He issued a series of exsiccates, *Plants of the Brno county* (*Gewächse des Brünnner Kreises*), which contained several hundred species, collected an extensive herbarium, and published the first comprehensive report on the flora of Moravia (Hochstetter 1825), which included species occurrence records from Brno.

Hochstetter's botanical activities stimulated interest in the local flora among the city's amateur naturalists, including W. Tkany, J. Wessely and R. Rohrer. However, the plant records from Brno in the first flora of Moravia (Rohrer & Mayer 1835) are mainly based on earlier records and herbarium specimens by Hochstetter. Nevertheless, this flora further supported interest in botanical exploration of the city and its surroundings, as shown by herbarium specimens now deposited in the herbaria of the Moravian Museum (BRNM) and Masaryk University (BRNU). Numerous specimens were collected by J. N. Bayer, F. Jellinek, S. Reissek and W. Tkany.

Systematic recording of the city flora was carried out by A. Makowsky between the early 1850s and the early 1900s. His explorations resulted in a list of 362 species that occurred spontaneously or were cultivated in Brno (Makowsky 1863a). By combining his new finds with the records of earlier researchers, he compiled a flora of the Brno county (*Die Flora des Brünnner Kreises*; Makowsky 1863b). Both works were published in the first volume of the journal of the Brno Natural History Society (*Naturforschender Verein in Brünn*), which was founded in 1861. Members of this society, including I. Czižek, F. Fiala, F. Haslinger and G. Niessl von Mayendorf contributed significantly to the knowledge of the local flora and deposited most of their herbarium specimens in the society herbarium, which is now included in the herbarium BRNU. Research into the local flora was also promoted by two editions of a field guide to the city's and county's flora (Haslinger 1869, 1880). The botanical knowledge gathered since the beginning of research into Moravian flora was summarized by A. Oborny in his *Flora of Moravia and Austrian Silesia* (*Flora von Mähren und österr. Schlesien*; Oborny 1883–1886), written in German, and its counterpart in Czech (Formánek 1887–1897).

In the early 20th century, research into the city's flora was continued mainly by J. Hruby, F. Teuber, O. Thenius and A. Wildt, who were all members of the German-speaking Brno Natural History Society. The specimens collected by these botanists, with the exception of Thenius, are mainly deposited in the herbarium BRNM. A. Wildt also compiled a field guide to the flora of the city and its environs with identification keys (Wildt 1910). Another guide to the city's flora, published two decades later (Hruby

1928), contained detailed lists of plant species at specific sites, including public parks near the city centre and well-known botanical sites near the city.

From the early 20th century, Czech speaking botanists also participated in the research into the flora of Brno. For instance, V. Filkuka collected a few hundred plants in the northern outskirts of Brno in the 1910s, while F. Švestka intensively studied the flora in various parts of the city and its environs in the 1920s and 1930s. The Natural History Club in Brno (Klub přírodovědecký v Brně), a Czech counterpart to the Naturforschender Verein in Brünn, was founded in 1905. In 1914, it launched its own journal, which soon became a publication venue for botanical records from the city and its surroundings. After the foundation of Masaryk University in 1919 and its Institute of General and Systematic Botany in 1921, the number of professional botanists in Brno increased. Nevertheless, there was no particular focus on the city's flora in the 1920s and early 1930s, except for two reports on ruderal plants (Krist 1935, 1940), which represent some of the earliest articles dealing with alien plants in this country.

In the second half of the 20th century, several local botanists, including F. Dvořák, J. Dvořák, F. Kühn, J. Müller, J. Saul, M. Smejkal and J. Unar recorded plant occurrences and collected specimens, which are now stored in the above-mentioned herbaria. Dvořák & Kühn (1966) published a list of alien plant taxa that were introduced with overseas wool import to Brno textile factories. Some of these species disappeared soon after their introduction, but some others are now a permanent part of the urban flora of Brno (e.g. *Amaranthus deflexus*, Grüll 1999). An overview of the synanthropic flora of the city, based on detailed knowledge of the flora of urban brownfields and waste lands, was published by Grüll (1979), who listed about 800 taxa from the city. The same author also conducted a systematic study of ruderal vegetation of Brno (Grüll 1981). An overview of the threatened plant species of Brno was published in a three-volume series by Šmiták & Tichý (1997) and Tichý et al. (1999, 2001).

Data sampling

We conducted a thorough floristic mapping of the Brno city between the years 2011 and 2021. To obtain a comparable density of floristic records across the city, we divided the study area into grid cells of 1.25' of longitude \times 0.75' of latitude, i.e. approx. 1.5 \times 1.3 km. These grid cells are derived from the third division of the grid system used for central European floristic mapping, with the basic grid cells of 10' \times 6' (Fig. 1A, B; Supplementary Data S1). The total number of grid cells covering the study area is 152. In each grid cell, we recorded the presence of all spontaneously occurring taxa of vascular plants. We visited each grid cell at least three times in different parts of the growing season. For grid cells situated on the city's administrative border, we collected separate information on taxa occurring within and outside the city. For the descriptive analyses, we used complete species lists from the entire borderline grid cells in order to have comparable data for all grid cells. The taxa that were only found outside the city are marked in Supplementary Data S1.

In the field, we used mobile GPS applications whenever possible to accurately pinpoint the location of plant records and boundaries of grid cells. We stored the collected data in the Vratička database (<https://www.sci.muni.cz/vraticka>). In September 2022, the database contained 69,314 occurrence records from Brno and its vicinity within the

studied grid cells. We imported these data into the Pladias Database of the Czech Flora and Vegetation (Wild et al. 2019, Chytrý et al. 2021, <https://www.pladias.cz>) in November 2022. Although we primarily involved professionals and qualified volunteer amateur botanists, several students also participated in the fieldwork. Their records were summarized in bachelor theses (Dršková 2013, Melicharová 2016, Harásek 2018, Musilová 2018, Svobodová 2018, Faltýnková 2020, Klepalová 2021) and master theses (Laštůvková 2017, Staviařová 2017, Melicharová 2019) at Masaryk University and Mendel University in Brno. In total, our team included 37 botanists.

