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Biodiversity of high-mountain woody plants in the East Carpathians in Ukraine

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Abstract: The highest parts of the European mountain massifs are covered by subalpine and alpine vegetation, with rich flora containing many relic woody plants adapted to cold temperatures and relatively short vegetation periods. In the Ukrainian Carpathians, only several highest mountain massifs form environmental conditions suitable for high mountain plants. The aim of the study was the detection of the centre of biodiversity of the high mountain plants in the East Carpathians in Ukraine. We expected the largest number of high mountain woody species in the Ukrainian East Carpathians would occur in the Chornohora, the largest and most elevated mountain chain in the country. To solve this problem, the geographic distribution of 16 woody species was analysed cartographically. We gathered georeferenced data of 919 localities of taxa, which occur in the subalpine and alpine vegetation belts, and prepared maps of their distribution using QGIS software. Additionally, we analysed vertical distribution and occurrence on different expositions of every taxon. Most of analysed subalpine and alpine species occur in the highest and the largest mountain massifs. The high mountain woody species occur in the Ukrainian parts of the East Carpathians mainly in the largest mountain massifs, the Chornohora, Svydovets, Chyvchyny, Marmarosh, and to a lesser extent, also in the Gorgany. The vertical distribution and predominant occurrence on the northern or close to northern expositions of most subalpine and alpine species indicate their demands for the relatively high level of humidity of the soil and high level of precipitation. These condition point to the relic character of most of analysed species, which origin from the glacial periods of the Pleistocene. Most of the taxa, which have centres of their distribution in the alpine and sub-alpine vegetation belts of the East Carpathians in the Ukraine territory are valuable but threatened elements of the Ukrainian flora.

Keywords: arctic-alpine plants, alpine plants, subalpine plants, East Carpathians, phytogeography

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Introduction

Mountains in general have very rich vascular floras due to flora history and large site heterogeneity. The highest parts of the majority of European mountain massifs cover subalpine and alpine vegetation. However, in these mountains except for the Alps, the subalpine and alpine belts are not very widespread and frequently formed only on the most elevated peaks. The expected altitudinal shift of the mountain vegetation to 2080 can strongly diminish areas with climatic conditions suitable for high mountain plants and reduce their geographic ranges (Körner, 2003). The heterogeneity of the climatic conditions in the mountains resulting from the microsite variation could mitigate plant extinction to some degree (Opedal et al., 2014; Rixen & Wipf, 2017). Nevertheless, many lower massifs would lose their subalpine plants with high probability.

In the high mountains, except common species found at different altitudes, occur the plants specific to the subalpine and alpine vegetation belts, adapted to the cold climate, high precipitation, short vegetation period, and relatively high UV radiation (Körner, 2003; Franzén & Molander, 2012). The latter plants compose two groups, the species that developed directly in the mountains and the species that developed in the arctic tundra (Hultén, 1937) and inhabited mountains during the glacial periods of the Pleistocene (Ozenda & Borrel, 2003). Several species of the subalpine and alpine plants of mountain origin have local, endemic distribution, and are the most valuable elements of the floras (Mráz & Ronikier, 2016; Gómez et al., 2020; Mirek, 2020). The arctic-alpine species reach the southern limits of their distribution in the mountains of Central Europe, are rare, and have a relic character from the glacial periods, constituting a valuable and specific element (Birks, 2008; Raduła et al., 2021). Both these groups of taxa deserve special attention and conservation efforts, especially in their southernmost localities (Ronikier, 2011; Niskanen et al., 2019).

The highest parts of the mountains conserve the most valuable elements of the floras (Ozenda & Borrel, 2003; Sulejman, 2011; Gómez et al., 2020; Mirek et al., 2020; Sciandrello et al., 2020), which developed during the Pleistocene history of plant cover (Pawłowski, 1937a, b; Kotov & Chopyk, 1976; Birks, 2008). At the same time, the subalpine and alpine vegetation belts in the mountains of Central Europe are considered to be endangered by climate changes (Gottfried et al., 2012; Pauli et al., 2012; Rixen & Wipf, 2017; Kobiv, 2018).

The subalpine and alpine vegetation belts in the Ukrainian part of the East Carpathians spread over a relatively restricted area. This mountain complex contains several dozens of massifs and mountain chains with developed high mountain plant cover only at their most elevated peaks (e.g. Zapałowicz, 1889; Coldea, 1991; Malynovski & Kricsfalushy, 2000, 2002; Malynovski et al., 2002; Nesteruk, 2003). In the Ukrainian East Carpathians, the cold-adapted subalpine and alpine plants appeared vulnerable to climate change with a tendency to reduce their habitats (Kobiv, 2018), and a number of them are threatened (Didukh, 2009).

The occurrence of most subalpine and alpine plants in the Carpathians is concentrated mainly in the Tatras, Făgăraş, and Retezat with relatively lower numbers of these species in other massifs (Mirek, 2020). The detailed analysis of geographic distribution and environmental conditions of *Empetrum hermaphroditum* Hagerup (Boratyński & Didukh, 2000), *Kalmia procumbens* (L.) Gift, Kron & P.F.Stevens ex Galasso, Banfi & F.Conti (Boratyński & Didukh, 2002), *Rhododendron myrtifolium* Schott & Kotschy (Boratyński et al., 2006) and *Pinus mugo* Turra (Tsaryk et al., 2006) in the East Carpathians revealed presence localities of these species close to the tops of the most elevated peaks and preferences of the northern slopes. The particular data concerning rare and threatened taxa in Ukraine were presented in the Ukrainian Red Data Book (Didukh, 2009) and described by Cherepanyn (2017). Considering the deficiency of such data, the documentation of subalpine and alpine plant species and analysis of their site conditions deserve the utmost attention. The aim of our study was an analysis of the occurrence of 16 taxa of woody plants, which have centres of their occurrence in the alpine and subalpine vegetation belts. We expected the distribution of the high mountain plants in Ukraine would be restricted to the most elevated and the most massive and compact mountain ridges. Additionally, we assumed that most of the subalpine and alpine taxa would be occurring mainly on the north and north-eastern exposed slopes of the mountains, as observed in *Pinus mugo* (Tsaryk et al., 2006), *Rhododendron myrtifolium* (Boratyński et al., 2006) and species of the genus *Empetrum* (Boratyński et al., 2000).

