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RESEARCH ARTICLE

Distribution and conservation status of *Ligularia sibirica* (Asteraceae) in Europe, with special reference to Ukraine

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Abstract. Based on our thorough analysis of bibliographical and herbarium data and field surveys of historical and existing localities of *Ligularia sibirica*, a detailed map of its distribution in Europe is presented, which significantly supplements and clarifies the previous information, particularly concerning Ukraine, Poland, and partly Russia. The distribution and status of the species in each European country within its range is described. A special map is also provided for Ukraine, where the species has suffered the greatest decline. In some regions, *L. sibirica* as a relic boreal species is endangered and has been undergoing decline and extirpation at least since the 19th century. The main threat factors are climate changes and anthropogenic activity, particularly the drainage amelioration of wetlands. Adverse consequences of climate changes mostly concern localities in the plain terrain south-westwards from the boreal zone. In general, mountain populations demonstrate better persistence because the colder and wetter climate conditions in the mountains are more favorable for *L. sibirica*.

Keywords: boreal species, climate change, drainage amelioration, extinction, locality, relict species

Introduction

Ligularia sibirica (L.) Cass. (Asteraceae/Compositae) is a boreal Euro-Siberian species with a rather wide geographical distribution in Eurasia. It occurs mostly in the boreal zone eastwards from the Gulf of Finland throughout the northeast of the European part of Russia and Siberia further to the Far East (Meusel, Jäger, 1992). South-westwards from that area in Europe, the species is very rare and occurs only in small, isolated localities in Estonia, Latvia, Ukraine, Poland, Slovakia, Czechia, Romania, Hungary, Austria, Bulgaria, Croatia, and France.

Ligularia sibirica is included in the Red Lists and Red Data Books of these countries. It is also listed in Appendix I of the Bern Convention (Convention..., 1979) for strictly protected flora species, Annex II of the Habitats Directive of the Council of European Communities (Council Directive..., 1992) for the species of community interest whose conservation requires the designation of special areas of conservation, and Annex IV of that Directive for species of community interest in need of strict protection.

The species also occurs in the Great and Lesser Caucasus. Its rarity, coupled with its noticeable ornamental habit, makes *L. sibirica* an excellent flagship

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species to promote the conservation of wetlands that harbor many other endangered plant species.

Existing maps of the species' geographic range (Hultén, Fries, 1986; Meusel, Jäger, 1992; Liu et al., 1994; Hendrych, 2003; Piękoś-Mirkowa, Mirek, 2003) and descriptions of its distribution in Europe (Kukk, 2003; POWO, 2024–onward) differ significantly, which is caused mostly by non-comprehensive and incomplete chorological data and by inconsistencies in the taxonomic circumscription of that species (see below). Our study is supposed to clarify the current distribution pattern of *L. sibirica* in the European subcontinent and, based on the historical data from literature and herbaria, to evaluate the trends in its spatiotemporal changes. Special attention has been paid to the species' distribution and the status of its populations in Ukraine, where it apparently has undergone the most severe decline. Besides, the Ukrainian localities, both existing and historical, are of special biogeographical interest because they can be regarded as milestones of the past east-to-west colonization route(s) and have an intermediate position between the plains in the boreal zone in the east and mostly mountainous habitats in the west. As *L. sibirica* is considered relict beyond the boreal zone (Šmídová et al., 2011), studying the distribution of its extant and extinct populations with regard to habitat conditions helps to reveal the limits of the species' ecological niche and identify the most vulnerable populations. Their response to anthropogenically and naturally driven changes in the habitats allows to predict the prospects for survival under different management scenarios (Hampe, Jump, 2011).

The aim of this study is to revise and summarize the knowledge about the distribution patterns of *L. sibirica* in Europe and to prepare a detailed and comprehensive map, to reveal and explain the causes of local extinction or decline, particularly in Ukraine and, hopefully, to understand how to mitigate these processes.

Materials and Methods

Study species

Ligularia sibirica is a short-rhizomatous tall-herb perennial hygrophytic species. Flowering plants are 60–180 cm high (Fig. 1). The populations are sustained by seed reproduction; therefore, a sufficient number of flowering individuals, successful germination of seeds, and further development of seedlings are crucial for effective recruitment. Efficient



Fig. 1. Habit of *Ligularia sibirica* in the Chornohora Mts, Ukrainian Carpathians



Fig. 2. Open microsite suitable for seed replenishment of *Ligularia sibirica* at the source of a travertine stream in the Chornohora Mts, Ukrainian Carpathians

replenishment of populations implies the existence of suitable microsites, i.e. open, unshaded patches (Kobiv, 2005; Nobis, 2012), which may harbor developing seedlings or immature plants (Fig. 2).

Because rhizomatous growth is slow, clonal reproduction is uncommon for the species, though rhizome fragmentation (i.e. splitting) may occur in old individuals (Kukk, 2003; Kobiv, 2005; Evstigneev, Kharlampieva, 2014). Nevertheless, such disintegration is not accompanied by any rejuvenation and, therefore, does not prolong the life span of a genet.

In natural habitats, flowering usually begins in 4–5-year-old individuals. Despite the possible temporary cessation of the flowering ability, the life cycle is unidirectional and lasts about 10 years (Kukk, 2003; Kobiv, 2005; Evstigneev, Kharlampieva, 2014). Stunted individuals in unfavorable ecological conditions (e.g. overshadowing or overdrainage) are often unable to flower (Olaczek, 2014).