Species

We supplemented our data with accurately localized records from the same time period (2011–2021) published or stored in the Pladias database (Wild et al. 2019), NDOP database of the Nature Conservation Agency of the Czech Republic (AOPK ČR 2022) and specimens stored in the herbarium of Masaryk University (BRNU) and catalogued in the online database JACQ (Rainer et al. 2023), and the herbarium of Mendel University in Brno (BRNL). The NDOP database contains records from several sources, including the citizen-science databases such as iNaturalist (<https://www.inaturalist.org>) or BioLog (<https://www.biolog.nature.cz>). From these sources, only data supported by a photo of the plant or sampled by trustworthy amateur or professional botanists were included in the analyses. Taxa determined only to the genus level were omitted from the dataset before analyses.

Most of the taxa grown in domestic gardens are also grown in botanical gardens (van Kleunen et al. 2018). Therefore, we compiled a list of taxa that have escaped from cultivation in the Botanical Garden of the Faculty of Science, Masaryk University. This list complemented the spontaneous urban flora with information on escapes within the botanical garden, which is typically not available for private gardens. We included the list of escaping taxa from the Botanical Garden into our dataset.

Our dataset contained 74,060 records of 1,614 taxa from different taxonomic categories. We merged varieties and forms to the species level. We use the subspecies rank only if there were no doubts about their identification, otherwise we merged subspecies to the species level as well. We merged species in the taxonomically challenging groups into aggregates or sections following the national excursion flora (Kaplan et al. 2019). We consolidated multiple records of one species from one grid cell and analysed the presence/absence data at the grid-cell level. This resulted in 55,671 records, which are included in Supplementary Data S1. Taxonomy and nomenclature of plants follow Kaplan et al. (2019). We also discovered several new taxa for the Czech Republic, which are not included in Kaplan et al. (2019): *Caryopteris ×clandonensis* A. Simmonds, *Cotoneaster multiflorus* Bunge, *C. splendens* Flinck et B. Hylmö, *Eclipta prostrata* (L.) L., *Muhlenbergia mexicana* (L.) Trin., *Nassella tenuissima* (Trin.) Barkworth, *Pachysandra terminalis* Siebold et Zucc., and *Scoparia dulcis* L. We supplemented our findings with published information regarding a new record of *Phacelia congesta* Hook. (Sutorý in Lustyk & Doležal 2021). We list these taxa with the author names, unlike the taxa included in Kaplan et al. (2019), which we list without author names. The complete list of taxa is in Supplementary Data S1.

Although our research focused on spontaneously occurring taxa, some of our records could represent remnants of cultivation. Especially in areas of former gardens, it was difficult to distinguish cultivation escapes from remnants of previous cultivation. Therefore, we denoted such doubtfully escaped taxa with the abbreviation “cult.” in the taxon list. Detailed information, including the definition of aggregates, and taxonomic notes is given in Supplementary Data S1. The final list comprised 1,492 taxa used for the analyses.

For each taxon, we prepared a map of its distribution within the city of Brno. We created more than one map for taxonomically difficult taxa, one for the higher taxonomic rank, such as a species aggregate, and one or more for the lower taxonomic ranks, such as the individual species within the aggregate. For example, we present separate maps for *Aethusa cynapium*, *A. cynapioides* and *A. cynapium* agg. However, in the dataset of 1,492 species used for the analyses, we only included *A. cynapium* agg. The distribution maps are in Supplementary Data S2. For simplicity, we use the term “species” hereafter.

Plant groups

We extracted characteristics of species origin, residence time and invasion status, ecological specialization index, and Red List categories from the sources included in the Pladias database (Chytrý et al. 2021). We classified species by their origin and residence time in the Czech Republic following Pyšek et al. (2022) into (i) native, (ii) archaeophytes (alien species introduced before the year 1500), and (iii) neophytes (alien species introduced after 1500). Alien species (i.e. archaeophytes and neophytes together) were further classified by invasion status into (iv) casual, (v) naturalized, and (vi) invasive. Species marked as cultivated only (88 species) and alien species not included in Pyšek et al. (2022) (46 species) were omitted from the analyses.

We further classified the species as (vii) threatened according to the Red List of vascular plants of the Czech Republic (Grulich 2017, IUCN categories). All critically endangered (CR), endangered (EN), vulnerable (VU) and near threatened (NT) species were grouped as threatened. As some threatened species could be planted or spread by humans, we only focused on undoubtedly natural occurrences of these species. Threatened species that are probably spreading from cultivations or occur in man-made habitats within the city are marked by red or orange colour, respectively in Supplementary Data S1.

We also characterized (viii) the affinity of species to the urban environment as urbanophilous, urbanoneutral or urbanophobic using the urbanity index (Klotz et al. 2002). However, this index was only available for about half of the species on the list. The remaining species were not classified.

Finally, we used the ecological specialization index (Zelený & Chytrý 2019) for each species and distinguished a group of (ix) specialized species with a narrow niche.

We calculated the proportions of each plant group within each grid cell and mean values for indices.

Land-use variables

We characterized the environmental conditions in the study area using data on land use from the CORINE Land Cover 2020 dataset (Copernicus Land Monitoring Service 2020). We aggregated the original land-use categories into seven broad types – residential,

industrial, urban green, agricultural, forest, grassland, and water. A description of these types along with the original land-use categories included can be found in Table 1. For the aggregated land-use types, we calculated proportions within each grid cell. The prevailing land-use types in the grid cells are shown in Fig. 1B.

We calculated correlations to test the relationships between the proportions of aggregated land-use types and the proportions of species assigned to individual plant groups across grid cells using R version 4.3.0 (R Core Team 2023).

Table 1. Aggregated categories of land-use types and their description, based on the CORINE land-cover dataset (Copernicus Land Monitoring Service 2020).