Materials and methods

Study area

The Carpathians are an eastern extension of the Alps and, although half lower, they have many similarities in geomorphology, soil cover, flora, and vegetation (Nagy et al., 2003). Due to geology and geomorphology, the Carpathians are divided into the West, East, and South Carpathians, the Apușeni (Western Mountains), and the Transylvanian plateau (Kondracki, 1989, 1998). The East Carpathians form the north-easternmost part of the main arc of the Carpathians and its northern part lies on the Ukrainian territory (Fig. 1). It is the narrowest part of the Carpathians, with a spread ranging from 50 to 100 km and a length of about 280 km. The total area is about 2,400 km^2 (Holubets et al., 1988). The mountain chains stretched from northwest to southeast. The relief of the mountains is asymmetric. The northeastern slopes of the ridges are steeper than the southwestern due to the specific geological structure and the influence of Pleistocene glaciations (Romer, 1909; Matoshko, 2004; Kłapyta et al., 2021). On the northern slopes are presented glacial cirques with steep walls and outcrops of rocks, while the southern slopes have not been affected by glaciers and are more gentle (Kłapyta et al., 2021).

The Ukrainian Carpathians are typical medium-high mountains with predominantly domed peaks, often connected into long ridges or massifs cut by deep river valleys. Only in the southeastern part of the Ukrainian Carpathians did the absolute heights increase, reaching 2061 m above sea level on Hoverla Mt., the highest peak of Ukraine. This smoothness of the terrain is due to the easy weathering of flysch deposits, which is the predominant underlying rock in the mountains (Földvary, 1988). The south-eastern part of the Carpathians on the Ukrainian territory contains several massifs, such as Gorgany, Chornohora, Svydovets, Marmarosh, and Chyvchyny, built of hard sandstones, crystalline, and metamorphic rocks, and consequently, their relief acquired more severe forms. Here the peaks are often in the form of impregnable rocks, with basal parts covered with talus. Traces of Pleistocene glaciers (glacial cirques, moraines, small lakes) are also well visible here (Rehman, 1895; Romer, 1909; Malynovski, 1980; Holubets et al., 1988).

The Carpathians harbour rich flora containing about 3900 taxa, which is 1/3 of the total European flora (Tasenkevich, 1998). The plant cover of the Carpathians presents a vertical zonation typical for the mountains of Central Europe, with eminent upper forest line forming the bottom border of subalpine vegetation. The lower border of the subalpine zone rises from about 1250 m in the north-west (East Bieszczady, Skole Beskydy, Rivna, Krasna, Borzhava) to 1500–1600 m in the south-east (Chornohora, Marmarosh, Chyvchyny) (e.g. Zapałowicz, 1889; Środoń, 1948; Malynovski, 1980; Nesteruk, 2003). However, in the Carpathians, the upper limit of the forest and dwarf shrubs belt was limited by human activities in several mountain massifs (Zapałowicz, 1889; Vincenz, 1936; Tasenkevich, 2009). The

Fig. 1. The East Carpathians of Ukraine in the Carpathian arc

current anthropogenic upper forest line passes frequently at elevations of about 1200–1300 m, and in areas with intensive pastoral pressure, dropped even to 1000 m (Zapałowicz, 1889; Środoń, 1948; Kolischuk, 1959; Malynovski, 1980).

Species and data on their distribution

The 16 woody species were selected for the particular analyses (Table 1) from the total number of 29 subalpine taxa of trees and shrubs. All of them have their Ukrainian centre of occurrence in the Carpathians in the subalpine and alpine vegetation belts or at least most of their localities lying in the subalpine vegetation layer. Five species represented Arctic-Alpine (after Zając, 1996; Zając & Zając, 2009), nine the Central-European, and two Euro-Asiatic floristic elements (Table 1).

Data on the species' localities were extracted from literature, herbaria, Global Biodiversity Information Facility (GBIF) database, and authors' field notes. Only natural localities were analyzed. The geographic coordinates and exposure of localities were determined using Google Earth, when not reported in the original data. We gathered more than 1600 data however, a great number of them replicated the same information from different sources, some were very general and others could not be identified geographically. The selection of data for sufficiently detailed geographic coordinates reduced the number of records to 919.

The data on the orographic factors, altitude, and aspect came from the localities description sources and the authors' field observations. The exposure was determined using the main and intermediate geographic directions. The geographic distribution of every taxon was analysed cartographically and presented on the map using QGIS 3.16 (QGIS Development Team, 2020). Altitudinal range, the aspects, and inclination of localities were analysed and presented on the graphs, according to the data accessed.

