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Research Article

Syringa josikaea (Oleaceae) biotopes in the Ukrainian Carpathians: Climatic conditions and current dynamics

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Abstract

This study aims to identify the key environmental conditions that support the protection and natural regeneration of *Syringa josikaea* J. Jacq. ex Rchb., a rare Carpathian endemic species listed in the Red Data Book of Ukraine. A detailed analysis of the climatic characteristics of the species' habitats within the Ukrainian Carpathians is provided. Understanding the climatic factors influencing this local species is crucial for identifying its most vulnerable habitats and developing effective conservation strategies. This approach aligns with international conservation priorities outlined in red lists and other environmental policy documents. The article synthesizes key physical and geographical data, ecological characteristics, and dominant phytocoenological features of 18 documented *S. josikaea* habitats in Zakarpattia and Lviv Oblasts (regions) (Ukraine). A climatic classification of the species' habitats was conducted using data from the CarpatClim climate database. Additionally, a Köppen-Geiger climate type map for the Ukrainian part of the species' distribution range was developed based on climate indicators derived from 338 selected nodes of the regular CarpatClim grid. The results indicate that the species is predominantly found in areas with a temperate continental climate (Dfb). The study presents and discusses the mean statistical values of 21 climate indicators for the period 1961-2010. A comparative analysis of different climatological periods reveals that among the 338 sites examined, only 159 (47% of the total area) have experienced a climatic shift from colder to warmer conditions over the past half-century.

Keywords: biotope; climate type; climate change; relict species; Köppen-Geiger classification; Zakarpattia Oblast (region)

Introduction

Hungarian lilac (*Syringa josikaea* J.-Jacq. ex Rchb., *Oleaceae*) is an endemic species with a highly disjunct distribution (Figure 1). It is found in the Ukrainian Carpathians and the Apuseni Mountains of Romania, where it occurs in small, isolated, relict populations. Molecular studies suggest that the species originated in theearly Pleistocene (Q_1) (Lendvay *et al.*, 2016). Its closest relatives are the East Asian species of the genus from

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ser. *Villosae*, specifically *S. villosa* Vahl. and *S. wolfii* S.K. Schneid (Chen, 2008; Lendvay *et al.*, 2016). Palaeobotanical evidence from interglacial sediments in eastern Germany indicates that *S. josikaea* once had a more extensive range than it does today. The species is believed to have diverged from its East Asian relatives during the cold and arid periods of the Pleistocene (Mania and Mania, 2008). Fossil remains from Middle Miocene sediments of the Carpathian Basin suggest that *S. josikaea*, is a Tertiary relict (Járai-Komlódi, 1990). However, its divergence within its current distribution likely occurred more recently, during the Ice Age (Lendvay *et al.*, 2013; 2016).

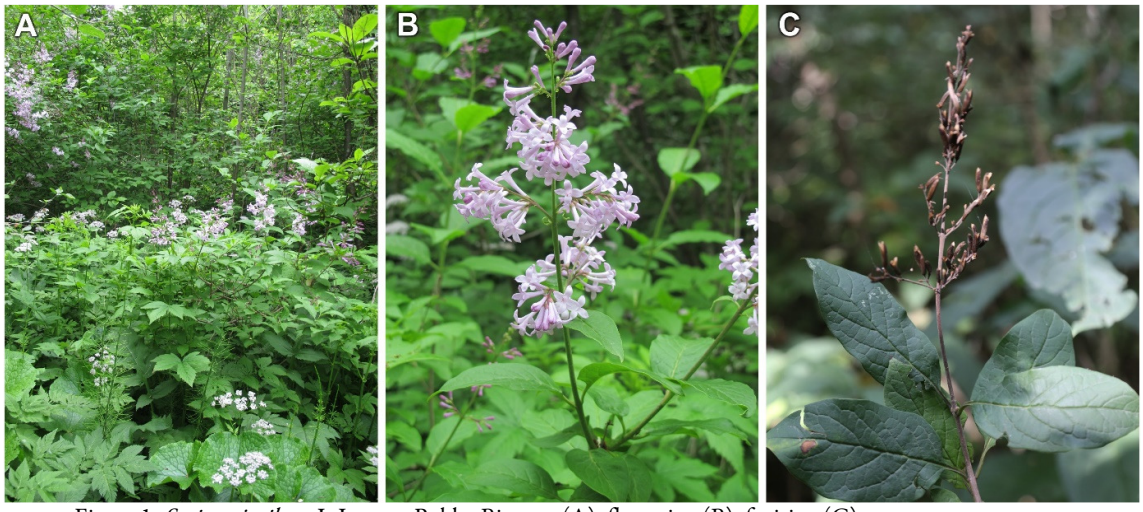

Figure 1. *Syringa josikaea* J.-Jacq. ex Rchb.: Biotope (A); flowering (B); fruiting (C)
*Note: The locations of biotope: Mukachevo Rayon, south of village Tyshiv (with former village Medvezhe), Ukraine. The coordinates are as follows: 48.80° N; 23.08° E; 475 m above sea level. The area is 0.5 ha

The species is currently classified as "Critically Endangered" (CR) in the Red Data Book of Ukraine (Didukh, 2009a; Nakaz, 2021). It is also listed in the European Red List (Bilz *et al.*, 2011) and appears in the Romanian Red Data Book, where it is noted as protected within the Apuseni Natural Park (Dihoru and Negrean, 2009). Furthermore, it is included in Resolution No. 6 (1998) of the Berne Convention, as amended in 2011 (EEA, 2024a) and is listed under Annexes I, IIb and IVb of the European Union (EU) Habitats Directive (EEA, 2024b, 2024c). In the International Union for Conservation of Nature Red List, the species was previously categorized as "Data Deficient" (DD) until 2018, but is currently assessed as "Endangered" (EN) (Höhn and Lendvay, 2018). It is likewise designated as "Endangered" (EN) in the Carpathian List of Endangered Species (Witkowski *et al.*, 2003).

According to the classification of the European Nature Information System (EUNIS, Annex I of the Habitats Directive), the majority of *S. josikaea* habitats fall under the category 91E0* – Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion, Alnion incanae, Salicion albae*) or Floodplain forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion, Alnion incanae, Salicion albae*). *S. josikaea* is assigned the code 2186 in the Annexes of the EU Habitats Directive. In accordance with the Directive's provisions, *S. josikaea* is to be strictly protected as a species of Community Importance (SCI), both in the Ukrainian flora and within its specific habitats. These protections align with the principles of the Natura 2000 network, which safequards biodiversity within EU member states, including areas both inside and beyond designated network boundaries (Kohut, 2013; Kuzemko, 2017). The plant communities that support *S. josikaea* are also recoreded in the Green Book of Ukraine (Didukh, 2009b), where the species holds a synphytosozological index of 16.2, placing it in Class I, Category 2, and designating its community status as "rare". Furhtermore, *S. josikaea* is listed as a protected species within Ukaine's Emerald Network at the following sites: UA0000013 (Skolivski Beskydy National Nature Park), UA0000032 (Uzhanskyi National

Nature Park), and UA0000269 (Vynohradivska Tysa) (Solomakha, 2016). However, the the presence of the species at the latter site has not been confirmed by the authors.