Ligularia sibirica is calcicolous and has a strong affinity to hygrophytic habitats — alkaline fens, peatlands, spring-water mires, and wet forests, particularly from the class *Alnetea glutinosae*. During the vegetative season, it requires rather constant groundwater level, preferably 4–7 cm below the soil surface. Summer droughts or drainage amelioration are adverse to its vitality and cause the rapid decline of populations. There are literature data (Mânzu et al., 2013) that *L. sibirica* markedly prefers coldwater habitats. The species is also rather heliophilic but tolerates semi-shade as well (Heinken-Šmídová, Münzbergová, 2012; Olaczek, 2014). However, in the shaded forest understory, the plants are stunted. Though *L. sibirica* is a tall-herb species, it is poorly competitive (Trojecka-Brzezińska, Nobis, 2024) and prone to replacement by other forbs (e.g. *Solidago canadensis* L.), shrubs (*Salix* spp.), trees (*Betula* spp., *Pinus sylvestris* L.), or graminoids that form dense stands (*Cladium mariscus* (L.) Pohl, *Phragmites australis* (Cav.) Trin. ex Steud., *Schoenus ferrugineus* L.) and encroach in the course of vegetation succession triggered by land abandonment (e.g. cessation of mowing or grazing) or climate warming.

The combination of all these ecological requirements — hygrophytic conditions with a rather constant groundwater level, cold-water supply, alkaline soil, sufficient insolation, and gaps in vegetation suitable for seedling recruitment — makes *L. sibirica* a highly stenotopic species. In addition, it is not expansive, i.e., it does not readily colonize adjacent suitable habitats. Though the achenes are equipped with a pappus, which is supposed to facilitate anemochory, particularly in the family

Asteraceae (Costas et al., 2024), the seedlings usually emerge close to the parental plants (Kobiv, 2005; Heinken-Šmídová, Münzbergová, 2012). Apparently, these biological characteristics of *L. sibirica* impose limitations on its past and current distribution.

Literature data on the germination rate differ significantly and show that the bulk of seeds germinates within 1.5–8 weeks after sowing *in vitro* (Fomina, 2016; Cișlariu et al., 2018; Budisavljević et al., 2021). It was established that a small percentage of seeds can maintain their viability for two years in the soil seed bank, as can some ‘dormant adults’ without any above-ground organs (Heinken-Šmídová, Münzbergová, 2012; Puchalski et al., 2014).

Altogether, this implies that after the cessation of flowering due to unfavorable changes in a population or its habitat, most probably it is doomed to rapid decline or even extinction.

Ligularia sibirica sensu lato exhibits significant polymorphism in its pubescence, height, number of capitula, shape of the leaves, and their edge (Krylov et al., 1949), which gave reasons to describe a range of taxa of different taxonomic ranks. For instance, based on the narrow species concept used in the *Flora of the USSR* (Kirpicznikov, 1969), which almost does not recognize any infraspecific categories and does not imply broad within-species variation over a large geographic range, the Soviet authors (Minderova, 1957, 1962; Poyarkova, 1961) distinguished the following closely related species in Europe: *L. lydiae* Minderova, *L. arctica* Pojark., *L. subsagittata* Pojark., and *L. bucovinensis* Nakai. However, later authors (Chater, 1976), including modern Russian botanists (Gubanov et al., 2004; Illarionova, 2009) recognize only *L. sibirica* within the infrageneric section *Ligularia* in Europe but optionally use the subspecies rank, viz. *L. sibirica* subsp. *lydiae* (Minderova) Tzvelev, referring to pubescent plants. Currently, the wide circumscription of *L. sibirica* also prevails in the peri-Caucasian countries (Eric, 1990; Avetisyan, 1995).

Concerning the relict origin of *L. sibirica*, there are paleodata on its occurrence in the Carpathian region already in the late Pleistocene (Stoicovici, 1982), and it is considered a relict of that period (Olaczek, 2014; Szatmari, 2022). However, because the present distribution pattern shows a strong affinity to the boreal climate, in Europe outside the territory of Russia the species is also referred to as