Results

Species characteristics

Alnus alnobetula, occurs in the temperate and sub-arctic parts of the northern hemisphere, in subsp. *alnobetula* in the mountains of Central Europe (Chery, 2015; POWO, 2022). The Carpathian part of its range does not cover the Western Carpathians, and the western limit of its distribution is considered a phytogeographical boundary between the West and East Carpathians (Wołoszczak, 1896; Zarzycki, 1964; Jasiewicz, 1965; Browicz & Kaczmarek, 1972; Pawłowski, 1972). In Ukraine, the largest populations of green alder, covering hundreds of hectares are concentrated in the subalpine vegetation belt of the Chornohora, Marmarosh, Chyvchyny, and Gorgany mountains, mainly on the northern slopes. To the West of Svydovets, areas occupied by *A. alnobetula* become narrower, with populations known in the Borzhava, Krasna, Polonyna Rivna, Pikuy, Skole Beskydy, and Bieszczady (Fig. 2a). Such pattern of distribution

Table 1. Studied species of woody mountain plants of the East Carpathians in Ukraine; names after Plants of the World (POWO, 2022), except *Vaccinium gaultherioides*

Species	General range	Occurrence in vegetation belt of Carpathians	Analysed localities number
Alnus alnobetula (Ehrh.) K.Koch subsp. *alnobetula* (=*Alnus viridis* (Chaix) DC.)	CEUR	Sub-Alpine-(Montane)	141
Clematis alpina (L.) Mill.	CEUR	Sub-Alpine-(Montane)	59
Dryas octopetala L.	ARALP	Alpine	9
Juniperus communis L. var. *saxatilis* Pall. (=*Juniperus communis* subsp. *alpina* (Sm.) Čelak., *J. commnis* subsp. *nana* (Baumg.) Syme)	ARALP	Sub-Alpine – (Alpine)	149
Lonicera caerulea L.	EUROS	Sub-Alpine	2
Pinus cembra L.	CEUR	Sub-Alpine – Montane	157
Prunus padus var. *borealis* A.Blytt (=*Padus petraea* Tausch; *Prunus padus* L. subsp. *petraea* (Tausch) Domin)	CEUR	Sub-Alpine – Montane	1
Ribes petraeum Wulfen	EUROS	Sub-Alpine – (Montane)	36
Salix alpina Scop. (=*S. jacquini* Host)	CEUR	Alpine	2
Salix bicolor Ehrh. ex Willd.	CEUR	Sub-Alpine	23
Salix hastata L.	ARALP	Sub-Alpine	17
Salix herbacea L.	ARALP	Sub-Alpine – Alpine	39
Salix kitaibeliana Willd.	CEUR, CARP	Sub-Alpine – Alpine	19
Salix retusa L.	CEUR	Sub-Alpine – Alpine	15
Salix silesiaca Willd.	CEUR	Sub-Alpine – Montane	102
Vaccinium gaultherioides Bigelow	ARALP	Sub-Alpine – Alpine	148

ARALP – Arctic-Alpine; CARP – Carpathians; CEUR – Central European mountains; EUROS – Euro-Sibirian.

could partly result from the strong reduction of the *A. alnobetula* thickets (named 'kryvolisya'), practiced since the time of Wallachian expansion during 14–16 centuries and later, to expand subalpine pasture areas (Zarzycki, 1964; Tasenkevich, 2009; Kłapyta, 2014). Currently, *A. alnobetula* enters the alpine zone to an altitude of 1900 m in Chornohora (Nesteruk, 2003) and goes down to 700 m in the Skole Beskydy (Slobodyan, 1966) and Uzhansky National Park in the East Bieszczady Mts. (Stoyko et al., 2007). It