Throughout the 20th century and into the present day, Hungarian, Polish and Ukrainian botanists have conducted extensive research on the distribution, ecological preferences, structural attributes, and phytocoenological characteristics of *S. josikaea*, including the cenogenetic relationships within its plant communities. These studies have not only underscored the ecological significance of this rare Carpathian endemic species but also highlighted the urgent need for its protection and the implementation of targeted conservation measures to preserve its genetic diversity within the Ukrainian Carpathians (Thaisz, 1912; Fekete and Blattny, 1914; Wierdak, 1923; Stoyko, 1966, 1980; Horb, 1984; Milkina, 1985; Felbaba-Klushyna, 2005). To evaluate the current distribution and conservation of *S. josikaea*, E. Kohut conducted a series of detailed studies between 2004 and 2024. These investigations aimed to clarify both historically known and newly recorded habitats of the species in the Ukrainian Carpathians (Kohut and Höhn, 2010; Lendvay, 2012; Kohut, 2013). A comprehensive floristic survey was carried out to document existing populations, including data on physical and geographical features, geographic coordinates and altitudinal distribution. At present, ongoing efforts involve monitoring established populations and searching for potential new habitats of *S. josikaea* in the Ukrainian Carpathians. To ensure the long-term survival of the species, further research is required to refine our understanding of its climatic, hydrological, and edaphic requirements. Continued phytocoenological monitoring of its habitats is also essential for effective conservation planning.

The primary aim of this study is to identify and analyse the climatic characteristics of *S. josikaea* habitats within the Ukrainian Carpathians. To achieve this goal, the following research tasks were formulated: (1) to classify the types of climates within the species distribution area using the Köppen-Geiger climate classification system; (2) to calculate the average statistical values of key climatic indicators across individual habitat sites; (3) to assess the dynamics of climatic conditions in the region; and (4) to identify indicators and possible trends of mesoclimatic change within the species' range. This includes an analysis of relationships between temperature and hydrological shifts, as well as an assessment of the species' survival prospects in the context of its narrow cenotic amplitude and the specific conditions of its refugial habitats.

A detailed study of the climatic conditions of *S. josikaea* habitats will contribute to the species' *ex situ* conservation, support the identification and potential restoration of forgotten habitats whose conservation is recognised as a priority in international documents and Red Lists.

Materials and Methods

For the climatic classification of *S. josikaea* habitats, we utilised the CarpatClim climate database (Szalai *et al.*, 2012), developed through an international collaboration involving research institutes across Central Europe. Ukraine was represented in the project by the Ukrainian Hydrometeorological Institute (UkrHMI) of the State Emergency Service and the National Academy of Sciences of Ukraine. The database contains 16 meteorological indicators with daily resolutions and 37 variables with monthly resolution, covering nearly all meteorological stations in the Carpathian region for the period from 1961 to 2010. The data were homogenised using specialized climatological software MASH (Multiple Analysis of Series for Homogenisation), and spatially interpolated with MISH (Meteorological Interpolation based on Surface Homogenised Data Base) to regular grid nodes at a spatial resolution of 0.1° × 0.1° (approximaely ≈7 × 11 km). The known occurrences of the species correspond to different nodes within the regular CarpatClim grid. Based on the data from 338 grid nodes and a total of 21 climate variables, a map depicting the distribution of Köppen-Geiger climate types was compiled (Kottek *et al.*, 2006). In addition to the species' habitats, the selected map section encompasses the entire Zakarpattia Oblast, parts of Lviv and Ivano-Frankivsk Oblasts, as well as a narrow strip of adjacent western countries.

The Köppen-Geiger climate classification is a multi-stage conventional system (Kottek *et al.*, 2006) based on biogeographical conditions and the specific temperature and precipitation regimes of a given area (Table 1). The system distinguishes 5 primary climate zones (A, B, C, D, E), of which C represents temperate warm climates, D corresponds to the boreal zone, and E designates the polar zone. In addition to these main categories, the second letter (w, s, f) indicates the distribution of precipitation, reflecting its seasonality during cold and warm periods. The third letter (a, b, c, d) denotes thermal characteristics and is used to differentiate degrees of continentality or climatic extremity. Within the Carpathian region, only the C, D, and E climate types are observed.

Table 1. Selected Köppen-Geiger climate types and their classification criteria (Kottek *et al.*, 2006)

Climate types Köppen-Geiger			Classification criteria		
1	**2**	**3**	**1**	**2**	**3**
C	s	a	$-3 < T_{cold} < 18$ and $T_{warm} > 10$	$P_{sdry} < 40$, $P_{sdry} < P_{wwet}/3$	$T_{warm} \geq 22$
	w	b		$P_{wdry} < P_{swet}/10$	$T_{warm} < 22$, $T_{mon10} \geq 4$
	f	c		neither (s) nor (w)	$T_{warm} < 22$, $1 \leq T_{mon10} < 4$
D	s	a	$T_{cold} \leq -3$ and $T_{warm} > 10$	$P_{sdry} < 40$, $P_{sdry} < P_{wwet}/3$	$T_{warm} \geq 22$
	w	b		$P_{wdry} < P_{swet}/10$	$T_{warm} < 22$, $T_{mon10} \geq 4$
	f	c		neither (s) nor (w)	neither (a) nor (b), $T_{cold} \geq -38$
		d			neither (a) nor (b), $T_{cold} < -38$
E		T	$T_{warm} < 10$		$0 < T_{warm} < 10$

*Notes: 1 – main climate types; 2 – seasonality of precipitation; 3 – temperature regime. T_{warm} = average temperature of the warmest month (°C); T_{cold} = average temperature of the coldest month (°C); T_{mon10} = number of months with average temperature above +10 °C; P_{sdry} = precipitation of the driest summer month (mm); P_{wdry} = precipitation of the driest winter month (mm); P_{swet} = precipitation of the wettest summer month (mm); P_{wwet} = precipitation of the wettest winter month (mm). In accordance with the established classification criteria, the designation of summer and winter months depends on the prevailing climatic conditions in either the first or second half of the year (6-month period = O-N-D-J-F-M and A-M-J-J-A-S)

The geolocation of *S. josikaea* habitats was determined using our own GPS measurements, as well as topographic maps, forest management maps from state forestry enterprises, and Google Earth imagery. Field-based ecological and phytocoenological observations, along with laboratory soil analyses, were carried out between 2004 and 2023.

The names of the species were taken from POWO (https://powo.science.kew.org/). Syntaxons were given according to Prodromus by Borhidi (2003).