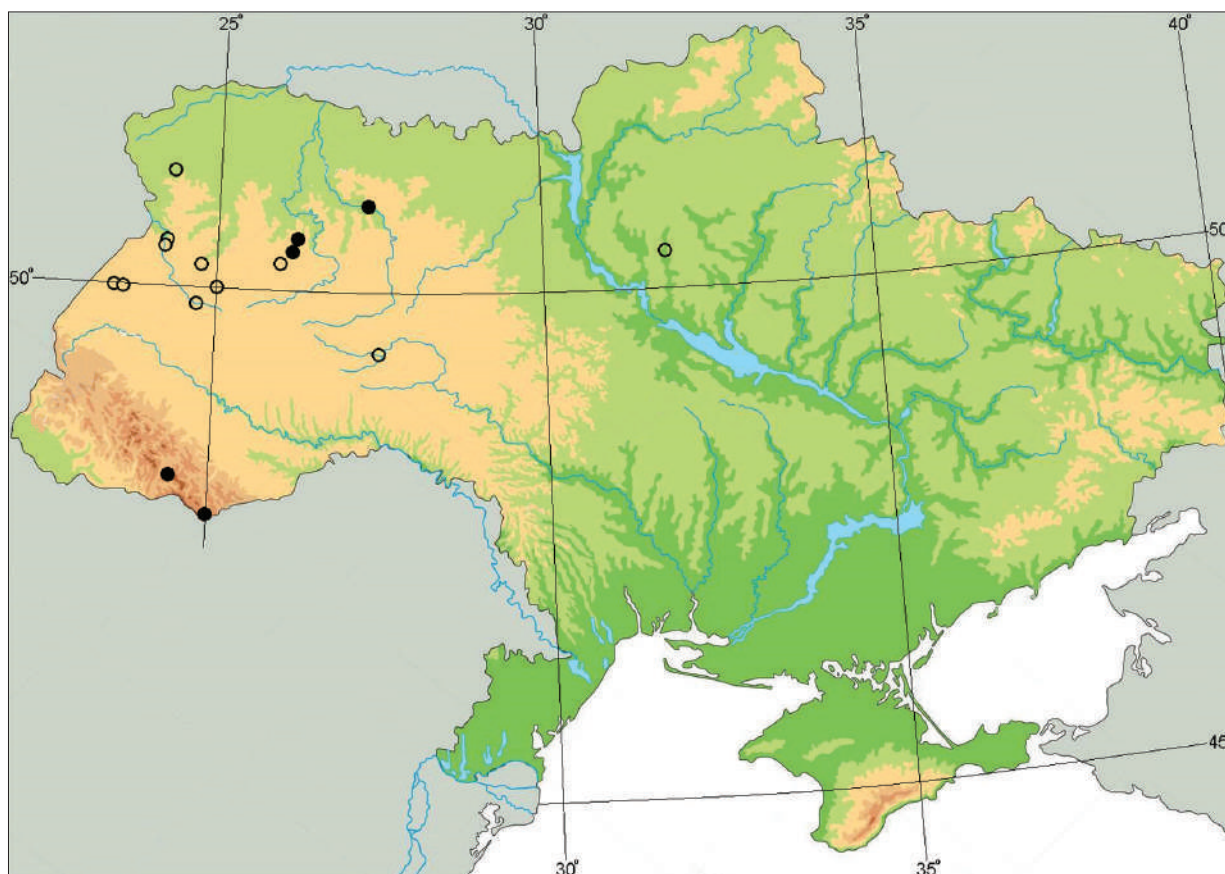


Fig. 3. Distribution of *Ligularia sibirica* in Ukraine: ● — existing localities; ○ — extinct localities

a relict of the early Holocene (Procházka, Pivničková, 1999; Hendrych, 2003; Cișlariu et al., 2018) when appropriate conditions were common to the vast part of today's temperate zone of the continent. Therefore, isolated localities of *L. sibirica* scattered throughout Europe beyond Russia are considered remnants of once larger populations (Šmídová et al., 2011).

Data collection

The study involved an extensive survey of bibliographic and herbarium data on the distribution of *Ligularia sibirica*. Herbarium vouchers of that species were studied in the KRAM, KW, LW, LWS, W, and WU herbaria (acronyms follow *Index Herbariorum*: Thiers, 2024–onward), as well as in other collections using online virtual herbaria databases, viz. JACQ (<https://www.jacq.org>) and GBIF (<https://www.gbif.org>).

A considerable amount of literature concerning the distribution of *L. sibirica* was analyzed. It includes articles on the species' occurrence in certain countries (Fischer, 1991; Kukk, 2003; Mirek, Piękoś-Mirkowa, 2006; Šmídová et al., 2011; Mânzu et al., 2013; Dítě, Eliáš, 2016; Mânzu, Cișlariu, 2019), national, regional, and local floras (Grossheim, 1934; Sofieva, 1961; Flora severo-vostoka..., 1977; Galushko, 1980; Tabaka et al., 1988; Avetisyan, 1995; Poluyanov, 2005; Mayevskiy, 2014), relevant Red Data Books and Red Lists (Andriyenko, 1996; Procházka, Pivničková, 1999; Kobiv, 2009; Demakhina, 2014; Olaczek, 2014; Bancheva, 2015; Schratt-Ehrendorfer et al., 2022), etc.

The sites in Ukraine where *L. sibirica* has been previously reported were surveyed in 2006–2024 to check the current status of populations. The species' localities were also visited in Poland in 2022–2023 during the seminars organized by the *Nature and Man Foundation*.

Botanical nomenclature mainly follows *Plants of the World Online* (POWO, 2024–onward).

Results and Discussion

Distribution of *Ligularia sibirica* in Ukraine

Most of the Ukrainian localities of *Ligularia sibirica* (both historical and present) lie in the west of the country (Fig. 3), which is explained by more humid climate conditions in that territory (Natsionalnyi atlas..., 2007).

In spatial terms, the Ukrainian localities of *L. sibirica* can be roughly subdivided into those occurring in the plain or mountainous parts of the country (Fig. 3). The first group of localities lies mostly in Volyno-Podillya (often Latinized as Volhyno-Podolia), a territory with mainly wavy and hilly landscapes.

The northernmost data on the species occurrence in Ukraine come from the Volyn' Region (Volyns'ka Oblast) ca. 10 km to the north of the town of Volodymyr (earlier known as Volodymyr-Volynskiy). It is evidenced by two vouchers gathered in the closely located sites: near Zamosty and Verba villages in the mossy fens and alder carrs. Both specimens were collected back in the late 19th century by the renowned botanists Paczoski (KW025751) and de Montresor (KW6443-6), while the latter author noted on the herbarium labels that *L. sibirica* was very rare already at that time. Later, Minderova (1957) used his vouchers to describe “*Ligularia ucrainica*”, a microspecies that has not been recognized by other authors. These findings, which are the only available for the Volyn' Region, have never been confirmed further and because that area has later undergone drainage amelioration, most probably the species has gone extinct there (Andriyenko, 1996; Kobiv, 2009).

Another cluster of historical localities lies in the Lviv Region eastwards from the town of Sheptytskiy (formerly known as Chervonohrad and Krystynopol) between Potorytsia, Pozdymyr, and Volsvyn villages. These data date back to the 19th — early 20th centuries and are documented by herbarium vouchers collected by Rehmann (KRAM178603, KRAM178607-09, WU s. n.) and an article by Wróblewski (1917), which describes the habitat of *L. sibirica* as a damp alder carr. Though the species was mentioned from several closely located sites, we failed to confirm its current occurrence there during our recent surveys of that area, which implies its extinction because of past amelioration.