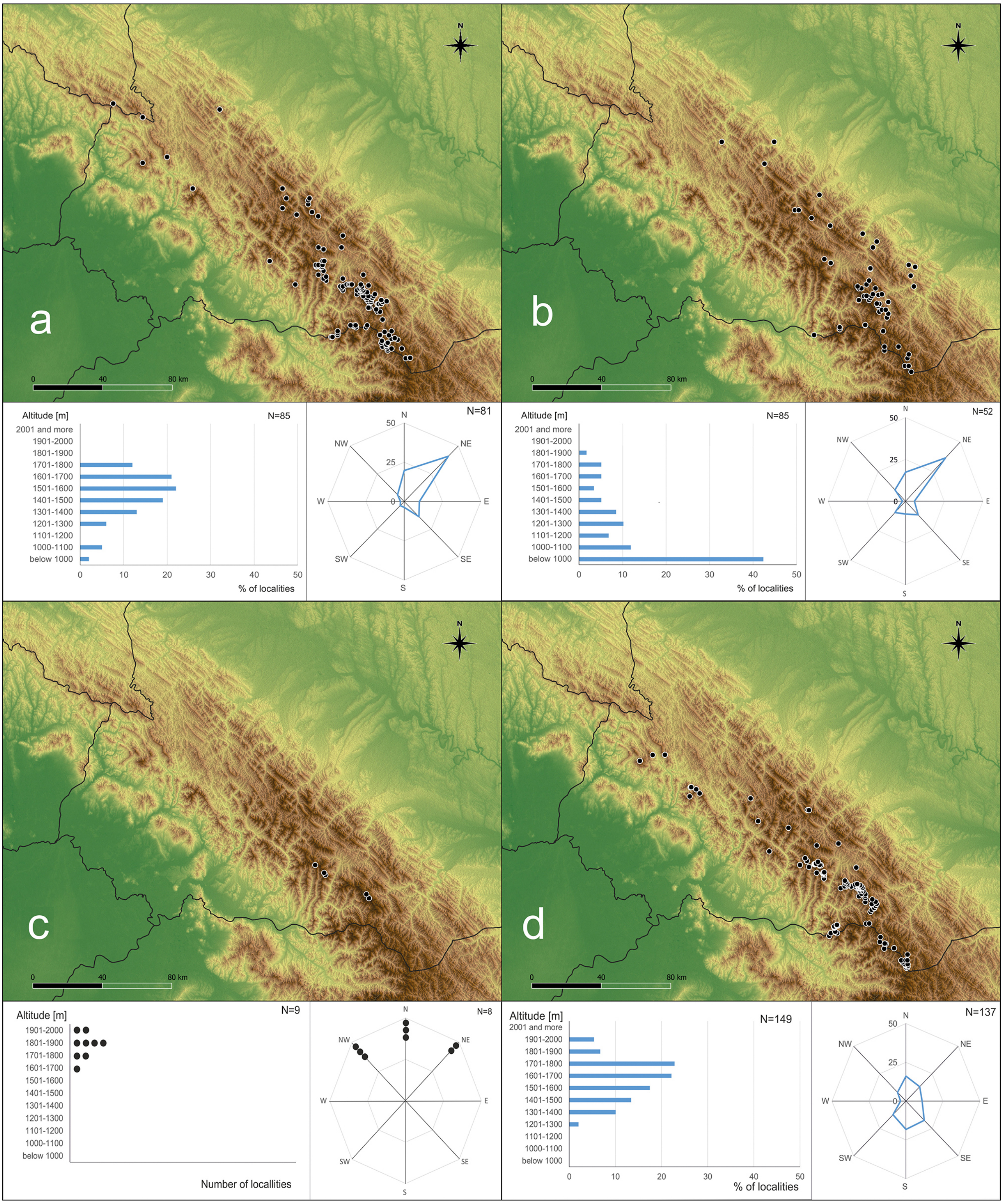

Fig. 2. Geographic distribution, altitudinal range and exposition of localities of (a) *Alnus alnobetula*, (b) *Clematis alpina*, (c) *Dryas octopetala*, (d) *Juniperus communis* var. *saxatilis*

grows on moist, shady, steep and frequently rocky slopes, in wet and relatively cold valleys, avalanche gorges, and along streams. In the subalpine vegetation belt, it sometimes overgrows the polonynas (subalpine meadows) after pasture ceased, at lowest locations also abandoned hay-meadows. In the eastern part of the Carpathians in Ukraine, the green alder forms large massifs of dense, crooked thickets, in some places competing with *Pinus mugo*. It is often possible to observe the division of ecological niches of these two species based on soil moisture (alder is more moisture-loving) and exposure (alder is associated with northern exposures). It is one of the diagnostic species of endemic to the East Carpathians association *Pulmonario-Alnetum viridis* Pawłowski et Walas 1949, widespread in the Krasna, Svydovets, Chornohora, Chyvchyny, Hrynyava, and Marmarosh massifs, at altitudes 1370–1750 m on the north-facing steep slopes, and the walls of glacial cirques and less frequently on the southern slopes. Under anthropogenic pressure (grazing, felling, burning), these phytocoenoses are transformed into dense turf grasslands (Malynovski, 1980; Winnicki, 2017). Another endemic for the East and South Carpathians association is *Alnetum viridis austro-carpaticum* Borza 1959. It was renamed to *Salici-Alnetum viridis* Čolić et al. 1962 and is treated as a South Carpathian variant of the association *Alnetum viridis* Berger 1922, the latter widespread in the Alps (Coldea et al., 1997; Mucina et al., 2016). This shrubby association is widespread in all high-mountainous regions of the Ukrainian Carpathians, descending in the valleys to elevations of 1150–1200 m on the southern, sometimes also on the northern slopes.

Clematis alpina is a woody deciduous vine with attractive flowers. Due to the broad geographic range covering sub-Arctic and mountain areas from Europe to the West to East Asia, it is divided into three subspecies (Yang et al., 2009). In the mountains of Central Europe, the Alps, Carpathians, and mountains of the Balkan Peninsula (Browicz & Gostyńska-Jakuszewska, 1966), occurs *C. alpina* subsp. *alpina*. In the Carpathians within Ukrainian territory, the species was observed mainly in the Chornohora, Svydovets, and Chyvchyny (Fig. 2b), with many localities below the upper forest line. The lowest places were found at about 350 m on the Tisa river valley, and the most elevated at 1895 m on Shpytsi in the Chornohora (Zapałowicz, 1889). Apart from a large number of localities in the montane vegetation zone, *C. alpina* frequently occurs at altitudes between 1200 and 1600 m, preferring north and north-eastern expositions. It grows most frequently on fresh, rich, and nutritious soils developed from the calcareous or neutral bedrock. It has overgrown the subalpine thickets of *Alnus alnobetula*, the thickets on the stream banks, and also forest edges.

Dryas octopetala is a glacial relict represented by great amounts of pollen in the fossil floras of the late Pleistocene, Last Glacial, and early Holocene (Noryśkiewicz et al., 2004; Skrede et a., 2006; Bradley, 2014). It is an arctic-alpine species (Zając & Zając, 2009) of base-rich habitats, with a generally wide and disjunctive distribution within the Arctic (Elkington, 1971; Hultén & Fries, 1986). In Central Europe, *D. octopetala* is present in the Pyrenees, Massive Central, Alps, Apennines, and in the mountains of the Balkan Peninsula (Elkington, 1971; Varsamis et al., 2020). In the West Carpathians it is quite frequent in the Tatras and rare in the Pieniny (Pawłowski, 1956; Browicz & Gostyńska-Jakuszewska 1970a; Zając & Zając, 2001). In the East and South Carpathians it occurs in the highest massifs (Buia, 1956; Mirek, 2020). The distribution of *D. octopetala* in the Ukrainian Carpathians is restricted to the most elevated summits as Blyznytsya, Drahobrat, and Zhandarmy in the Svydovets and Pop Ivan and Brebeneska in the Chornohora (Zapałowicz, 1889; Malynovski, 1980; Andrienko & Mosyakin, 2009), mostly at elevations of 1900–2000 m (Fig. 2c). It grows on limestone rocks, on stony soil, predominantly on the northern slopes. It is a diagnostic species for the Class *Carici rupestris-Kobresietea bellardii* Ohba 1974. The association *Dryadetum* described from the Svydovets (Domin, 1930) can be considered as impoverished *Achilleo schurii-Dryadetum* Coldea 1984 (syn. *Salix reticulata-Dryas octopetala* Beldie, 1967) from Ordo *Elynetalia* Oberd. 1957, Alliance *Oxytropido-Elynion* Br.-Bl.1949 (Malynovski & Kricsfalusy, 2002), known from the East and South Carpathians in Romania (Coldea, 1991). These plant communities occupy small areas on the northern, humid slopes at altitudes of 1650–1990 m, protected by a thick layer of snow in winter, on poorly developed, shallow soils. The plant communities are formed by *D. octopetala*, which is an evergreen, prostrate shrub 8–10 cm in height forming dense mats with sparse patches of grasses, sedges, mosses, and lichens (Malynovski, 1980).