Results and Discussion

Characteristics of Biotopes for *Syringa josikaea (Oleaceae)* in the Ukrainian Carpathians

A total of only 26 local populations of *S. josikaea* have been recorded in the species' current habitat (Figure 2): 18 (on the map 1-16 represent Zakarpattia (Zk) and 17-18 represent Lviv (Lv)) – in the Ukrainian Carpathians (16 in Zakarpattia and 2 in Lviv Oblast) and 8 (1-8 Romania (Ro)) – in the Apuseni Mountains (Bihor, Cluj and Alba County, Romania) (Milkina, 1985; Didukh, 2009a; Karabchuk *et al.*, 2010; Kohut and Höhn, 2010; Lendvay *et al.*, 2016).

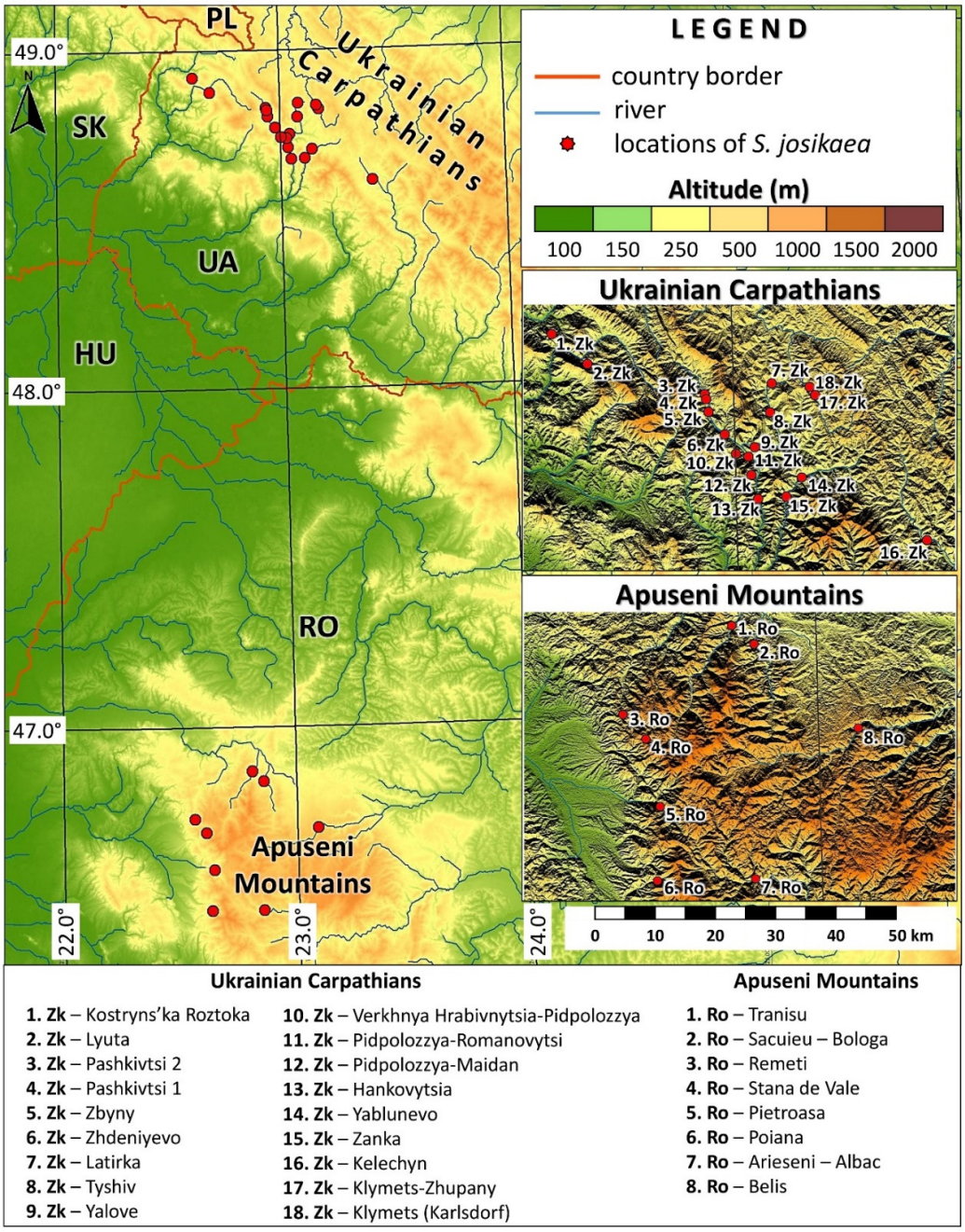

Figure 2. Present distribution and the locations of *S. josikaea* in the Carpathians

The main physiographic, geographical, ecological and coenological features of 18 fixed localities (1-18. Zk) of *S. josikaea* in the Ukrainian Carpathians (Kohut and Höhn 2010; Kohut, 2013), which are located in the catchments of the Uzh, Bystrytsia, Liuta, Latorica, Zhdenivka, Vecha, Rika, Repinka and Stryi rivers, are summarised.

1. Zk, Uzhhorod Raion, near the village of Kostryns'ka Roztoka. The site is located in the Borsuchyna or Bolotyn tract of Kostryna forestry, square 21, on the right bank of the Borsuchyna stream (a left tributary of the Uzh River). It lies on the western slope of Lishchynka mountain, which is covered by a dense beech forest. The coordinates are as follows: 48.92° N; 22.61° E; 550 m above sea level. The area of the population is 0.5 ha;

regeneration is mainly vegetative. The site has the status of a "nationally important nature monument 'Mount Yavirnyk'" (created to preserve virgin beech and sycamore forests with Hungarian lilacs in its undergrowth), within Uzhanskyi National Park; not subject to direct forestryactivities. The ecological and cenotic conditions of the site are influenced by a small willow bog, which remains waterlogged due to the presence of a nearby spring. The soil is dark and peaty, with undecomposed plant material accumulating in some areas. The flora of the region includes lilac shrubs, which occur among the willow trees. The associated species include: *Fraxinus excelsior, Fagus sylvatica, Corylus avellana*, *Chrysosplenium alternifolium, Caltha palustris, Carex remota, Dryopteris carthusiana*.

2. Zk, Uzhhorod Raion, between the villages of Chornoholova and Lyuta. The site is located in the Bystrychi forestry, square 30, and spans approximately one kilometre in lenght. The site is situated primarily on the right bank of the Bystrytsya River, a tributary of the Lyuta River. It is located on the lower slopes of the south-western and western aspects of Babynkovo mountain, which is covered by a dense fir-beech forest. The coordinates of the site are as follows: 48.88° N; 22.69° E; elevation ranges from 430 to 570 m above sea level. The area is 1.0 ha. Protection status is "territory of Uzhanskyi National Park". The ecological and cenotic conditions are as follows: the area is characterised by a rocky, narrow, V-shaped valley composed of sedimentary rocks (flysch). The lilac plants are observed growing directly over the stream. Regeneration is predominantly vegetative, with high density of large, old clones. The population status is stable. The associated species include: *Lonicera xylosteum, Rosa pendulina, Dryopteris cristata, D. dilatata, D. expansa, Cystopteris fragilis, Polystichum aculeatum, Phegopteris connectilis, P. polyploides*. There is almost no anthropogenic influence.