The next cluster comprises localities near the villages of Shklo, Stavky, and the town of Ivano-Frankove (former Yaniv) in Lviv Region located about 15 km apart from each other. They are evidenced by Tomaschek (1859) and herbarium vouchers gathered in the middle of the 19th century (LW127549, LW127553-5, LW127556, LWS99880-1, LWS99886, KW02572, WU s. n.), whose labels refer to wetlands. These findings have never been confirmed later, and because of the frequent botanical surveys of the area it is suggested that the species is long-extinct there. The wetland locality near Ivano-Frankove is well known as a habitat of other rare and threatened hygrophytic species and belongs to Roztochia Nature Reserve now (Soroka, 2004).

Another cluster of historical localities was also confirmed by herbarium vouchers (LWS99883-5), gathered in the middle of the 19th century in two wetland localities near the village of Lopatyn, Lviv Region. Later, that area was drained and subjected to peat excavation, therefore *L. sibirica* has apparently gone extinct there.

One more species' historical locality in Lviv Region was situated ca. 6 km westwards from the town of Brody. It was mentioned by Motyka (1947) and evidenced by herbarium vouchers from 1937 (LW12550, LW12552). The habitat was described as a moist oak and hornbeam forest with gyttja soil at the calcium-rich water outflow. The population was low-numbered already at that time (Motyka, 1947) and our survey of that area proved that most probably it has not survived.

There is also a mention of the occurrence of *L. sibirica* near the village of Pidlyssya, Zolochiv District, Lviv Region (Kagalo, 2012), referring to the herbarium record from the 1970s, which, however, has been lost and therefore these data are unverified. Former wetlands near that village have been severely drained, which implies that the species' persistence in that area is highly unlikely.

The largest cluster of localities lies near the town of Ostroh (Rivne Region) at the edge of three physiographic regions: the Volynian Upland, Lesser (Male) Polissya Plain, and Podolian Upland. It is a biodiversity hotspot that harbors many rare and threatened vascular plant species (Melnik et al., 2001) included in the *Red Data Book of Ukraine* (Red Data Book..., 2009). Some of them, similarly to *L. sibirica*, are both calcicole and hygrophilic, e.g. *Cladium mariscus*, *Carex buxbaumii* Wahlenb., *C. davalliana* Sm., *C. hostiana* DC., *Dactylorhiza incarnata* (L.) Soó,

Epipactis palustris (L.) Crantz, *Iris sibirica* L., *Liparis loeselii* (L.) Rich., *Pinguicula vulgaris* L., *Schoenus ferrugineus*, *Swertia perennis* L., *Betula humilis* Schrank, *Pedicularis sceptrum-carolinum* L., *Saxifraga hirculus* L., and *Salix starkeana* Willd. Notably, the latter four species have also a boreal affinity (Meusel, Jäger, 1992). That cluster consists of three patches of distribution of *L. sibirica*. The westernmost one lies at the very border between the Rivne and Ternopil Regions ca. 4 km west of Ruska Huta village, Kremenets District. In the first half of the 20th century, it was documented by a herbarium record (LW127551) while the locality was described by Motyka (1947) as the edge of a peat fen, and according to him the species was scarce there already at that time. We found out that this habitat was destroyed due to massive peat excavation in that area.

Another locality from that cluster is situated about 20 km north-westwards of the previous one near the village of Derman in the significantly drained calcareous peatland, which now belongs to the Derman-sko-Mostivskyi Regional Landscape Park (Andriyenko, Antonova, 1986; Andriyenko, Pryadko, 2001; KW009335). The population inhabiting the edge of that peatland was quite viable in the 1980s (Andriyenko, Antonova, 1986) but according to our observations, it has declined considerably during the last decades and is on the brink of extinction now.

The largest existing Ukrainian population of *L. sibirica* belongs to the same cluster and lies about halfway between the two mentioned sites between the villages of Mosty, Bushcha, and Illyashivka in the Derman-Ostroh National Nature Park. That entity can be best referred to as a metapopulation, i.e. a group of local populations inhabiting nearby but spatially disconnected patches with similar ecological conditions required by *L. sibirica*, i.e. calcareous wetlands. Thus, the species is scattered in two wetland parts of the Derman-Ostroh National Nature Park, namely in the Zbytnyky River Floodplain and Bushchanskyi Botanical Reserves. The distribution of *L. sibirica* is highly discontinuous and the patches where it occurs are situated up to about 2.5 km apart from each other. The species' occurrence there is documented by literature (Andriyenko, Antonova, 1986; Andriyenko et al., 2012; Pryroda..., 2015; Golovko et al., 2020) and herbarium (LW215472, KW025744, KW096184, LWS113020) data. Here *L. sibirica* is distributed in calcareous fens, which undergo gradual overgrowth with shrubs and trees



Fig. 4. Encroachment of shrubs and trees into the habitat of *Ligularia sibirica* in the Derman-Ostroh National Nature Park, Ukraine

after the abandonment of land use (Fig. 4). That metapopulation includes several thousand flowering plants (Golovko et al., 2020) distributed within the patches with a total area of above 200 ha. Apparently, its size is the largest among the lowland European localities beyond Russia.

One more record comes from the east of Rivne Region at the edge of Zhytomyr Polissya. It is evidenced by herbarium vouchers (KW138861, KW138863) gathered in the grassland on the bank of the Pereveznia River. Though the vouchers date from 1997, they were added to the KW herbarium quite recently; therefore, the current status of the population remains unknown.