Juniperus communis var. *saxatilis* (POWO, 2022), the Arctic and European high mountain juniper, is one of several proposed and disputed names for this taxon (eg. Farjon, 2005; Raab-Straube, 2014; Mirek et al., 2020; Boratyński & Boratyńska, 2021). The unclear taxonomy and complicated nomenclature resulted from the evolutionary history of the common juniper, especially in the southernmost parts of its geographic range (Mao et al., 2010; Adams & Schwarzbach, 2012; Adams, 2014). In Europe, *J. communis* var. *saxatilis* is common in the Pyrenees, the Alps, Carpathians and mountains of the Balkan Peninsula (Browicz et al., 1971; Hultén & Fries, 1986; Gómez et al., 2020; Boratyński & Boratyńska, 2021). In the Ukrainian Carpathians this juniper occurs above the upper forest line, in the subalpine and the lower part of the alpine zone, at altitudes from (1100)

1250 to 2000 m (Fig. 2d). It frequently forms association *Juniperetum nanae* Br.-Bl. et al. 1939 from Alliance *Juniperion nanae* Br.-Bl. in Br.-Bl., Sissingh & Vlieger 1939, for which is a diagnostic species. That plant community covers even broad areas, independently of the slope inclination and exposition, frequently with rock outcrops, shallow, very gravelly, and relatively dry soils (Malynovski & Kricsfalushy, 2002).

Lonicera coerulea is a variable species with several taxa distinguished within them at the subspecies or

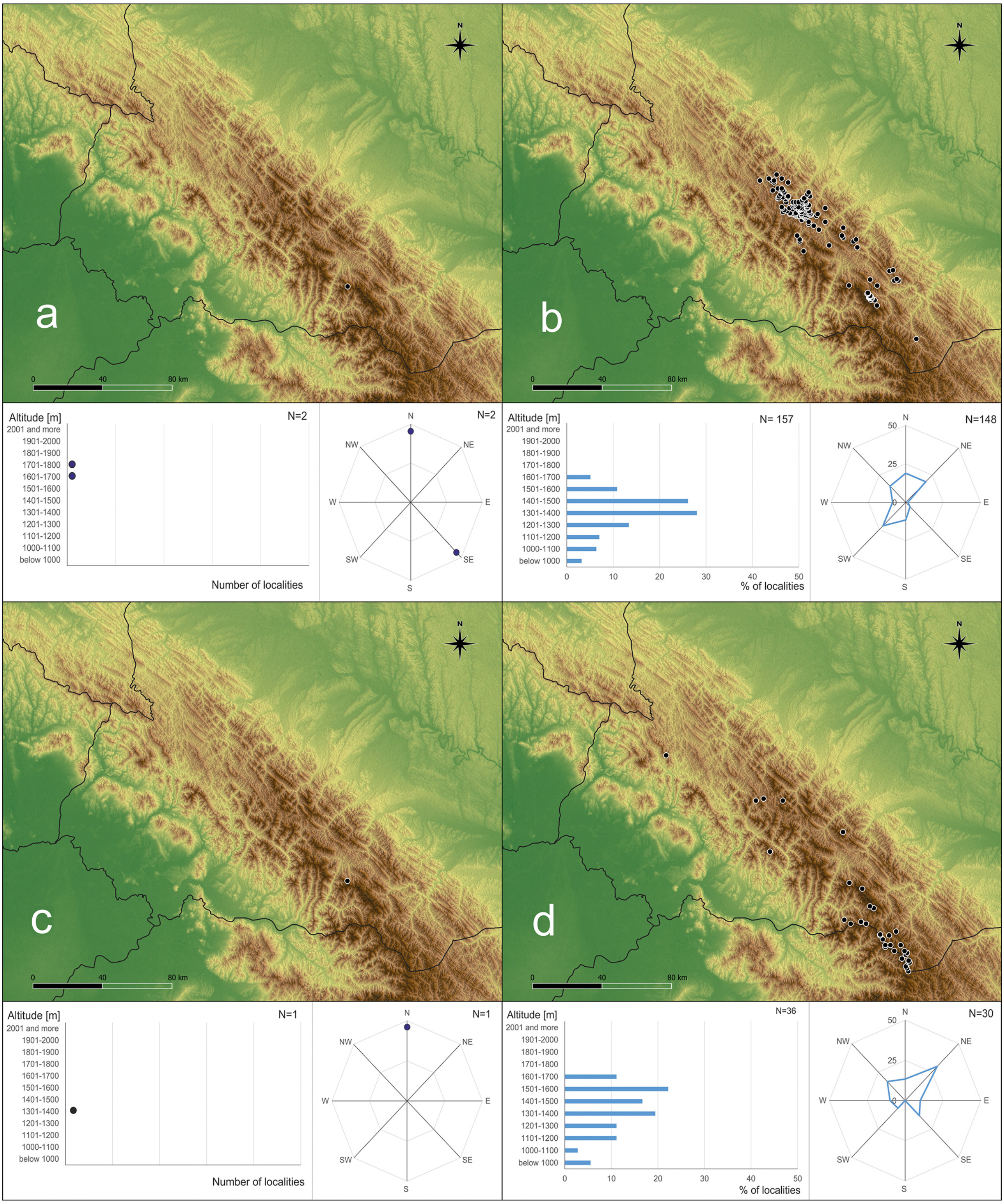

Fig. 3. Geographic distribution, altitudinal range and exposition of localities of (a) *Lonicera caerulea*, (b) *Pinus cembra*, (c) *Prunus padus* var. *borealis*, (d) *Ribes petraeum*

varieties rank widespread in the circumboreal zone (POWO, 2022; USDA, 2022). In Europe occurs a typical subspecies, *L. coerulea* subsp. *coerulea*. In Ukraine it grows in four places close to each other at the summit of the Petros in the Chornohora (Fig. 3a), at an elevation of 1650 to 1750 m (Igoshina, 1955) at the edge of the spruce forest from alliance *Piceion excelsae* Pawłowski et al. 1928 (=*Vaccinio-Piceion*) and in the mountain pine plant community of alliance *Pinion mugo* Pawłowski et al. 1928. It is a Red book species in Ukraine (Melnyk & Batochenko, 2009).