Category	Description	CORINE land-cover nomenclature
Residential	Areas mainly occupied by dwellings and buildings used by administrative/public utilities, including their connected areas (associated lands, approach road network, parking lots).	111 Continuous urban fabric 112 Discontinuous urban fabric
Industrial	Areas mainly occupied by industrial activities of manufacturing, trade, financial activities and services, transport infrastructures for road traffic and rail networks, airport installations, river port installations, including their associated lands and access infrastructures. Includes industrial livestock rearing facilities. Areas also occupied by extractive activities, construction sites, human-made waste dump sites and their associated lands.	121 Industrial or commercial units 122 Road and rail networks and associated land 124 Airports 131 Mineral extraction sites 133 Construction sites
Urban green	Areas created for recreational use. Includes green or recreational and leisure urban parks, sport and leisure facilities.	141 Green urban areas 142 Sport and leisure facilities
Agricultural	Arable land, permanent crops, and heterogeneous agricultural areas	211 Non-irrigated arable land 221 Vineyards 222 Fruit trees and berry plantations 242 Complex cultivation patterns
Forest	Areas occupied by forests and woodlands	311 Broad-leaved forest 312 Coniferous forest 313 Mixed forest 324 Transitional woodland/shrub
Grassland	Grasslands under no or moderate human influence; lands that are permanently used for fodder production	231 Pastures 321 Natural grassland
Water	Lakes, ponds and pools	512 Water bodies

Results

Species richness of Brno flora

We found 1,492 species of vascular plants, including 1,465 within the city of Brno and additional 27 species growing in the parts of grid cells outside the city boundaries. The numbers and proportions of species assigned to individual plant groups within the city flora are shown in Table 2 and Fig 2.

Table 2. Numbers and proportions of species belonging to individual plant groups found in the city of Brno between the years 2011–2021. The figures include species found outside the city in the mapped grid cells. Numbers of threatened and near threatened species do not include the species whose occurrence is secondary.

Plant groups	Number	Proportion (%)
Origin and residence time		
Native species	902	60.5
Archaeophytes	205	13.7
Neophytes	339	22.7
Cultivated only (incomplete record, not analysed)	46	3.1
Invasion status		
Casual	216	14.5
Archaeophytes	40	2.7
Neophytes	176	11.8
Naturalized	260	17.4
Archaeophytes	146	9.8
Neophytes	114	7.6
Invasive	67	4.5
Archaeophytes	18	1.2
Neophytes	49	3.3
Threatened and near threatened species	255	17.1
Critically endangered (CR)	10	0.7
Endangered (EN)	49	3.3
Vulnerable (VU)	44	2.9
Near threatened (NT)	152	10.2
Affinity to the urban environment		
Urbanophilous species	181	12.1
Urbanoneutral species	200	13.4
Urbanophobic species	486	32.6
Specialized species (index of specialization > 0)	1,027	68.8
All species	1,492	

The most frequent species in the city flora, i.e. those occurring in every grid cell, were generalists, such as *Achillea millefolium* agg., *Artemisia vulgaris*, *Plantago major*, *Sambucus nigra*, *Taraxacum* sect. *Taraxacum*, *Trifolium repens*, and *Urtica dioica*. The most frequent invasive neophytes were *Erigeron annuus* (150/98.7% grid cells), *Robinia pseudoacacia* (144/94.7%) and *Solidago canadensis* (143/94.0%).

Native species prevailed in the overall urban flora, followed by neophytes and archaeophytes (Table 2, Figs 3A, B). However, archaeophytes were, on average, more numerous in the grid cells than neophytes (Fig. 3B). Archaeophytes also exhibited a higher number of species with naturalized status in the total flora and higher average number per grid cell than naturalized neophytes. In contrast, there were more neophyte species with invasive status than archaeophyte species with invasive status, both in the total city flora and in grid cells (Figs 3A, B).

Overall, the proportion of native species in the grid cells ranged from 47% in highly urbanized grid cells to 91% in forested areas on the urban periphery. The proportion of