The southernmost locality within the plain part of Ukraine was reported at the end of the 19th century by Schmalhausen (1897) from Podillya between the towns of Medzhybizh and Lityn, Kmnelnystkyi



Fig. 5. Distribution of *Ligularia sibirica* in Europe: ● — existing; ○ — extinct; □ — introduced localities; ? — status unknown

Region. Its exact location remains unknown, and the species has never been confirmed in that area later. As the climatic conditions are distinctly drier there in comparison with the rest of the localities (Natsionalnyi atlas..., 2007), it is hardly unlikely that *L. sibirica* could have survived the ongoing global warming in that site; therefore, it is considered extinct (Andriyenko, 1996; Kobiv, 2009).

The easternmost Ukrainian locality, which is also the only one in the Left-Bank part of Ukraine (east of the Dnipro River) is documented by the herbarium specimen (MW0248941) collected in 1848 near the town of Yahotyn, which now belongs administratively to Kyiv Region. It has never been confirmed later and most probably is long-extinct.

In Ukraine, *L. sibirica* occurs also in the Carpathians (Fig. 3). Its mountain populations are separated from the plainland group of localities by an over 200 km disjunction. However, they are located rather close, i.e. 15–65 km from the nearest habitats of *L. sibirica* in Romania (Mânzu et al., 2013). One of the Ukrainian mountain localities is situated near the village of Lazeshchyna in Zakarpattia (Transcarpathian) Region on the southern slope of the Chornohora Range. In 2001 that population included about 1500 generative individuals, inhabited several tufa-forming springs, and stretched along the travertine stream within the altitude of 915–1000 m a.s.l. (Kobiv, 2005). Unfortunately, later that area was subjected to massive clear-cutting, which

almost destroyed the habitat. As a result, only the remnants of that population have survived, which comprise about 40 generative individuals located in an area of ca. 200 m². Despite the lack of limestone bedrock in the Chornohora Mts, there are some calciferous streams where CaCO₃ is washed out from the deeper rocks. That results in the deposition of travertine on the surface near the springs and further downstream. That significantly alkalizes the soil, whose pH(H₂O) value exceeds 7.0, which enables suitable conditions for *L. sibirica* (Kobiv, 1999, 2005). Annex I of the Habitats Directive 92/43/EEC (Council Directive..., 1992) and later documents of the European Commission (Interpretation manual..., 2013) assign priority conservation status to that type of habitats — 7220* Petrifying springs with tufa formation (*Cratoneurion*).

Another Carpathian locality is in the Chernivtsi Region, namely in the Chyvychny Mts (which belong to the Marmarosh Massif) near the village of Sarata, a few kilometers from the border with Romania. The species occupies two nearby habitats in the river valley at the Bilyi Potik Stream (KW025752, KW139174). These wetland patches are also related to the calcium-rich stream (Chorney, 1999; Chorney et al., 2008). The site is included in the Cheremosh National Nature Park; therefore the population is not threatened.

Distribution in other European countries

The most westward outposts of *Ligularia sibirica* in Europe are located in the mountains of France (Fig. 5), namely in the East Pyrenees, Massif Central, and Morvan where over 30 localities have been documented (Bensettiti et al., 2002). In the former two mountain systems, some populations are rather large-sized, and the species occurs mostly within 1000–1200 m a.s.l. (Danton, Baffrae, 1995; Bensettiti et al., 2002); however, it reaches 1400–1500 m a.s.l. in the Pyrenees (Meusel, Jäger, 1992). In several stations, mostly in the Massif Central, extinctions have been reported (Bensettiti et al., 2002). In the Morvan Mts (Burgundy), the species is very scarce and occurs in a single locality at ca. 350 m a.s.l. (Bugnon, 1952; Bensettiti et al., 2002).

The main non-Boreal European region of the species' distribution is associated with the mountains of Central and Central-East Europe in Czechia, Slovakia, Poland, Hungary, Romania, and Ukraine.

In Czechia, *L. sibirica* occurs in a single locality in the Šumava Mts at 730 m a.s.l. and in two clusters at the foothills of the Western Sudetes at 215–260 m a.s.l. (Hendrych, 2003; Heinken-Šmídová, Münzbergová, 2012).

The only Austrian locality is situated in the low-mountain area of the North-Eastern Prealps (nordöstlichen Voralpen) in Lower Austria (Niederösterreich) at 420 m a.s.l. Though *L. sibirica* is included in the country's Red List (Schratt-Ehrendorfer et al., 2022), a thorough analysis of all the existing data proves that most probably the species is not native there (Fischer, 1991).

In Slovakia, the species occurs in three regions of the Western Carpathians, viz. the Nízke Tatry, Slovenský Raj, and Bachureň within 400–1000 m a.s.l. In one of them, Slovenský Raj, its populations are rather large-sized and form a cluster of several localities (Šmídová et al., 2011; Heinken-Šmídová Münzbergová, 2012; Dítě, Eliáš, 2016).

In Poland, five localities were known in the plain terrain of the central-southern and eastern parts of the country. Two more stations have been reported from the foothills of the Tatra Mts, Western Carpathians; however, one of them (in the Zakopane Depression) went extinct in the 20th century (Nobis, 2012). Most of the remaining Polish populations are low-numbered and prone to decline (Mirek, Piękoś-Mirkowa, 1989, 2006). Because the Polish and Slovak West-Carpathian localities are only about 40 km away from each other, they can be treated as the same group.