Pinus cembra is a large tree forming specific forests with *Larix decidua* Mill. at the upper forest line. It occurs in the Alps and Carpathians as a relic of the Pleistocene age (Obidowicz et al., 2004; Caudullo & de Rigo, 2016; Farjon, 2017). In the Carpathians, the stone pine grows in the Tatras and in the East and South Carpathians highest massifs (Beldie, 1952a, Jasičová, 1966; Jalas & Suominen, 1973; Browicz & Gostyńska-Jakuszewska, 1974; Zając & Zając, 2001). Information on *P. cembra* occurrence, ecology, and state of protection in the Ukrainian part of the Carpathians was published in many papers (e.g. Rehman, 1873; Hołowkiewicz, 1877; Zapałowicz, 1889; Spausta, 1896; Szafer, 1914; Wierdak, 1927; Hilitzer, 1934; Środoń, 1936; Kontny, 1938; Smaglyuk, 1969; Stoyko et al., 1999, 2004; Klimuk, 2006). Localities of the species are dispersed and form a strip on the north-eastern macro-slope of the Carpathian arc, mainly on the upper parts of the river basins of Svicha, Limnytsia, Bystrytsia Solotvynska, Bystrytsia Nadvirnyanska, Brusturyanka, and Prut, at altitudes of 900 – 1700 m, with a minimum at 830 on Grofecki Koń in the Gorgany, and maximum at 1700 m on Petros and Kedrovaty-Pohorilets in the Chornohora (Fig. 3b). The vast majority of localities are concentrated in Gorgany (4159.9 ha), on the slopes of Syvulya, Popadya, Artytsia, Matahiv, Gorgan, Yavirnyk, Chomyak, Strymba, Kedryn, Yayko, Verkhniy Pasichny, etc. (Środoń, 1936; Chopyk, 1976; Stoyko et al., 1999). The species was well conserved in the Gorgany due to site conditions limiting competition from *Picea abies* (L.) H.Karst and as a result of protection by owners, the State Forests and Greek-Catholic Metropolis, which established large nature reserves in 1919 and 1935, respectively (Środoń, 1936; Kontny, 1938). In the Chornohora, the species spread over an area of 34.7 hectares on the Petros, Gadzhyna, Kizi-Ulohy, Kedrovaty-Pohorilets, and Dzembronya, mainly in form of small groups of trees or single specimens, which historically results from overexploitation (e.g. Vincenz, 1936). *Pinus cembra* grows on the steep slopes of various exposures, frequently covered with boulders, on the poor, acid, fresh, and sometimes wet soils in the upper forest belt and among the thickets of *Pinus mugo* (Środoń, 1936; Didukh et al., 2000). It is an indicator of Alliance *Piceion excelsae* Pawłowski et al. 1928, when the role of spruce is weakened due to site conditions, as in the Gorgany, or upper forest line zone. To preserve this species, several isolated populations were conserved in nature protection sites of different statuses, the strict nature reserve (zapovidnyk) *Gorgany* established in 1919 (Środoń, 1936), Carpathian National Park and state reserves Grofa, Tavpishyrsky, Yaykivsky, Bradulsky, Kedryn, and Chorny Dil. In the Red Book of Ukraine it is considered in IUCN category VU (Tasenkevich et al., 2009).

Prunus padus var. *borealis* (*Padus petraea*) is known only from Petros in the Chornohora, from one locality at an altitude of 1400 m, in the subalpine vegetation belt (Fig. 3c), where it was collected by J. Mądalski in 1936: 'na N stoku Pietrosa w Czarnoh.', zielnik Instytutu Botaniki im. W. Szafera PAN w Krakowie (KRAM_M).

Ribes petraeum is a Central-European, mountain species known from the Pyrenees on the West to the Carpathians on the East and to the mountains of the Balkan and Apennine Peninsulas on the South, with single localities in the mountains of North Africa (Jalas et al., 1999; Boratyński & Browicz, 1976a). In the Carpathians, it occurs mainly in the most elevated massifs (Mirek, 2020). In the East Carpathians in Ukraine, *R. petraeum* represents the subalpine floristic element, with localities in the montane vegetation belt. The species is relatively frequent in the Chyvchyny, Marmarosh, and Chornohora, and is known from several localities dispersed in the other mountain chains. It grows at altitudes between 1300 and 1600 m (Fig. 3d), but sporadically goes down to 900 m along the Chorny Cheremosh river in the Chyvchyny. The most elevated localities were detected at 1695 m on Polonyna Vertopy in the Chornohora (Zapałowicz, 1889). It grows in the thickets of *Alnus alnobetula* and enters the *Picea abies* forests, especially along the stream valleys (Pawłowski & Walas, 1949).