3. Zk, Mukachevo Rayon, 1 km north of the village Pashkivtsi. The site is situated in the Pashkivtsi forestry, square 18, on the right bank of the Zhdenivka River, a tributary of the Latorica River. It lies withina narrow strip between the E0722 road and the foot of the Polonyna Bukyuska ridge. Polonyna Bukyuska (1304 m) is forested with beech and spruce. Its coordinates are as follows: 48.83° N; 22.94° E; 490 m above sea level. The area is 0.1 ha. Protection status is "not protected". The ecological and cenotic conditions are those of a small willow bog, an area that is constantly waterlogged and sometimes covered with water. The species occurs in high density among willow trees. The associated species include: *Alnus incana, Fraxinus excelsior, Frangula alnus, Salix cinerea, Corylus avellana, Caltha palustris, Chrysosplenium alternifolium, Veratrum album*. Due to the proximity of the motorway and adjacent agricultural land, the habitat is subject to heavy anthropogenic pressure.

4. Zk, Mukachevo Raion, northern edge of the village Pashkivtsi. The site is situated in the Pashkivtsi forestry, square 34, on the right bank of the Zhdenivka River, between the road (E0722) and the foot of the Polonyna Bukyuska ridge. Polonyna Bukyuska (1304 m) is covered with a mixed forest of beech and spruce. Its coordinates are as follows: 48.82° N; 22.94° E; 470 m above sea level. The area is 0.1 ha. Protection status is "not protected". The ecological and cenotic conditions of the area are characterized by the presence of a narrow bog forest dominated by grey alder (*Alnus incana*) adjacent to peat deposits, which is in turn border a peat bog. The site is subjected to continuous waterlogging, with periods of inundation, and a high density of dead trees. The associated species include: *Corylus avellana, Salix caprea, Caltha palustris, Filipendula ulmaria, Chaerophyllum hirsutum subsp. glabrum, Cirsium oleraceum*. Due to the proximity of the motorway and the built-up area, the biotope is threatened with extinction.

5. Zk, Mukachevo Raion, between the villages of Pashkivtsi and Zbyny. The site is located in the Pidpolozzya forestry, section 28, on the left bank of the Zhdenivka River, at the eastern foot of the mountain (611 m). The exact coordinates are as follows: 48.80° N; 22.95° E; 450 m above sea level. The area is 0.06 ha. Protection status is "not protected". The ecological and cenotic conditions of the area are characterized by the presence of a small willow bog situated between a meadow with narrow-leaved cottongrass (*Eriophorum angustifolium*) and mountain foothills covered with beech-fir forest. The area is subjected to constant inundation, although there are also some dried grey alder (*Alnus incana*) trees present, with a notable population of lilac exhibiting fruiting specimens. The associated species include: *Frangula alnus, Salix cinerea,*

Caltha palustris, Chrysosplenium alternifolium, Juncus effusus, Ranunculus repens. Due to the proximity of the motorway built-up area, the biotope is threatened with extinction.

6. Zk, Mukachevo Raion, on the western edge of village Zhdeniyevo. The site is situated in Chereshneve tract, Zhdeniyevo forestry, square 18, on the right bank of the Zhdenivka River, on the north-eastern foot of Shyrokyi Munchel mountain (1102 m). The coordinates are as follows: 48.77° N; 22.98° E; 440 m above sea level. The area is 0.7 ha. Protection status is "botanical reserve of local importance, designated as the Hungarian Lilac Reserve". The territory serves as a seed base for the species, facilitating its artificial distribution in the region. The ecological and cenotic conditions of the territory are characterized by a continuous alder swamp, with the area exhibiting high levels of soil moisture. Water is supplied by two subterranean springs, with precipitation and runoff from the slope representing additional sources. The water is brown in colour and exhibits a sulphurous odour. In the swampy area, the tree layer is dominated by grey alder (*Alnus incana*), with the lilac population exhibiting a satisfactory condition. The associated species include: *Fraxinus excelsior, Salix caprea, Salix cinerea, Acer pseudoplatanus, Corylus avellana, Caltha palustris, Carex elongata, C. brizoides C. remota, C. pseudocyperus, Chrysosplenium alternifolium.* Due to the proximity of the built-up area of the village, the biotope is in danger of extinction.

7. Zk, Mukachevo Raion, in the built-up area of village Latirka. The site is situated on the right bank of the Latorica River. The coordinates are as follows: 48.84° N; 23.08° E; 570 m above sea level. It includes only 3 specimens. Protection status is "not protected". The ecological and cenotic conditions of the area in question are those of an anthropogenic environment, situated directly on the riverbank. According to local residents, no lilacs were planted in this location; rather, they were already established in the area prior to the construction of the human edifice. This is evidenced by the presence of old stems and roots of bushes. The villagers pay special attention to their preservation.

8. Zk, Mukachevo Raion, South of village Tyshiv (with former village Medvezhe). It is located in Nyzhni Vorota forestry, sq. 9, on the right bank of the Latorica River, at the north-eastern foot of Hulyayka mountain (1038 m) in a relatively flat terrain. The coordinates are as follows: 48.80° N; 23.08° E; 475 m above sea level. The area is 0.5 ha. Protection status is "not protected". The ecological and cenotic conditions of the area are characterized by a bog with stagnant water and helophytes. The associated species include: *Alnus incana, Ribes uva-crispa, Chaerophyllum hirsutum subsp. glabrum, Filipendula ulmaria, Cirsium oleraceum, Thalictrum aquilegifolium.* The site is situated in close proximity to a woodworking plant, which poses a significant threat to the continued existence of the species.

9. Zk, Mukachevo Raion, South of village Yalove (with former village Pudholichka). It is located in Nyzhni Vorota forestry, sq. 17, on the left bank of the Latorica River, at the north-western foot of the mountain (791 m). The coordinates are as follows: 48.75° N; 23.04° E; 390 m above sea level. Only a few specimens are left. Protection status is "not protected". The ecological and cenotic conditions of the area are characterized by an alder swamp with willows, extending between a hornbeam forest and a stream that flows into the Latorica River. The presence of bushes is notable near a small surface depression, which is frequently inundated. The associated species include: *Alnus incana, Salix caprea, Sambucus nigra, Cirsium oleraceum, Juncus effusus, Scirpus sylvaticus.* The entire area is subject to intense anthropogenic pressure, and the construction of a gas pipeline has resulted in the degradation and partial disappearance of the biotope.

10. Zk, Mukachevo Raion, between villages Verkhnya Hrabivnytsia and Pidpolozzya. It is located in Pidpolozzya forestry, sq. 17, along a one-kilometre section on the left bank of the small right tributary of the Latorica River, at the south-eastern foot of Kinskyi Verkh mountain (981 m). The coordinates are as follows: 48.74° N; 23.00° E; 380 m above sea level. There are approximately 10 bushes. Protection status is "not protected". The biotope is situated within a wet beech and hornbeam forest on a rocky stream bank, with surrounding bushes leaning over the water. An illegal solid waste dump is located on the bank of a stream near the habitat.