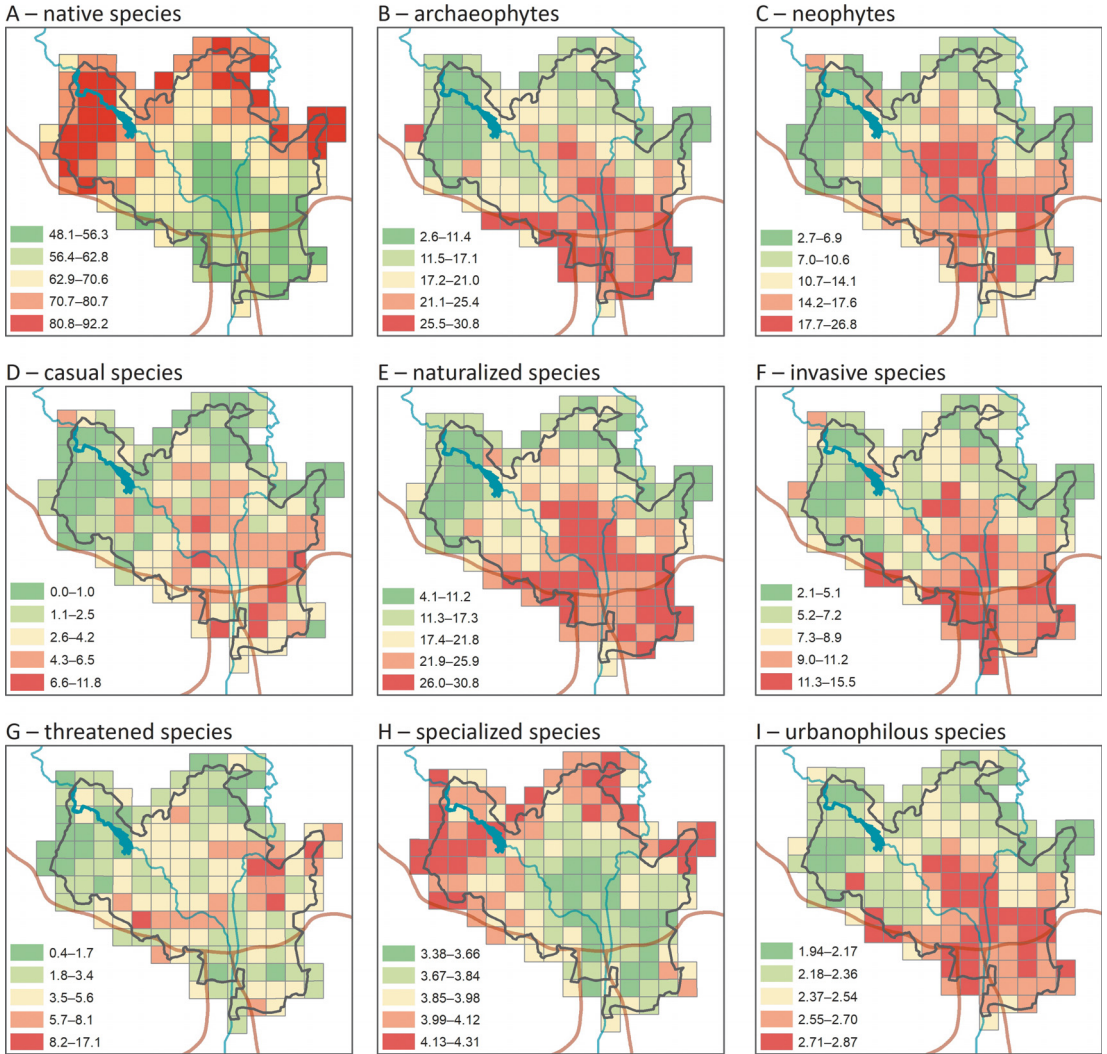


Fig. 2. Distribution of individual plant groups within the city of Brno. The numbers given in the maps are proportions for plant groups and mean index values for specialized and urbanophilous species per grid cell. Threatened species include near threatened species. Information on urbanity was only available for about half of the species.

archaeophytes varied between 3% and 32%, with higher values found in the agricultural parts of the city. The proportion of neophytes ranged from 2% to 26%, with higher values in the most urbanized areas (Figs 2A–C). The numbers of alien species grouped according to their residence time and invasion status in the city flora and their average numbers per grid cell are given in Figs 3A, B. Distributions of casual, naturalized and invasive species groups are shown in Figs 2D–F.

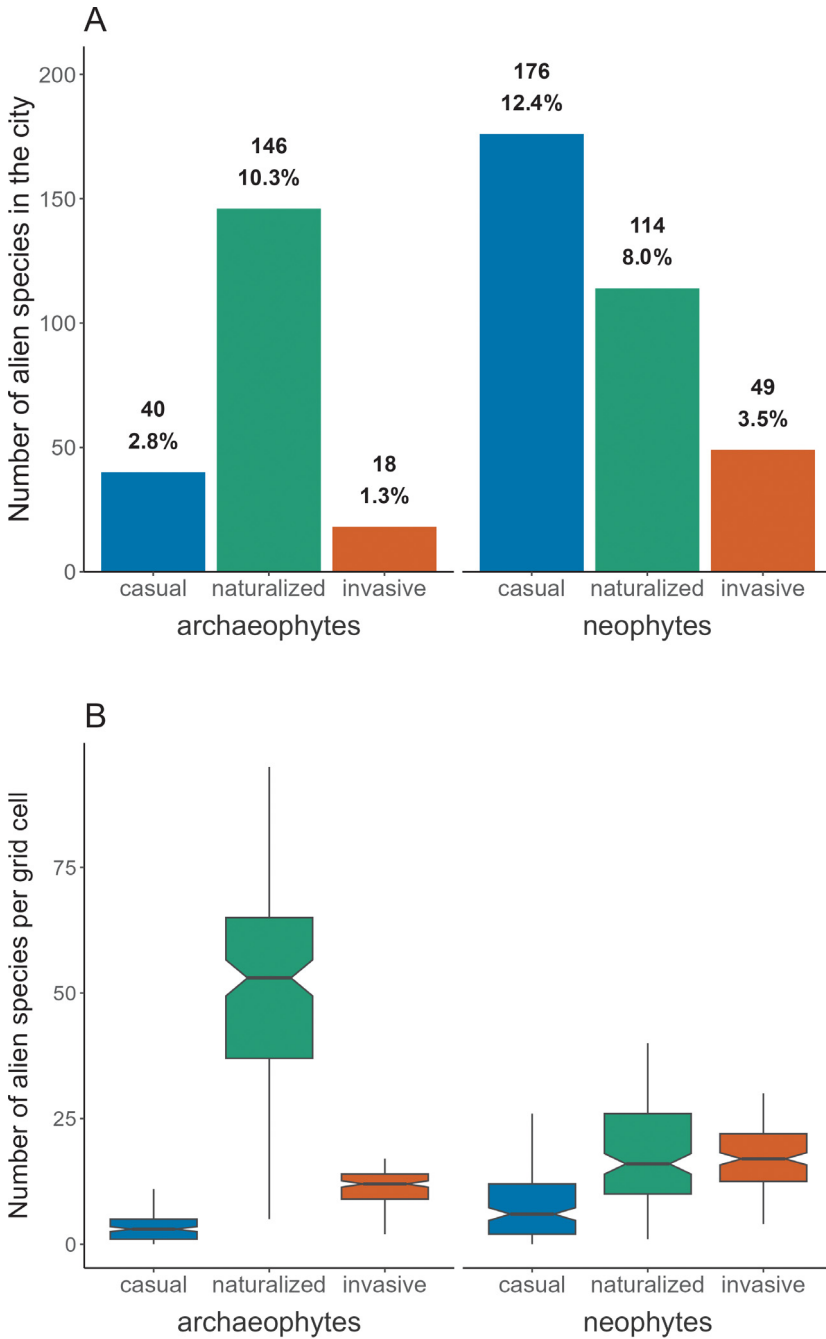


Fig. 3. Number of species assigned to alien plant groups in the city flora (A) and average numbers of species assigned to alien plant groups per grid cell (B). Percentages represent the proportions of the plant groups in the total city flora.

Table 3. Complete list of threatened species found in the study area during the years 2011–2021. Near threatened species are excluded. The species not used for the analyses because they could be potentially spreading from cultivation, remnants of cultivations or secondary occurrences in man-made habitats are marked by asterisks. Species found outside the city only are marked by two asterisks.