Salix alpina is a small, creeping shrub with densely branched twigs clinging to the ground or rocks and a few long and thin shoots. It grows in the Alps and Carpathians (Jalas & Suominen, 1976), in the latter, in the Tatras, Svydovets, Rodna, Bucegy, and Făgărăş (Beldie, 1952b; Browicz & Gostyńska-Jakuszewska, 1970b; Mirek, 2020). In the Ukrainian East Carpathians it is represented by a single isolated population (Fig. 4a), occupying a restricted area with a small number of individuals in the alpine belt of the Svydovets massif (Blyznytsya, 1880 m), participating in association *Salicetum herbaceae* Br.-Bl. 1931. This is one of the rarest species of the Ukrainian Carpathians' flora, listed in the Red book of Ukraine in IUCN category EN. Its' occurrence is limited by specific ecological demands, the narrow local ecological-phytocoenotic amplitude, and threatened due to the influence of recreation (Danylyk, 2009a).

Salix bicolor is an European, mountain species occurring from the Pyrenees in the West to the Carpathians in the East (Jalas et al., 1999). In the Carpathians its localities are dispersed in the most elevated massifs (Mirek, 2020), most frequently in the subalpine vegetation (Zieliński, 1976a). In the Carpathians of Ukraine, it occurs in the Chornohora and in the single localities in the Chyvchyny, Borzhava, and Gorgany, within the subalpine, but enters also the alpine vegetation belt. It grows mainly in wet

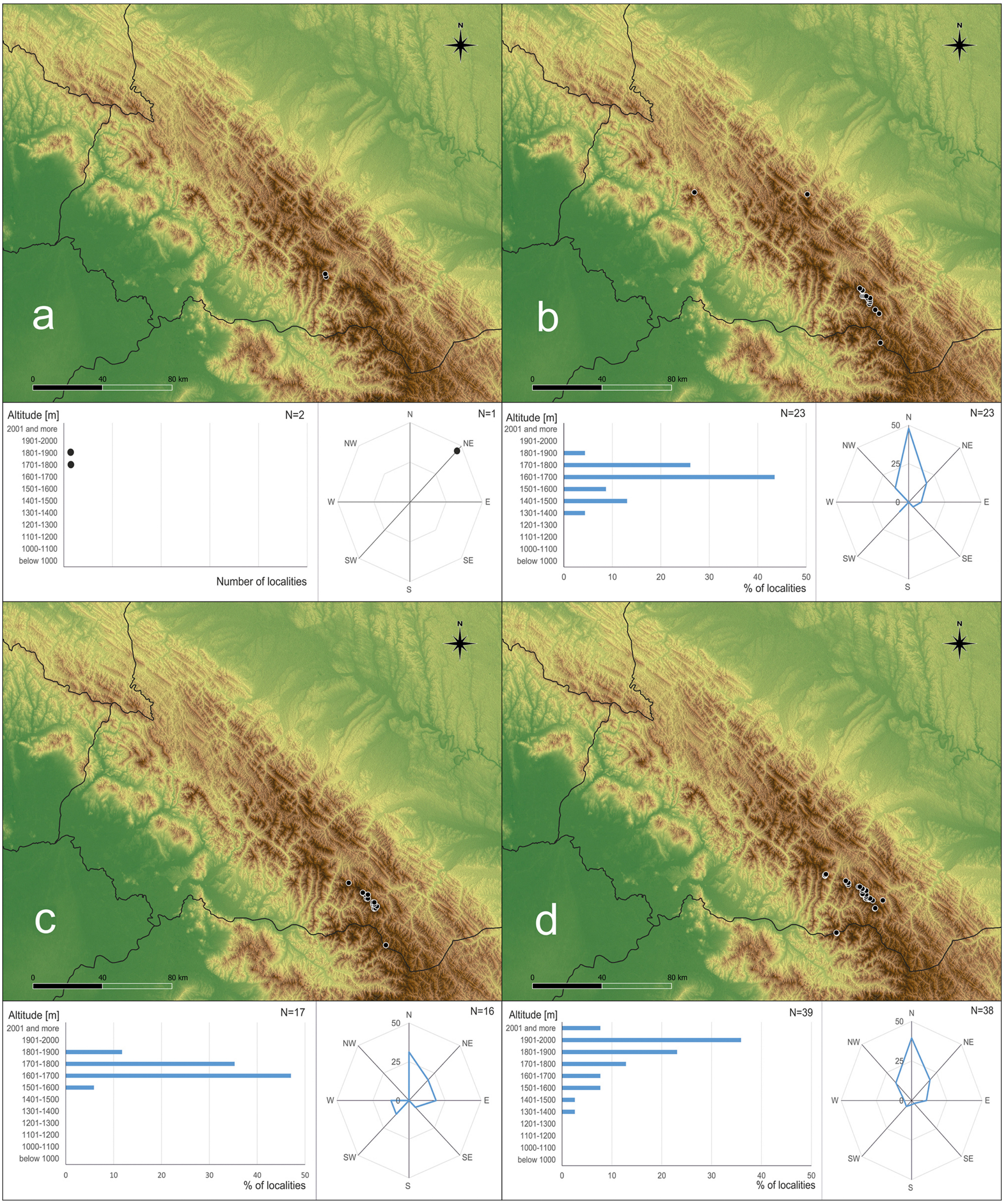

Fig. 4. Geographic distribution, altitudinal range and exposition of localities of (a) *Salix alpina*, (b) *Salix bicolor*, (c) *Salix hastata*, (d) *Salix herbacea*

conditions, on the North slopes (Fig. 4b). Its lowest localities were detected at about 1350 m on Velyky Verh in Borzhava and 1450 m on Mala in the Gorgany, the most elevated at about 1980–2000 m in Kizie Ulohy and Munchel in the Chornohora (Zapałowicz, 1889).

Salix hastata has a broad geographic range covering the Arctic and subarctic regions and high mountains of the northern hemisphere (Hultén & Fries, 1986). In Europe out of Scandinavia, it occurs mainly in the Pyrenees, Alps, and Carpathians (Jalas et al., 1999). In Ukraine, *S. hastata* occurs in the Chornohora, with only one locality in the Chyvchyny (Fig. 4c). It grows mostly on the northern, eastern, and intermediate between N and E slopes, with the altitudinal minimum at 1545 m on Skorushny in the Chornohora and 1610 m on the slopes of Chyvchyn, and maximum at 1850 m on the Kizie Ulohy in the Chornohora (Zapałowicz, 1889). The species occurrence is connected with slightly inclined sloped and humid places among *Pinus mugo* thickets, where it grows in single individuals.