11. Zk, Mukachevo Raion, south-east of village Pidpolozzya. It is located in Romanovytsi tract, Pidpolozzya forestry, sq. 31, on the left bank of the Romanovets stream (right tributary of the Latorica River),

at the northern foot of the mountain (1054 m). The coordinates are as follows: 48.74° N; 23.03° E; 350 m above sea level. The area is 0.2 ha. Protection status is "not protected". The ecological and cenotic conditions of the area are characterized by a swamp forest with grey alder (*Alnus incana*) and lilacs, which are typical for wet habitats. The population status of the lilac is deemed to be satisfactory. The associated species include: *Sorbus aucuparia, Viburnum opulus, Sambucus nigra, Euonymus europaeus, Chaerophylum hirsutum subsp. glabrum, Caltha palustris, Filipendula ulmaria.* The site is situated behind a building (on an uninhabited farm) in close proximity to a pasture, which is drained by drainage ditches. The habitat was probably larger in the past.

12. Zk, Mukachevo Raion, 3.5 km south of village Pidpolozzya. It is located in Maidan tract, Pidpolozzya forestry, sq. 25, on the right bank of the Latorica River, directly near the motorway (E471), on the eastern foot of the mountain (1054 m). The coordinates are as follows: 48.71° N; 23.04° E; 340 m above sea level. The area is 0.5 ha. Protection status is "local importance botanical nature monument 'Hungarian Lilac'". The ecological and cenotic conditions of the area are characterized by a swamp forest with grey alder *(Alnus incana)* and spring geophytes. This habitat is drier than the surrounding areas and features small streams and a high density of flowering specimens. The following species are associated with this habitat: *Alnus glutinosa, Fraxinus excelsior, Acer campestre, Carpinus betulus, Corylus avellana, Euonymus europaeus, Sambucus nigra, Allium ursinum, Lilium martagon*. The construction and maintenance of the Chop–Kyiv highway in the 1980s resulted in the destruction of a portion of the habitat. This, in turn, led to disturbances in the hydrological regime of the biocenosis, rendering it one of the most threatened areas.

13. Zk, Mukachevo Raion, 4.5 km north of village Hankovytsia. It is located in Ihnatyk tract, Hankovytsia forestry, sq. 3, between Dozhdzhatyi and Ihnatyi streams (right tributaries of the Latorica River), at the eastern foot of Lypcha mountain (859 m) that is covered with beech forest. The coordinates are as follows: 48.68° N; 22.05° E; 320 m above sea level. The area is 0.6 ha. Protection status is "not protected", former (since 1969) protected status of the territory is terminated. The ecological and cenotic conditions of the area are characterized by a swamp forest with grey alder *(Alnus incana)* and black alder *(Alnus glutinosa)*. This is interspersed with heavily silted patches, which alternate with areas that are either periodically or permanently flooded. The following species are associated with this habitat: *Corylus avellana, Sambucus nigra, Daphne mezereum, Carpinus betulus, Acer pseudoplatanus, Leucojum vernum, Allium ursinum, Lilium martagon, Scopolia carniolica, Lunaria rediviva, Equisetum telmateia, Matteuccia struthiopteris, Cardamine bulbifera, Cardamine glanduligera*. The direct anthropogenic impact is minimal.

14. Zk, Mukachevo Raion, 2.5 km west of village Volovets, in the former village of Yablunevo. It is situated in Verkhnyiy Volovets forestry, sq. 28, on the left bank of the Vecha River (left tributary of the Latorica River), along the river in the pasture, at the north-western foot of the mountain (688 m). The coordinates are as follows: 48.71° N; 23.14° E; 440 m above sea level. The area is 2×0.5 ha. Protection status is "not protected". The ecological and cenotic conditions of the area are characterized by the presence of small bogs, which are dominated by grey alder *(Alnus incana)* and tall, old lilacs with trunk diameter up to 15 cm. The territory is subjected to a constant water cover. The following species are associated with this habitat: *Chaerophyllum hirsutum subsp. glabrum, Caltha palustris, Cardamine amara, Scirpus sylvaticus, Filipendula ulmaria, Petasites hybridus*. The territory is located in a village. It is under threat of extinction.

15. Zk, Mukachevo Raion, 500 m north of the railway station Zanka. It is situated in Nyzhnyiy Volovets forestry, sq. 2, on the left bank of the Vecha river (left tributary of the Latorica River, on a 150 m long stretch near the railway tracks, at the western foot of the mountain (991 m), covered with beech forest. The coordinates are as follows: 48.68° N; 23.11° E; 420 m above sea level. The area is 0.2 ha. Protection status is "not protected". The ecological and cenotic conditions of the territory are characterized by the presence of a vast mountain alder forest, comprising grey alder *(Alnus incana)* and common ash *(Fraxinus excelsior)*. While the territory exhibits patches of willow bogs, the landscape displays a mosaic of dry and wet areas. The following species are associated with this habitat: *Corylus avellana, Sambucus nigra, Filipendula ulmaria, Petasites hybridus, Chaerophyllum*

hirsutum subsp. glabrum, Cirsium oleraceum. The habitat was probably larger, but during the construction of a power line, a wide swathe of endangered forest was cut down.

16. Zk, Khust Raion, village Kelechyn. It is located in Izky forestry, sq. 18, on the right bank of the Repinka River (right tributary of the Rika River), directly near the road (T0718), at the north-eastern foot of Dilok mountain (723 m). The coordinates are as follows: 48.61° N; 23.41° E; 500 m above sea level. The area is 0.15 ha. Protection status is "not protected". The ecological and cenotic conditions of the area are characterised by a small alder forest comprising grey alder *(Alnus incana*) and black alder *(Alnus glutinosa)*, as well as a rich, high vegetation cover. The landscape displays a mosaic of heavily waterlogged depressions alternating with dry areas and is characterised by a constant water supply from a sulphurous mineral water spring. The following species are associated with this habitat: *Salix caprea, S. caprea, Picea abies, Viburnum opulus, Thalictrum aquilegifolium, Chaerophyllum hirsutum subsp. glabrum, Filipendula ulmaria*. The biotope is located next to a mineral water source, but the area is noticeably drying out due to drainage ditches between roads and is under particularly strong anthropogenic influence.