Critically endangered (CR)	Endangered (EN)	Vulnerable (VU)
<i>Agrostemma githago</i> *	<i>Althaea officinalis</i> *	<i>Adonis vernalis</i>
<i>Ajuga chamaepitys</i>	<i>Anemone sylvestris</i> *	<i>Amaranthus blitum</i>
<i>Asplenium ceterach</i> *	<i>Antennaria dioica</i>	<i>Asplenium scolopendrium</i>
<i>Chenopodium murale</i>	<i>Anthriscus caucalis</i>	<i>Campanula bononiensis</i>
<i>Erysimum repandum</i> **	<i>Carex hordeistichos</i>	<i>Carex alba</i> *
<i>Filago germanica</i>	<i>Centaurea montana</i> *	<i>Carex stenophylla</i>
<i>Herniaria hirsuta</i>	<i>Cephalanthera rubra</i>	<i>Caucalis platycarpus</i>
<i>Hibiscus trionum</i>	<i>Chamaecytisus albus</i> **	<i>Centaurium pulchellum</i>
<i>Montia arvensis</i>	<i>Chenopodium vulvaria</i>	<i>Chondrilla juncea</i>
<i>Polycnemum arvense</i>	<i>Cotoneaster laxiflorus</i>	<i>Corallorhiza trifida</i>
<i>Polycnemum majus</i>	<i>Crepis praemorsa</i>	<i>Cypripedium calceolus</i>
<i>Puccinellia distans</i> *	<i>Crepis setosa</i>	<i>Epipactis palustris</i>
<i>Spergularia marina</i> *	<i>Dactylorhiza incarnata</i>	<i>Equisetum ramosissimum</i>
<i>Tordylium maximum</i> **	<i>Dactylorhiza sambucina</i>	<i>Euphorbia angulata</i>
	<i>Dianthus gratianopolitanus</i> *	<i>Euphorbia falcata</i>
	<i>Dianthus superbus</i> **	<i>Gagea bohemica</i>
	<i>Draba muralis</i>	<i>Gagea villosa</i>
	<i>Drymocalis rupestris</i>	<i>Gentianopsis ciliata</i>
	<i>Echium maculatum</i>	<i>Hydrocharis morsus-ranae</i> *
	<i>Epipactis albensis</i>	<i>Hyoscyamus niger</i>
	<i>Epipogium aphyllum</i>	<i>Iris graminea</i> *
	<i>Equisetum xmoorei</i>	<i>Iris pumila</i> *
	<i>Equisetum hyemale</i> **	<i>Iris variegata</i>
	<i>Erigeron podolicus</i>	<i>Lithospermum officinale</i>
	<i>Festuca drymeja</i> **	<i>Melampyrum arvense</i>
	<i>Gentiana cruciata</i> **	<i>Melampyrum cristatum</i>
	<i>Gypsophila paniculata</i> *	<i>Monotropa hypopitys</i>
	<i>Hippuris vulgaris</i> *	<i>Muscari neglectum</i> *
	<i>Inula germanica</i>	<i>Odontites luteus</i>
	<i>Kickxia spuria</i>	<i>Orobanche elatior</i>
	<i>Lepidium coronopus</i>	<i>Platanthera bifolia</i>
	<i>Leucojum aestivum</i>	<i>Platanthera chlorantha</i>
	<i>Linum hirsutum</i> *	<i>Potentilla alba</i>
	<i>Malva pusilla</i>	<i>Pulsatilla grandis</i>
	<i>Melilotus dentatus</i>	<i>Pulsatilla pratensis</i> subsp. <i>bohemica</i>
	<i>Minuartia rubra</i>	<i>Ranunculus rionii</i>
	<i>Misopates orontium</i>	<i>Reseda luteola</i>
	<i>Nymphoides peltata</i> */**	<i>Rosa gallica</i>
	<i>Orchis purpurea</i>	<i>Rosa micrantha</i>
	<i>Orlaya grandiflora</i> *	<i>Rosa spinosissima</i>
	<i>Ornithogalum boucheanum</i>	<i>Rubus saxatilis</i>
	<i>Orobanche picridis</i>	<i>Sclerochloa dura</i>
	<i>Parietaria officinalis</i>	<i>Senecio erucifolius</i>
	<i>Phelipanche purpurea</i>	<i>Stachys annua</i>
	<i>Pilosella leucopsilon</i>	<i>Stipa dasyphylla</i>
	<i>Prunus fruticosa</i>	<i>Taxus baccata</i> *
	<i>Rumex stenophyllus</i>	<i>Trifolium fragiferum</i>
	<i>Salsola tragus</i> subsp. <i>tragus</i>	<i>Trifolium rubens</i>
	<i>Scrophularia vernalis</i>	<i>Urtica urens</i>
	<i>Sideritis montana</i>	<i>Valerianella carinata</i>
	<i>Stachys germanica</i>	
	<i>Stipa smirnovii</i>	
	<i>Tephrosieris integrifolia</i> **	
	<i>Thesium dollineri</i>	
	<i>Thymelaea passerina</i>	
	<i>Torilis arvensis</i>	
	<i>Verbascum blattaria</i>	
	<i>Verbascum speciosum</i> *	
	<i>Xanthium strumarium</i>	

We found 255 threatened (including near threatened) species (17% of the overall city flora, Table 2). Of these, eight critically endangered species occurred spontaneously within the city (*Ajuga chamaepitys*, *Chenopodium murale*, *Filago germanica*, *Herniaria hirsuta*, *Hibiscus trionum*, *Montia arvensis*, *Polycnemum arvense* and *P. majus*). In areas of the studied grid cells outside of the city boundaries, we also found *Erysimum repandum* and *Tordylium maximum* (Supplementary Data S2). Additionally, 49 species found are endangered (e.g. *Anthriscus caucalis*, *Echium maculatum*, *Inula germanica*, and *Scrophularia vernalis*), 44 species are vulnerable (e.g. *Asplenium scolopendrium*, *Carex stenophylla*, *Ranunculus rionii*, and *Stachys annua*), and 152 species are near threatened (e.g. *Androsace elongata*, *Bothriochloa ischaemum*, *Crepis tectorum*, and *Viola rupestris*). All threatened (excluding near threatened) species are listed in Table 3. The proportions of threatened and near threatened species in the individual grid cells are shown in Fig. 2G.

The flora of Brno also contains 181 urbanophilous species (Table 2, Fig. 2H). Mean index of specialization per grid cell is shown in Fig. 2I.

Relationship of flora with urban land use

We found distinct distribution patterns of individual plant groups within the city. The proportions of species assigned to the studied plant groups in the grid cells reflected the proportions of aggregated land-use categories, although the strength and direction of response to specific land-use categories differed markedly between plant groups (Fig. 4).