In addition, we discovered a previously overlooked herbarium specimen of *L. sibirica* (W0276340), collected in 1841 near the town of Stargard in Pomerania, now NW Poland (Fig. 6). Originally misidentified as "*Heloseris palustris* Rchb." (= *Tephroseris palustris* (L.) Schrenk ex Rchb.), it was distributed by O.C. Schramm as an exsiccate of that species. Noteworthy, other vouchers of the same exsiccate issue kept in the B, BR, K, L, and WAG herbaria do belong to *T. palustris*. Their digitized images are accessible online in JACQ (<https://www.jacq.org>) and GBIF (<https://www.gbif.org>) virtual herbaria databases. Both species, *Ligularia sibirica* and *Tephroseris palustris*, occur in peatlands, and the labels on corresponding vouchers say that they came from a peat-cutting site, which might imply that they grew together, and because of their mutual resemblance, the collector confused *L. sibirica* with *T.*



Fig. 6. A newly discovered herbarium specimen (W0276340) of *Ligularia sibirica* from Pomerania, NW Poland

palustris in at least one of his herbarium samples. However, the date on all these herbarium vouchers, viz. “the end of May” corresponds to the flowering period of *T. palustris*, while *L. sibirica* produces generative shoots about 1–1.5 months later, therefore, the collection date of the above-mentioned specimen is hardly correct, though there is no reason to doubt the place of its origin, because the collector, O.C. Scramm lived and worked in Western Pomerania at that time (Breitfeld et al., 2020). Moreover, calcareous fens, which are suitable habitats for *L. sibirica*, are situated near Stargard (Sotek, 2010); therefore, the species’ occurrence there (at least in the past) seems very likely. However, the current status of that population is unknown (Fig. 5).

The only Hungarian population was situated at the north-eastern edge of the Pannonian Basin about 70 km from the Romanian Carpathians at an unusually low altitude (about 140 m a.s.l.), which is the lowest among the non-boreal localities of *L. sibirica* in Europe. Though it occurred in the long-protected area of the Bátorliget mire, the species went extinct there in the middle of the 20th century. The attempt of its reintroduction from Slovakia in the 1980s failed (Papp, Dudas, 1989; Papp, Lesku, 1998; Király, 2007).

Romania is the only country in the non-boreal territory of Europe where *L. sibirica* is not very rare. Thus, about 120 populations are documented and mapped in that country (Mânzu, Cişlariu, 2019). Almost all of them refer to the territory of the Eastern and Southern Carpathians, and some of them form clusters. In the Romanian Carpathians, the species occurs at the vast altitudinal range within 400–2100 m a.s.l. (Meusel, Jäger, 1992) in a wide spectrum of plant communities (Matei, 2014). There is also a record from the Transylvanian Basin and another one from the plain terrain at the eastern foothills of the Carpathians (Mânzu et al., 2013).

Ligularia sibirica is known in two countries of the Balkan Peninsula. One of its stations is situated in the Plitvice Lakes National Park in the Dinarides, Croatia, at 660 m a.s.l. (Stančić et al., 2010). There are also two localities in the Pirin Mts in Bulgaria at 1140 and 1400 m a.s.l. (Bancheva, 2015). These Balkan outposts are significantly separated from the rest of the European stations. The Bulgarian localities, along with the Caucasian ones, are the southernmost known records of the species in Europe.

Ligularia sibirica also occurs in the Baltic countries Latvia and Estonia where it is rare, low-numbered, and prone to extinction. Thus, in Latvia, it was found only in the northern and eastern parts of the country (Tabaka et al., 1988), while in Estonia, the species has survived in merely 8 out of 18 previously documented localities (Kukk, 2003).

Distribution of *L. sibirica* in the boreal part of the European Russia is usually referred to and pictured as continuous (Meusel, Jäger, 1992; Liu et al., 1994; Piękoś-Mirkowa, Mirek, 2003; Šmídová et al., 2011), which might imply that the species is quite common throughout that part of its range. However, it contains significant gaps, especially at its edge. Thus, the species is rather rare and included in the local Red Data Books of the Murmansk, Leningrad, Pskov, Novgorod, Bryansk, Tver, Moscow, Ivanovo, Yaroslavl’, Kostroma, Vologda, Kirov, and Ulyanovsk regions, which also concerns the Republics of Mari El, Chuvashia, Tatarstan, and Udmurtia in the Russian Federation.

It is worth mentioning that *L. sibirica* has gone extinct in the Kursk and Oryol regions of Russia (Yelenevskiy, Radygina, 1997; Poluyanov, 2005; Mayevskiy, 2014), i.e. at the southern edge of its distribution (Fig. 5), where it was documented in literature (Schmalhausen, 1897) and by herbarium specimens collected over 100 years ago (MW0248896-7, MW0248899, MW0248900-3). The species does not occur in the Voronezh, Saratov, Ryazan’, Lipetsk, Kaluga, and Samara regions, as well as in the Republic of Mordovia, which shows that it is far from being common across the European part of Russia.

In the north of Russia beyond the boreal zone, *L. sibirica* occurs also near the coast of the Arctic Ocean and its northernmost localities reach the 69th N parallel (Fig. 5), i.e. its range slightly extends into the Arctic tundra (Demakhina, 2014).

A disjunct part of the species’ range lies in the Caucasian Mountains (Fig. 5) where *L. sibirica* is rather common in the subalpine wetlands throughout most of the mountain massifs in the Great and Lesser Caucasus (Grossheim, 1934; Sofieva, 1961) and reaches 3300 m a.s.l. (Galushko, 1980). The species occurs in Krasnodar Krai and in all the North-Caucasian republics of the Russian Federation (Galushko, 1980), as well as in Georgia / Sakartvelo, Armenia / Hayastan, and Azerbaijan. In addition, the species’ range slightly extends into the Kars Province of Turkey (Erik, 1990).