17. Lv, Stryi Raion, between villages Klymets' and Zhupany. It is located in Klymets' forestry, sq. 21, on the right bank of the Stryi River, on the north-eastern slope of Verkhovyna Watershed ridge, 1.5 km from Veretskyi Pass (839 m). The coordinates are as follows: 48.82° N; 23.17° E; 740-760 m above sea level. The area is 1.2 ha. Protection status is "protected in the local nature monument 'Hungarian Lilac'" (Lviv Oblast), population status is stable. The ecological and cenotic conditions of the area are characterized by a swamp forest with grey alder *(Alnus incana)*, which grows on waterlogged alluvial substrate. The majority of flowering specimens are located on the edge of the habitat. The following species are associated with this habitat: *Picea abies, Sorbus aucuparia, Salix caprea, Sambucus racemosa, Lonicera xylosteum, Filipendula ulmaria, Cirsium oleraceum, Aconitum variegatum subsp. paniculatum*. – There is almost no anthropogenic influence.

18. Lv, Stryi Raion, on the western outskirts of village Klymets, founded by a former German colony called Karlsdorf. It is located on the right bank of the Stryi River. The coordinates are as follows: 48.84° N; 23.16° E; 741 m above sea level. There are only a few specimens left in the area. Protection status is "not protected". The plant is popular among local people and can be found near almost every house where large, old bushes grow in front gardens. The ecological and cenotic conditions are those of a swamp forest with grey alder *(Alnus incana)*, in a fir forest on a waterlogged alluvial substrate. The following species are associated with this habitat: *Picea abies, Salix caprea, Sambucus racemosa, Lonicera xylosteum, Filipendula ulmaria, Cirsium oleraceum, Aconitum variegatum subsp. paniculatum*.

The majority of the habitats are situated in mountain valleys, around rivers and streams, on small, low floodplains, and on waterlogged riverine terraces, which are characterized by the presence of swampy or alder gallery forests. The species is also found in narrow habitats within willow bogs situated in the beech-fir and beech vegetation zone, at an altitude of 350-750 metres above sea level. The species is primarily found in the following communities: *Querco-Fagetea* Br.–Bl. et Vlieg. 1937, *Salicetea purpureae* Moor 1958 and *Alnetea glutinosae* Br.-Bl., Tx. ex Westhoff *et al*., 1946. The main biotopes of *S. josikaea* are swampy, hygrophytic forests, where the following species are the main identifiers *Alnus incana*, *A. glutinosa*, *Fraxinus excelsior*. In terms of species richness, the locality (16 Zk) is the most distinctive in the Repinka River valley near the village of Kelechyn (Kohut and Höhn, 2010; Kohut, 2013).

Studies of soil samples from habitats in the vicinity of the villages of Pidpolozzya, Zhdenijevo, Kostryns'ka Roztoka, and Klymets' indicate that *S. josikaea* grows on moist and heavily peated, boggy soils, mineral-rich soils characterised by low acidity (pH ranges from 3.5 to 5.8), high nitrogen and potassium content, and low mobile phosphorus. In particular, the upper soil layers exhibit a pronounced concentration of mobile zinc, manganese, cobalt, and iron (Csoma *et al*., 2016).

Currently, only 5 habitats are protected: in Zakarpattia Oblast, the main areas of occurrence are in Uzhanskyi National Park (in Bystryy, Zhdenijevo, Kostryna, Pidpolozzya forestry) and Lviv Oblast (in Klymets' forestry), with the majority of occurrences concentrated in local natural monuments. In order to fully preserve the species' gene pool, it is necessary to reserve all its recorded habitats.

The climatic features of the habitat of S. josikaea

S. josikaea is distributed in areas with a temperate continental climate classified as Dfb (boreal snowy climate with sharply defined differences between winter and summer (D), without a dry season, evenly humid throughout the year (f), with warm summers (b)), (Figure 3). In some territories near the present-day range of *S. josikaea* the warm temperate climate type Cfb (temperate climate without regular snow cover (C), without a dry season, evenly humid throughout the year (f), and with warm summers (b)) and the subarctic continental climate type Dfc (boreal snow climate with sharply defined differences between winter and summer (D), without a dry season, evenly humid throughout the year (f), and with cool summers and harsh winters (c)) also occur. Given that all climate types (Cfb → Dfb → Dfc) in the study area include the symbol 'f', indicating a uniform distribution of precipitation throughout the year, it may be argued that the climates corresponding to individual nodes of the regular CarpatClim grid in the species' range and habitats differ primarily in their thermal characteristics. In terms of spatial distribution of precipitation, the climate types are distinguished to a lesser extent, while due to the temporal homogeneity of precipitation, they are not distinguished at all.

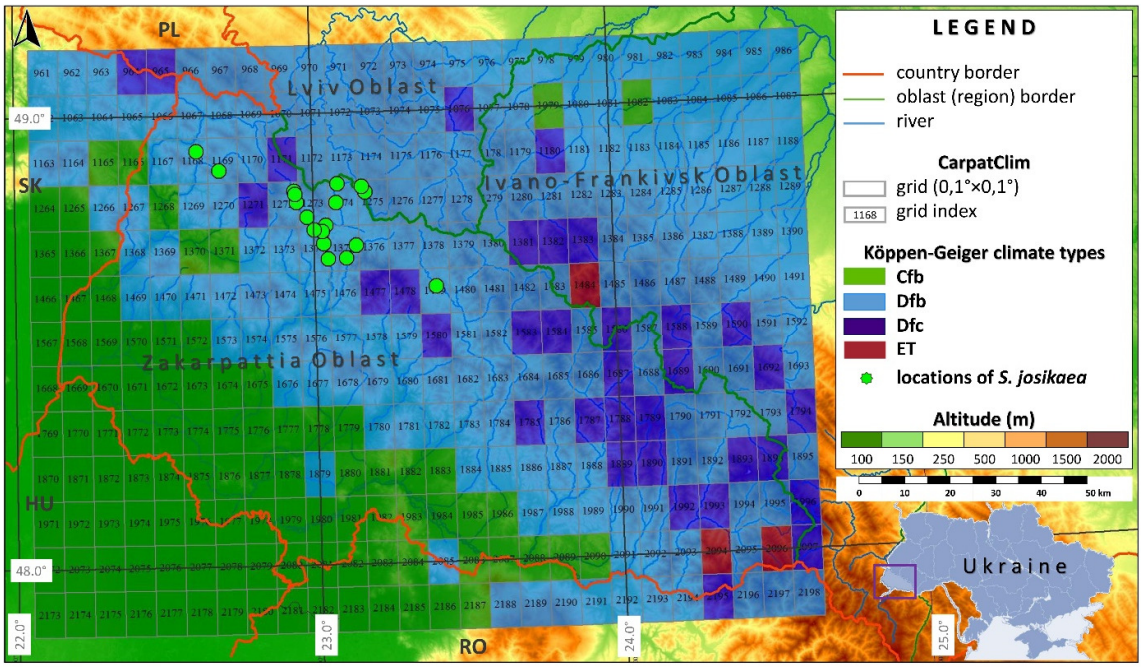

Figure 3. Köppen-Geiger climate types in the distribution area of *S. josikaea* from the Ukrainian Carpathians (habitats of the species are marked with bright green dots)

The mean statistical values of climatic indicators pertaining to the corresponding nodes of the regular grid in the territory of *S. josikaea* distribution for the period from 1961 to 2010 were summarised and characterised in Table 2.