The proportion of forest area within grid cells was the most important factor for each plant group except for threatened species. The high proportion of forest was positively related to the proportion of native and specialized species, whereas it was negatively related to the proportions of all groups of alien species and urbanophilous species. However, the proportion of forest area does not correlate with the total species richness and the proportion of threatened species in Brno. The importance of other land-use types varied among plant groups. Besides forests, other important factors included residential and industrial land use, which supported the high proportion of neophytes and naturalized alien species and were negatively related to specialized species. The high proportion of archaeophytes was maintained mainly by agriculture and less by residential land use. Less important correlates were water bodies, urban green spaces, and grasslands (Fig. 4). The proportion of threatened species was slightly positively correlated with the proportion of grasslands in the grid cells.

Discussion

Current flora of the city of Brno

During 11 years of field mapping of the flora in the city of Brno, we recorded about one third of the total flora of the Czech Republic (Kaplan et al. 2019). Our results are consistent with other studies showing that cities can harbour remarkably high plant diversity (Pyšek 1998, Chocholoušková & Pyšek 2003, Kühn et al. 2004, Wania et al. 2006, Godefroid & Koedam 2007).

	Species richness	Proportion of native species	Proportion of archaeophytes	Proportion of neophytes	Proportion of casual species	Proportion of naturalized species	Proportion of invasive species	Proportion of threatened species	Proportion of specialized species	Proportion of urbanophilous species
Number of land-use types	0.38*	0	-0.08	0.08	0.05	0.02	-0.12	0.29*	-0.13	-0.08
Proportion of agricultural areas	-0.15	-0.41*	0.55*	0.17	0.24	0.42*	0.42*	-0.05	-0.11	0.39*
Proportion of forests	-0.03	0.88*	-0.87*	-0.76*	-0.67*	-0.88*	-0.76*	-0.16	0.67*	-0.84*
Proportion of grasslands	0.13	0.11	-0.11	-0.1	-0.1	-0.08	-0.17	0.43*	0.05	-0.18
Proportion of industrial areas	-0.01	-0.47*	0.43*	0.45*	0.4*	0.45*	0.43*	0.18	-0.5*	0.47*
Proportion of residential areas	0.24	-0.52*	0.37*	0.64*	0.46*	0.52*	0.37*	0.18	-0.56*	0.5*
Proportion of urban green areas	-0.06	-0.04	-0.01	0.11	0.05	0.05	0	-0.07	-0.06	0.08
Proportion of water bodies	-0.04	0.11	-0.11	-0.09	-0.11	-0.11	-0.08	-0.17	0.15	-0.08

Fig. 4. Correlation matrix with proportions of individual plant groups and urban land-use types within grid cells in Brno. The colour scale goes from red for positive correlation to blue for negative correlation. * $P < 0.05$. Threatened species include near threatened species. Note that information about urbanization affinity was only available for about half of the species.

Urban area is a highly dynamic fine mosaic of habitats that changes in space and time. Our data are also affected by such dynamics. We are aware of numerous species occurrences that have disappeared during the survey period (e.g. *Montia arvensis* occurred casually in the university campus Bohunice in 2016 and subsequently disappeared). It is also likely that we have overlooked some species. One such example could be *Corydalis intermedia*, which was documented by Miroslav Smejkal in the 1990s and may still be growing in the city. On the other hand, some species have been found at new sites, i.e. *Asplenium ceterach* subsp. *bivalens* (Řepka et al. in Lustyk & Doležal 2020), *Caryopteris xclandonensis* (Danihelka et al. 2020), *Cotoneaster multiflorus* (Sedlák & Řepka in Lustyk & Doležal 2022), *C. splendens* (Řepka in Lustyk & Doležal 2022), *Eclipta prostrata* (Doležal & Řepka in Lustyk & Doležal 2022), *Lemna minuta* (Landucci in Hadinec & Lustyk 2014), *Muhlenbergia mexicana* (Řepka et al. in Lustyk & Doležal

2022), *Nassella tenuissima* (Řepka et al. in Lustyk & Doležal 2021), *Panicum virgatum* (Chytrý & Danihelka in Hadinec & Lustyk 2015), *Phacelia congesta* (Sutorý in Lustyk & Doležal 2021), *Polypogon viridis* (Řepka et al. in Lustyk & Doležal 2021), and *Scoparia dulcis* (Řepka in Lustyk & Doležal 2019). It should be noted that the occurrences of some of the above-mentioned species are either results of probable intentional planting (e.g. *Asplenium ceterach* subsp. *bivalens*) or it is difficult to differentiate whether their occurrence is spontaneous or not (see notes in Supplementary Data S1).

Since the end of our fieldwork in 2021, we have found or learned about new localities of several previously found rare species and entirely new (mainly ornamental) species that have escaped from cultivation. Such an example is *Perovskia abrotanoides* × *P. atriplicifolia*, which was found as an escape from cultivation in a paved area near the city centre in 2023 (Chytrý in Lustyk & Doležal 2024 in prep.).

Decline of native species and archaeophytes

Although many species occurrence records were published from the study area in the past, most of them concerned geographically or ecologically unusual plant species. We do not have complete historical data to give a more accurate overview of the dynamics of urban flora in the city of Brno. Nevertheless, a comparison of our data with previously published floristic records documents the loss of many, mostly highly specialized species. Makowsky (1863b) was the last who collected *Himantoglossum jankae* on the southern slope of Hády hill in 1855. He documented several rare plant species of primarily nutrient-poor habitats that have completely disappeared from the city (e.g. *Achillea nobilis*, *Centunculus minimus*, *Daphne cneorum*, *Goodyera repens*, and *Pseudognaphalium luteoalbum*). Most records of the above-mentioned plants in the study area date back to the 19th century, and the most recent ones are from the 1950s–1960s. An important group of species that have disappeared from Brno are wet-meadow specialists (e.g. *Viola elatior*, 1836 Tkany BRNU), including those related to fens and mineral-rich soils (e.g. *Pedicularis palustris*, s. d. Formánek BRNM; *Juncus subnodulosus*, 1977 Řepka BRNU and *Scirpoides holoschoenus*, 1977 Řepka BRNU, published by Řepka in Hadinec & Lustyk 2017). Several formerly relatively frequent native species are recently restricted to small populations, such as the orchids *Corallorhiza trifida*, *Cypripedium calceolus*, *Dactylorhiza sambucina*, and *Orchis purpurea*.