Distribution patterns of *Ligularia sibirica* in Europe

A general outlook on the species' distribution in Europe shows that it is highly disjunctive (Fig. 5). Its localities scattered beyond the boreal zone, i.e. south-westwards of Russia and the Baltic states (Latvia and Estonia), can be roughly divided into two groups: those associated with either plain or mountainous terrain. It is noteworthy that in the vast territory of the non-boreal part of the Great European Plain, which spans the whole continent from the Atlantic Ocean to the east, *Ligularia sibirica* occurs only in Poland and Ukraine. The disjunction between the existing localities in these countries on the one hand and those in Russia on the other is significant, but the chain of documented extinct stations between them (Fig. 5) implies that they may be treated as the remnants of an ancient colonization route, which might have been connecting these parts of the species' range in the past. The distribution pattern of *L. sibirica* infers that it does not currently inhabit many of the suitable habitats within the perimeter of its dispersal; moreover, its occurrence in Central and Central-Eastern Europe probably was rather limited even in the past periods when the climatic conditions were more favorable for the species.

Relict non-boreal plain-inhabiting European populations of *L. sibirica* are especially vulnerable and prone to decline, by contrast to the mountainous or boreal areas with colder climate and, consequently, lower evapotranspiration, which prevents overdrying of the habitats. In that context, the ongoing climate warming adversely affects the lowland populations because it causes drying up of peatlands and the encroachment of shrubs and trees (Heijmans et al., 2013). However, based on the literature and herbarium data, the decline of these populations can be traced already from the 19th — first half of the 20th century. It could be contributed by the drying trend in the European peatlands during the last centuries (Swindles et al., 2019). It is noteworthy that the verified data on the occurrence of *L. sibirica* in the forest-steppe zone, i.e., under pessimum thermal-humidity conditions in Ukraine and the European part of Russia (Fig. 5), date back to the 19th century, and have never been confirmed later due to their extinction. It concerns the Khmelnytskyi and Kyiv Regions of Ukraine as well as the Kursk and Oryol Regions of Russia. Thus, the documented climate-driven extinctions of *L. sibirica*

have been happening for more than a century. A similar extinction event occurred in the middle of the 20th century to a lowland population in the Pannonian Basin, Hungary (Papp, Lesku, 1998). Recent rapid species' decline and extinction of range-edge populations in the Baltic states (Kukk, 2003) can also be attributed to climate change. Modern studies (Hájek et al., 2022) show that warming causes the shift of the pH niche in *L. sibirica* and some other rare fen species to more basophilic values, which makes them more stenotopic and facilitates their extinction. That could have also contributed to the narrowing of their geographic ranges during past Holocene warmings (Hájek et al., 2022).

Another adverse factor, which has an extremely negative effect on *L. sibirica* is drainage amelioration of the habitats. Its consequences are most evident in Ukraine where the expropriation of land by the state in the Soviet period allowed the implementation of gigantic projects of massive amelioration. That process intensified after World War II and reached an enormous scale in the 1950–1980s (Balashov et al., 1982). It was aimed mostly at increasing the areas of arable land at the expense of the territory, which was “overmoisted” in agricultural terms. Eventually, over 3.3 million ha of such areas were drained in Ukraine (Pankiv, 2008). This concerns mainly the west of the country where most of the historical localities of *L. sibirica* have been previously reported (Fig. 3). For instance, in the most affected Lviv, Rivne, and Volyn' administrative regions the drained lands account for as much as 19.5–23.5 % of their total area. Thus, natural or semi-natural wetlands and humid grasslands have mostly been converted into arable land (Pankiv, 2008). That has been accompanied by the modification and canalization of riverbeds, which resulted in a profound transformation of the floodplains. This caused a huge loss of biodiversity in the west of Ukraine, including the extinction and decline of many populations of *L. sibirica* and other hygrophytic and mesohygrophytic species (Balashov et al., 1982).

The above overview of the historical localities of *L. sibirica* in Ukraine shows that it has died out in 10 such sites, while at least in 6 of them the main cause of extinction was habitat disturbance resulting from drainage amelioration. Four of these extinctions happened in Lviv Region (2 in Sheptytskyi, 2 in Yavoriv, 2 in Zolochiv districts), one in Volyn' Region (Volodymyr District), and one in Ternopil'

Region (Kremenets District). Thus, most extinctions refer to Lviv Region, where the percentage of ameliorated lands (23.5 %) is the highest (Pankiv, 2008). In addition, one of the remaining populations, namely near the village of Derman' (Rivne Region) is currently on the brink of extinction due to intense amelioration of the site. Thus, Ukraine's populations of *L. sibirica* have suffered the severest losses in comparison to other European countries.

It is worth mentioning that the localities of *L. sibirica* are often grouped in clusters, i.e. are situated only a few kilometers apart, which is most evident in the Pyrenees and Massif Central in France (Danton, Baffray, 1995; Bensettiti et al., 2002), Western Sudetes in the Czech Republic (Heinken-Šmídová, Münzbergová, 2012), Western Carpathians in Slovakia (Heinken-Šmídová, Münzbergová, 2012; Dítě, Eliáš, 2016), Lesser Polissya Plain in Ukraine, Pirin Mts in Bulgaria (Bancheva, 2015) and in multiple regions of Romania (Mânzu, Cișlariu, 2019). Such a pattern can be attributed to the past colonization history.

The specificity of the distribution of *L. sibirica* in Europe can be revealed by comparison with the ranges of other relict boreal species with similar habitat requirements, i.e., occurring in alkaline wetlands, e.g. *Betula humilis*, *Pedicularis sceptrum-carolinum*, and *Saxifraga hirculus*.

In this regard, the geographic range of *L. sibirica* is quite peculiar. Not only is it highly disjoined, but the species' isolated localities occur as far to the west as in the Pyrenees and as far to the south as in the Balkan Peninsula and the Caucasus.

Unlike most European boreal species, *L. sibirica* does not occur in the Scandinavian Peninsula and Finland. Moreover, there was no evidence of the species' occurrence near the southern Baltic coast until the above-reported locality in Pomerania, Poland, which is rather exceptional.