Table 2. Climatic characteristics of *S. josikaea* habitats for the period 1961-2010

CarpatClim climate indicators, their abbreviations and units	1. Zk	2. Zk	3. Zk; 4. Zk; 5. Zk	6. Zk	7. Zk; 8. Zk	17. Lv; 18. Lv	9. Zk; 10. Zk; 11. Zk; 12. Zk; 13. Zk	14. Zk; 15. Zk	16. Zk	Coefficient of variation
Number (index) of grids in the CarpatClim	1168	1169	1272	1273	1274	1275	1374	1375	1479	
Average long-term temperature (T_a), °C	6.4	7.3	6.4	6.6	6.0	5.9	5.9	5.2	7.8	0.11
Average minimum long-term temperature (T_{amin}), °C	2.2	3.1	2.5	2.4	1.6	1.9	1.6	0.8	3.5	0.38
Average maximum long-term temperature (T_{amax}), °C	10.7	11.4	10.4	10.7	10.4	9.9	10.3	9.5	12.0	0.06
Average temperature of the coldest month (T_{cold}), °C	-3.4	-3.2	-5.0	-4.7	-4.9	-5.2	-4.6	-4.9	-3.6	0.13
Average temperature of the warmest month (T_{warm}), °C	15.3	16.3	17.2	17.1	15.9	15.6	15.9	14.9	17.9	0.06
The number of months with an average temperature over 10 °C (NT_{mon} > 10 °C), month/year	5	5	5	5	5	5	5	5	5	0.00
The number of months with an average temperature under 0 °C (NT_{mon} < 0 °C), month/year	3	3	4	4	4	3	4	4	3	0.12
The number of frosty days (NT_{dmin} < 0 °C), day/year	126	118	143	138	144	140	144	162	112	0.09
The number of winter days (NT_{dmax} < 0 °C), day/year	54	44	69	64	72	71	73	74	53	0.13
The number of severe days (NT_{dmin} < −10 °C), day/year	23	22	30	32	30	29	8	33	24	0.34
The length of the vegetation period (NT_{dmin} < 5.5 °C), day/year	212	223	175	205	209	206	199	188	222	0.07
The number of summer days (NT_{dmin} > 25 °C), day/year	15	18	18	20	20	13	20	11	39	0.35
The number of hot days (NT_{dmin} ≥ 30 °C), day/year	0	1	1	1	1	0	1	0	4	0.00
Average long-term precipitation (P_a), mm	1067	1088	1250	1161	1193	1175	1158	1305	1279	0.06
Average precipitation in the driest winter month (P_{wdry}), mm	66	73	79	66	73	75	72	90	76	0.11
Average precipitation in the wettest winter month (P_{wwet}), mm	91	92	121	92	98	87	105	128	120	0.15
Average precipitation in the driest summer month (P_{sdry}), mm	71	71	81	81	82	87	76	78	85	0.06
Average precipitation in the wettest winter month (P_{swet}), mm	116	121	137	148	159	156	153	159	152	0.09
The number of days with precipitation (NP_{dwet} ≥ 1 mm), day/year	151	152	164	156	156	162	153	161	158	0.03
The number of wet (rainy, snowy) days (NP_{dwet} ≥ 20 mm), day/year	9	9	11	12	10	10	11	13	13	0.12
Average snow depth (cm) in the coldest month (ST_{cold})	24	23	53	35	40	41	36	59	28	0.28

The complex orographic structure of the studied area is reflected in the temporal and spatial disproportions of climatic indicators. Populations of the species can be considered stenobiont in terms of temperature and hydrological conditions, being adapted to a narrow range of environmental factors. The habitats are located in areas with an average annual temperature (T_a) 6.2 °C (minimum: 5.2 °C, maximum: 7.8 °C). The average maximum long-term temperature (T_{amax}) did not exceed 12 °C in any of the habitats during the period from 1961 to 2010. Furthermore, the variability of this indicator is among the lowest across the habitats, with a coefficient of variation of 0.06. The average temperature difference between the coldest (T_{cold}) and warmest (T_{warm}) months is less than 21 °C. In the species' distribution area, the average monthly temperature exceeds above 10 °C ($NT_{mon} > 10$ °C) for only 5 months, and falls below 0 °C ($NT_{mon} < 0$ °C) for almost 4 months. On average, the daily minimum temperature remains below freezing i.e. below 0 °C ($NT_{dmin} < 0$ °C) for approximately 40% of the year (141 days), is below freezing, , of which 26 days (18% of the year) are so-called severe days ($NT_{dmin} < -10$ °C), when the minimum temperature drops below −10 °C. Winter days ($NT_{dmax} < 0$ °C) account for 18% of the year (67 days) when the daily maximum temperature does not exceed 0 °C even in the warmest hours. The length of the vegetation period ($NT_{dmin} < 5.5$ °C), defined in CarpatClim as the number of days with an average temperature above 5.5 °C, covers an estimated 201 days in the species' habitat, i.e. 55% of the year. In its distribution area, summer days ($NT_{dmin} > 25$ °C) occur in only 5% of the days annually, with an average of about 18 days when the maximum daily temperature rises above 25 °C. Maximum daily temperatures above 30 °C ($NT_{dmin} \geq 30$ °C) have been recorded on average for only 1-4 days per year over the 50-year period.

The species prefers humid areas with a positive water balance and an even distribution of precipitation and water supply throughout the year. Its habitats receive an average of at least 1000-1100 mm of annual precipitation (P_a). The average precipitation in the driest winter (P_{wdry}) and summer (P_{sdry}) months, and in the wettest winter (P_{wwet}) and summer (P_{swet}) months across the distribution area is 75 - 80 - 105 - 149 mm, respectively, corresponding to 6.3% - 6.7% - 8.8% and 12.4% of the annual precipitation (P_a). Thus, the absolute difference between the precipitation of the two most extreme months, which can be separated by the temporal distribution of precipitation, is only 74 mm, which is 6.1% of the annual precipitation. The habitat receives a minimum of 1 mm ($NP_{dwet} \geq 1$ mm) of precipitation per day, in the form of either liquid or solid precipitation, on an average of at least 151 days per year, representing 41% of the total annual precipitation. In January, which is considered the coldest winter month in the range, the average snow cover is 41 cm.

The above mentioned 9 grids presented in table 2, a further 13 grids were identified as potential habitats of the species, based on hydrological, relief and climate data (Hadnagy and B. Balog, 2021).

Changing climatic conditions of S. josikaea habitats

Global trends in climate change (Rubel-Kottek, 2010; IPCC, 2023) are reflected in hydrothermal conditions (Wilson *et al.*, 2021), as well as in qualitative and quantitative trends in the development, alteration, or transformation of vegetation cover in the western regions of Ukraine (Didukh and Chorney, 2016; Kyyak *et al.*, 2022). The general features of climate change in western Ukraine, particularly in the Carpathian region, during the period 1991-2020, compared to the climatic norm of 1961–1990, indicate an increase in average annual temperatures by 0.8-1.6 °C, and a shift in heat and moisture conditions toward warmer and more arid bioclimatic zones (Kyyak *et al.*, 2022).