At the beginning of the 20th century, the landscape of the current urban periphery was predominantly agricultural. From that time, researchers reported several weed species that have disappeared from the whole city or even country due to changes in agricultural practice (e.g. *Bifora radians*, 1922 Thenius BRNU; *Linaria arvensis*, Laus 1908). Šmiták & Tichý (1997) listed 76 extinct plant species in Brno. However, our detailed survey found that 19 of these species still occur there, e.g. *Adonis aestivalis*, *Inula germanica*, and *Verbascum phoeniceum*.

Threatened and specialized species

Our results show that highly urbanized areas within the city select for urban-tolerant generalist species. Fragmentation and isolation of natural and seminatural habitats in residential and industrial areas, combined with high levels of disturbance, thus exhibit a significant impact on urban plant community structure. However, we also found that the city

provides refuge for some specialized and threatened species that cannot survive in the open, intensively managed agricultural landscape. The threatened species that occur in the city form a very heterogeneous group. Most of them survive in patches of natural or seminatural habitats, such as in dry grasslands (Šmiták & Tichý 1997, Tichý et al. 1999, 2001). Still, some threatened species have found their secondary niche in artificial habitats, e.g. *Saxifraga tridactylites* on railways and pavements, and halophilous plants such as *Puccinellia distans* and *Spergularia marina* along roads, which is consistent with observations at the national level (e.g. *Saxifraga tridactylites* in Ducháček 2009; *Spergularia marina* in Kaplan et al. 2016). Threatened species also include several weed and ruderal species that were dependent on previous management practices, such as *Ajuga chamaepitys*, *Anthriscus caucalis*, and *Chenopodium murale*. These species, which have recently become rare in agricultural landscapes, survive at some sites in urbanized areas. Because only natural occurrences of threatened plants were considered, escapes of threatened species from cultivations were not included into relevant statistics. This species group is quite numerous and includes particularly ornamental plants that have spread from cultivation (e.g. *Leucojum vernum*, *Menyanthes trifoliata*, and *Spiraea salicifolia*).

Alien species in the flora of Brno

The loss of specialized native species or archaeophytic weeds has been partly complemented by new introductions. Dvořák & Kühn (1966) and later on Grüll (1972, 1979, 1994, 1999) documented several plants introduced along railways, in sandpits, and with wool imported from overseas and processed by the textile industry in the 1950s–1980s. Most of these new taxa disappeared soon after their introduction (e.g. *Bromus scoparius*, *Cotula australis*, *Lawrenzia glomerata*), but some remnants of these introductions (e.g. *Amaranthus deflexus*, *Artemisia tournefortiana*, *Geranium sibiricum*, and *Rumex patientia*) are established and naturalized in the urban flora till now. Nowadays, *Amaranthus deflexus* is a common species of urban lawns, *Artemisia tournefortiana* occurs in vacant lots and back yards in the city centre, *Geranium sibiricum* grows in ruderal places, and *Rumex patientia* is common in brownfields and along the railways and roads.

The introductions of alien species to the city is continuing. There are two main factors underlying the observed distribution patterns of alien plant species: (i) high habitat invasibility in urbanized areas associated with frequent or severe disturbances, often coupled with high nutrient inputs and (ii) high propagule pressure (Davis et al. 2000, Pyšek et al. 2005, Pyšek & Chytrý 2014, van Kleunen et al. 2015, Kühn et al. 2017). Our results show that alien species in urbanized areas increase their richness by combining two main introduction pathways – intentional cultivation and unintentional transfer. Most alien species are cultivated in private gardens and public green spaces and escape from cultivation (Čeplová et al. 2017, van Kleunen et al. 2018). This is why a high proportion of alien plants are found in residential areas and their surroundings. Some alien species are introduced unintentionally with traffic (von der Lippe & Kowarik 2007, Hulme 2009, Schadek et al. 2009, van Kleunen et al. 2018). Such species are frequent in grid cells with more roads and railways (see e.g. distribution maps for *Atriplex micrantha*, *Dittrichia graveolens*, *Rumex patientia*, and *Senecio inaequidens*; Supplementary Data S2). Many alien species (e.g. *Artemisia tournefortiana*, *Bromus hordeaceus*, *Echinops sphaerocephalus*,

and *Lepidium ruderale*) have been found mainly at industrial sites and brownfields, in accordance with findings from other cities (Schadek et al. 2009).

The cumulative numbers of species from alien plant groups indicate that even though archaeophytes are less numerous in total, they exhibit higher average proportions within grid cells than neophytes. A similar pattern is shown for invasive alien species, indicating that few common alien species dominate in the whole study area (Pyšek et al. 2005, Lososová et al. 2012a, b).

Effects of land use on urban flora

Several studies of urban floras have shown that different land-use types harbour different assemblages of species (e.g. Celesti-Grapow et al. 2006, Knapp et al. 2008, Lososová et al. 2012a, b, Čeplová et al. 2017, Planchuelo et al. 2019). This also applies to the city of Brno.

Our maps show that mosaics of natural and seminatural habitats represent centres of species diversity within the city (Fig. 2). These areas can serve as urban refugia for specialized native flora, similar to protected areas in agricultural landscapes (Pyšek et al. 2002, Knapp et al. 2008, Planchuelo et al. 2019).

Our results indicate a high importance of forested areas for the diversity of native and specialist species, i.e. species with narrow ecological niches that are normally confined to (semi)natural habitats. Moreover, forests with natural species composition seem to prevent the occurrence of many alien species and provide suitable habitat supporting many understory herbaceous species even if surrounded by densely built-up areas (Wang et al. 2016). The territory of the city of Brno includes a small part of the Protected Landscape Area Moravian Karst and numerous small-scale specially protected areas (Šmiták 1992; <https://www.mapy.cz>) with preserved forest remnants that have a high diversity of native forest species (e.g. *Asarum europaeum*, *Cyclamen purpurascens*, *Lathyrus niger*, *Polygonatum multiflorum*, and *Tanacetum corymbosum*). By contrast, in unprotected urban forests, we often found alien species, such as *Impatiens parviflora*, and *Robinia pseudoacacia*.