In most countries of Europe beyond the boreal zone, except Poland and Ukraine, *L. sibirica* exhibits a strong affinity to the mountains. Therefore, its distribution in Europe to some extent can be characterized as boreal-montane (boreomontane). The species' localities are scattered in the following European mountain systems: the Pyrenees, Massif Central, Morvan, Šumava, Western Sudetes, Carpathians, Dinarides, Pirin, and Caucasus. However, these localities are very isolated and disjoined and hardly line up in a possible stepwise dispersal route (Fig. 5). For example, there is a considerable

700–900 km long hiatus between the localities in Western and Central Europe, viz. between the mountains in France and in the Czech Republic caused by their absence in the Alps and low mountain massifs of Germany called Mittelgebirge. A possible explanation for the absence of *L. sibirica* in the Alps and peri-Alpine region is the past existence of large Alpine ice shields in that territory in the Pleistocene (Schönschwetter et al., 2005).

The size and viability of the mountain populations does not depend on the distance from the main part of the species' range in the boreal zone. For instance, some outlying populations occurring in the subalpine zone of the Pyrenees and Massif Central in France (Danton, Baffray, 1995; Bensettiti et al., 2002) and the North Caucasus in Russia (Galushko, 1980) are large-sized and prospering, which shows that cold and wet mountain climate is favorable for the species viability.

Conclusion

The geographic range of *Ligularia sibirica* in Europe is highly discontinuous, which is most conspicuous beyond the boreal zone (Fig. 5). Because in that part of Europe the species is considered a Late Pleistocene — Early Holocene relict (Šmídová et al., 2011), significant disjunctions in its current distribution can be attributed to numerous later extinction events. It is noteworthy that even in the main part of the species range, i.e. in the boreal zone, its distribution can be hardly characterized as continuous due to its low colonization ability, stenotopic requirements for cold-water alkalic wetlands, and, consequently, the lack of suitable localities in many regions. Therefore, the species is also rare in most regions of Russia and is included in regional Red Data Books in that country. Apparently, that refers to the West-, Central- and South-European countries. Thus, the pan-European conservation concern for *L. sibirica* reflected in international documents, namely Appendix I of the Bern Convention (Convention..., 1979) and Annexes II and IV of the Habitats Directive (Council Directive..., 1992) is completely reasonable.

Nevertheless, the species' localities are often gathered in clusters and in some regions, e.g. in the Romanian part of the Carpathians, in the Caucasus, North Urals, the eastern shore of the Kola Peninsula, and the Udmurt Republic of Russia it is not rare. Because of the concentration of localities in the

territory of the East-South-Carpathian region, that area may be considered the secondary center of the species distribution in Europe beyond the boreal zone. In addition to numerous Romanian localities, this area also includes the stations of *L. sibirica* in the Ukrainian Carpathians.

In some regions, *L. sibirica* is endangered and has been undergoing decline and extinction at least since the 19th century. The main factors of threat to the species are climate change and anthropogenic activity, particularly drainage amelioration of wetlands. Adverse consequences of climate change (including the long-term period) mostly concern lowland localities peripheral to the main (i.e. boreal) range situated in the peri-Baltic region and in the forest-steppe zone of Ukraine and Russia where the climatic (thermal-humidity) conditions have long become unfavourable for *L. sibirica*. That also refers to the extinct population in the Pannonian Basin, Hungary.

Another threat factor, namely drainage amelioration of the species' habitats, had the greatest impact in Ukraine, where it was the main cause of extinction for at least 6 populations, mostly in the second half of the 20th century. To that matter, Ukrainian populations have suffered the most severe losses, because in total as many as 10 of them have gone extinct for different reasons, which concerns the plain part of the country.

Extinction due to anthropogenic habitat alterations has been also reported in France (Bensettiti et al., 2002).

In general, mountain populations (even some of the most outlying) demonstrate better persistence, because colder and wetter climate conditions in the mountains are more favorable for *L. sibirica*.

The adverse alterations in the ecological conditions due to both climate changes and amelioration not only cause the unfavourable decrease in the groundwater level but also trigger the vegetation successions, which results in the encroachment of more competitive shrub, tree, and forb species and leads to the replacement of *L. sibirica*. Mitigating these processes needs active conservation measures, which imply restoration of mild traditional land use activities, particularly mowing (Sienkiewicz-Paderewska et al., 2020; Hájková et al., 2022).

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ETHICS DECLARATION

The authors declare no conflict of interest.

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Поширення та охоронний статус *Ligularia sibirica* (Asteraceae) в Європі з особливою увагою щодо України

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Реферат. На основі ретельного аналізу бібліографічних і гербарних даних, а також польового обстеження історичних та існуючих локалітетів *Ligularia sibirica* укладено докладну мапу поширення цього виду в Європі, що істотно доповнює і прояснює попередні відомості, зокрема стосовно України, Польщі і Росії. Описано поширення та стан виду в кожній країні Європи. Окрему мапу поширення створено для України, де вид зазнав найбільших втрат. У деяких регіонах *L. sibirica* як реліктовий бореальний вид є загрозеним і зазнає регресування й вимирання принаймні ще з XIX століття. Основними факторами загрози є кліматичні зміни та антропогенна діяльність, зокрема осушувальна меліорація боліт. Негативні наслідки кліматичних змін стосуються здебільшого рівнинних локалітетів, розташованих південно-західніше від бореальної зони. Натомість, гірські популяції назагал виявляють більшу стійкість, оскільки холодніший і вологіший клімат у горах є сприятливішим для *L. sibirica*.

Ключові слова: бореальний вид, вимирання, зміни клімату, локалітет, осушувальна меліорація, реліктовий вид