To identify the trends in the climatic conditions of *S. josikaea* habitats, we analysed time series data on annual and monthly average air temperature and precipitation from specific CarpatClim nodes (9 in total) located closest to the species' habitats. A comparison between the periods 1961-1980 and 1991-2010 (Figure 4) reveals that the more recent 20-year interval was characterized by an increase in the average annual temperature by 0.7 °C and an increase in annual precipitation of 47 mm (≈4%). The most pronounced warming occurred in January (+1.7 °C), June (+1.0 °C), July (+1.7 °C), and August (+1.6 °C) while temperature variation during the spring and autumn months was less marked. An increase in monthly precipitation, except for June and August, was recorded throughout the year, with the most substantial increases observed in September (+27

mm), October (+21 mm), and January (+11 mm). Differences between the time series for the two selected 20-year periods were analysed and compared using the χ^2 test. At the 5% significance level (p=0.05), the χ^2 tests indicated the presence of heterogeneity in the time series of average annual air temperature and precipitation between the two periods in the species' habitat nodes. Consequently, over a 50-year period, the climate within the species' habitat has changed in accordance with regional trends (Didukh and Chorney, 2016; Wilson *et al.*, 2021; Kyyak *et al.*, 2022), with winters becoming milder and wetter, and summers warmer and less rainy.

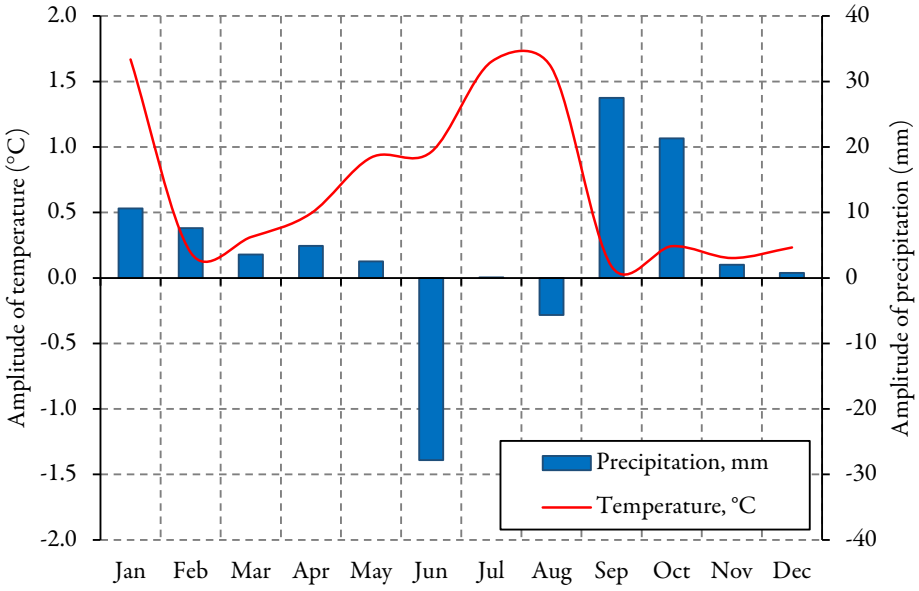

Figure 4. Amplitude in average monthly temperatures and precipitation between the periods 1961-1980 and 1991-2010 in habitats of the *S. josikaea*

Changes in climatic conditions are evidenced by the number of nodes in the regular CarpatClim grid corresponding to specific climate types, when comparing the periods 1961-1980 and 1991-2010 (Table 3). Of the 338 nodes analysed, only 159 (representing 47% of the total area) exhibited a shift in climate from colder to warmer types over the past half-century. The increase in heat stress and transpiration during summer poses a serious threat to the survival of *S. josikaea*, a species that favours well-moistened habitats within peculiar mountain willow and alder communities. This climatic shift may lead to a decline in both the number of populations and the extent of the species' habitat in the future.

Table 3. The number of CarpatClim grids with the corresponding Köppen-Geiger climate type in comparison of the periods 1961-1980 and 1991-2010

Köppen-Geiger climate types	Number of grids by periods		Change in climate types between periods	Average values for the period 1961–2010
	1961–1980	1991–2010		
Cfa	0	3	Cfb → Cfa = 3	0
Cfb	21	161	Dfb → Cfb = 143	102
Dfb	274	139	Dfc → Dfb = 8	199
Dfc	37	34	ET → Dfc = 5	34
ET	6	1	→ ET = 0	3
Total	338	338	159	338

Conclusions

The results of the research show that the total number of *S. josikaea* localities in the territory of the Ukrainian Carpathians is 18 of which six have been confirmed for more than 50 years: (8 Zk. – Tyshiv, 9 Zk. – Yalove, 14 Zk. – Yabluniv 1-2, 15 Zk. – Zanka 18 Lv. – Klymets'-Karlsdorf).

The ecological niche of the species in the Ukrainian Carpathians comprises areas with a temperate continental climate (Köppen-Geiger climate type – Dfb) characterised by an average annual temperature of 6.2 °C and humid conditions with a positive water balance and an even distribution of precipitation and water supply throughout the year. These areas receive at least 1000–1100 mm (on average, 1067 mm) of precipitation annually. Analysing the trend of changes in climatic indicators, especially temperature, the amount and distribution of precipitation, indicates that *S. josikaea* habitats are stenotopic. In addition to intense anthropogenic pressure, potential future threats to the species' habitat may include heat stress, increased evaporation and transpiration, particularly during the spring and summer months. Although the recent period has witnessed an increase of 47 mm (≈4%) in average annual precipitation, its seasonal distribution has become variable. Notably, the species' habitat has experienced an average increase of +1.4 °C in mean monthly temperatures during June-August. Climatic aridification, prolonged summer droughts, soil dehydration, and increased dryness during the growing season negatively affect the biological productivity and reproductive capacity of hygrophilous phytocoenoses, including *S. josikaea*. If current global warming trends continue, a reduction in the species' habitat can be predicted.

The species' habitats are situated in deeply incised valleys, characterized by distinctive meso- and microclimatic features resulting from latitudinal norms. The exposure and morphological features of the terrain influence local temperature, moisture regimes, and precipitation distribution. While the interpolation grid of CarpatClim adequately reflects spatial properties and changes in climatic variables, a more comprehensive understanding requires an integrated methodology. This should combine numerical modelling with targeted surveys of specific species' habitats using instrumental measurements.

Authors' Contributions

Conceptualization: E.K., I.H.; methodology: E.K., I.H., M.H.; investigation: E.K., I.H., I.K.; data curation: I.H., I.K.; visualization: I.H., I.K., writing - original draft: E.K., I.H.; writing - review and editing: E.K., M.H., supervision: E.K., M.H. All authors read and approved the final manuscript.

Ethical approval

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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