Several studies have revealed the importance of the patches of (semi)natural grasslands for biodiversity (Onandia et al. 2019, Planchuelo et al. 2019). Also in Brno, small patches of dry grasslands promote the survival of several rare and threatened species, such as *Campanula sibirica*, *Inula oculus-christi*, *Linum tenuifolium*, and *Stipa* spp.

Typical urban habitats are vacant lots and brownfields with early- or mid-successional stages of seminatural vegetation. These habitats can be species-rich, as can be seen in many European cities (Knapp et al. 2008, Lososová et al. 2011, Bonthoux et al. 2014). We found that brownfields, situated mainly in the industrial parts of the city, provide suitable living conditions for both common urbanophilous species and specialized rare species. For example, the area of the former textile factory Mosilana hosts several urbanophilous generalists (e.g. *Bassia scoparia*, *Eragrostis minor*, and *Paulownia tomentosa*) together with several habitat specialists (e.g. *Scrophularia umbrosa*, *Sparganium erectum*, and *Veronica beccabunga*) occurring in the artificial water channel.

Larger proportions of both residential and industrial land-use types, together with the great length of roads and railways promotes many alien species and generalists. These plants are adapted to a high frequency and/or intensity of disturbance, resist strong

changes in the physical environment and may use traffic as a dispersal vector (von der Lippe & Kowarik 2007, Hulme 2009, Schadek et al. 2009, Šumberová & Ducháček 2017). In the city of Brno, examples of such plants are *Rumex patientia* and *Senecio vernalis*.

Public green areas are often considered hotspots of urban biodiversity (e.g. Forman 2014, Salinitro et al. 2018). However, it has been repeatedly shown that this is not true for temperate European cities, at least not for vascular plants (see e.g. Lososová et al. 2012a, Jogan et al. 2022). Also in Brno, the proportion of urban green areas in the grid cells has likely a little effect on plant diversity. Urban green areas, including parks and lawns, are established by sowing a few grass species and intensively managed by frequent mowing. Beds with ornamental plants are usually well-maintained, leaving limited habitats for spontaneous flora. Recently, there has been a debate in the Czech Republic about the frequency of mowing of urban lawns, involving both citizens and managers. This has resulted in some lawns being mown in mosaics, but it is still too early to detect the effect of this management on spontaneously occurring native plants in cities. We recognize that urban green spaces are an important component of a healthy human environment supporting citizen well-being and offering several non-material ecosystem services (Amati & Taylor 2010), but their contribution to the diversity of spontaneous plants is currently relatively small.

Conclusions

Our study presents a dataset of 1,492 species found in Brno and their distributions within the city, recorded in a grid of 152 cells. These species are classified by their origin, residence time, invasion status, threat status in the Czech flora, index of ecological specialization, and affinity to the urban environment. Of these, 902 are native, 205 are archaeophytes, and 339 are neophytes. The remaining 46 species are probably remnants of cultivation. The flora of Brno contains 255 species classified as threatened or near threatened in the Czech Republic.

Our results confirm that current spontaneous flora of Brno is species rich. However, urbanization affects the proportions of different plant groups. A high level of urbanization has a negative impact on the survival of native, highly specialized plants. Our study detected areas with a high diversity of native, threatened, and specialized plants within the city. These areas are mainly located on the periphery of the city, especially in the northwestern, forested part. Areas with natural and seminatural habitats, especially forests and grasslands, are essential for maintaining high plant diversity in the city.

Supplementary materials

Data S1. List of spontaneously occurring taxa found in the study area in the years 2011–2021 and their occurrences in grid cells.

Data S2. Distributional maps of individual taxa.

Supplementary materials are available at www.preslia.cz

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Flóra města Brna

V této studii představujeme výsledky podrobného floristického průzkumu města Brna. V letech 2011–2021 jsme systematicky mapovali spontánní výskyty cévnatých rostlin v Brně (okr. Brno-město), a to v síti mapovacích polí o rozměrech 1,3 × 1,5 km (1/64 základního pole středoevropského síťového mapování). Zaznamenali jsme výskyt 1492 taxonů, jejichž rozšíření jsme dokumentovali jednotlivými mapami. Nalezené taxony jsme klasifikovali podle jejich původu, doby zavlečení, invazního statusu, vazby na městské prostředí, indexu specializace a kategorie ohrožení v České republice. Zjistili jsme významné rozdíly v rozšíření jednotlivých skupin rostlin v rámci města a městských biotopů. Brněnská flóra se převážně skládá z druhů původních v ČR (902), následovaných neofyty (339) a archeofyty (205). Podíl původních druhů byl nejmenší v silně urbanizovaných oblastech, zatímco archeofyty a neofyty zde byly častější. Nejběžnější taxony v Brně byly rostliny hojně i jinde v České republice, a to řebříčky *Achillea millefolium* agg., pampelišky *Taraxacum* sect. *Taraxacum*, bez černý (*Sambucus nigra*) a jitrocele *Plantago lanceolata* a *P. major*. Nejběžnější invazní neofyty byly turan roční (*Erigeron annuus*), trnovník akát (*Robinia pseudoacacia*) a zlatobýl kanadský (*Solidago canadensis*). Celkem bylo v Brně nalezeno 255 ohrožených taxonů. Kromě ohrožených rostlin vyskytujících se v chráněných územích se v urbanizovaných biotopech nacházejí např. *Ajuga chamaepitys*, *Chenopodium murale*, *Filago germanica*, *Herniaria hirsuta*, *Hibiscus trionum*, *Polycnemum arvense* a *P. majus*. Některé neofyty české květeny zatím zdomácněly především v Brně; k nim patří např. *Amaranthus deflexus*, *Artemisia tournefortiana* a *Geranium sibiricum*. Plochy městské zeleně, jakkoliv důležité pro příjemnější pobyt obyvatel města, mají jen omezený význam pro spontánní flóru v důsledku velmi časně a časté seče a převahy okrasných výsadeb. Pro druhovou bohatost městské flóry je důležitá především různorodost městského prostředí v gradientu od urbanizovaných a industriálních oblastí v centru města po zachovalé zbytky lesních a travinobylinných biotopů při jeho okraji.

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