Salix herbacea is a prostrate, dwarf shrub with creeping, branched underground stems and aerial twigs up to 5 cm, with 2–5 leaves. Geographically, it belongs to Hultén's Amphi-Atlantic category with wide arctic-alpine distribution in Eurasia and North America (Hultén & Fries, 1986; Alsos et al., 2009; Zając & Zając, 2009). In Europe, it occurs in the Arctic zone and further south in the high mountains from the Pyrenees on the West to the Carpathians on the East (Beerling, 1998; Jalas & Suominen, 1976). In the Carpathians *S. herbacea* is a glacial relict, forming fragmented populations isolated from each other mainly on non-calcareous bedrock in the Tatras, Chornohora, Rodna, Bucegi, Făgăraș, Parâng, Retezat and Țarcu-Godeanu mountains (Beldie, 1952b; Boratyński & Browicz 1976b; Mirek, 2020). In the Ukrainian Carpathians, it is known from the subalpine and alpine vegetation belts, from the altitudes between 1750 and 2000 m (Fig. 4c), with the lowest localities at about 1500 m on Pozhyzhevska and most elevated at 2020 m on Petros in Chornohora (Malynovski & Kricsfalushy, 2002; Cherepanyn, 2017). It grows mainly in depressions on summits and northern slopes, on the rocks, turfed rocky areas, screes, and sites with sufficient snow protection, most often in chyonophilic plant communities of snow-beds (association *Salicetum herbaceae* from Class *Salicetea herbaceae* Br.-Bl. 1948). Two small populations of *S. herbacea* confined to snowbeds are located at elevations of 1855 and 1925 m on the north and north-western slopes of Pop Ivan Marmarosky (Deyl, 1940; Cherepanyn, 2017; Kobiv et al., 2017). *Salix herbacea* forms there dense mats, and its patches cover small areas of 15 and 4 m^2 respectively. A detailed investigation in the herbaria and in the field allowed the discovery, that the previously published data probably concerned one small population located on the cliff along a rocky tourist path between the peaks of Pop Ivan and Mt. Rapa (1872 m) (Hleb et al., 2020). The next isolated population of *S. herbacea* locality lies on the Blyznytsya in Svydovets massif, where it occupies an area of about 300 m^2 in the snow-bed, and does not form a continuous cover (Malynovski, 1980). *Salix herbacea* is a poor competitor and requires some degree of regular disturbances, such as exposure, snow cover, solifluction, and avalanche disturbances or grazing, to ensure the development and persistence of an open community (Beerling, 1998; Kobiv et al., 2017). In the Red book of Ukraine it is included as glacial relict species in the category rare (R) (Danylyk, 2009b). All *S. herbacea* sites are located within the Carpathian Biosphere Reserve in the zone of strict protection.

Salix retusa and *S. kitaibeliana* are two closely related taxa with not resolved and still disputed taxonomic position of the latter, treated as a synonym of *S. retusa* (Zieliński, 1976b; Skvortsov, 1999), or as a separate species (Koblížek, 2006; Kosiński et al., 2017, 2019 and literature cited herein). Typical *S. retusa* is a prostrate shrub generally to 10 cm high, forming close tufts in exposed places. It is native to the subalpine and alpine belts of the Pyrenees, Alps, Apennines, Carpathians, Dinarides, and Rila Mts (Jalas et al., 1999; Aeschimann et al., 2004; Gómez et al., 2020). In the Carpathians, *S. retusa* occupies the highest massifs of the West, East, and South Carpathians (Mirek, 2020). In the Ukrainian part of the East Carpathians, it occurs in the Svydovets and Chornohora (Fig. 5a). In the Svydovets only one population is known close to the top of Blyznytsya at an altitude of 1800–1810 m, where it forms a plant association *Salicetum retuso-reticulatae* Br.-Bl. 1926 (together with *S. reticulata* L.), on the turfed scree of the steep (40–45°) slopes of the northern and south-western exposures (Malynovski & Kricsfalusy, 2002; Chopyk & Fedoronchuk, 2015). In the Chornohora, patches of *S. retusa* disjoined populations occur on steep rocky slopes (40–60°), on the ledges of sandstone rocks at altitude of 1750–2000 m of the Petros, Hoverla, Turkul, Rebra, Shpytsi, Gutyn Tomnatyk, Brebeneskul, and Pop Ivan. They cover areas of 10 to 500 m^2, on both, north-eastern and south-western macro-slopes. The species is rare (R) and conserved in the Carpathian Biosphere Reserve and the Carpathian National Park (Danylyk, 2009c).

Salix kitaibeliana was described from the Carpathians by Willdenow in 1806 (IPNI, 2022). It distinguishes from the typical *S. retusa* by more robust growth and two times larger leaves (Pawłowski, 1956; Gostyńska-Jakuszewska, 1992; Koblížek, 2006; Kosiński et al., 2017), despite, these two taxa do not show differences in ploidy level (Kosiński et al., 2019). *Salix kitaibeliana* is endemic to the Carpathians (Gostyńska-Jakuszewska, 1992; Nesteruk, 2003; Koblížek, 2006; Kliment et al., 2016; Mirek, 2020), occurs in the more elevated and more humid places than *S. retusa* (Gostyńska-Jakuszewska, 1992; Koblížek, 2006). The higher demands as concerns the soil humidity could also explain the occurrence of *S. kitaibeliana* on the north-facing slopes in the East Carpathians in Ukraine, while *S. retusa* covers also more xeric and dry southern slopes. In these

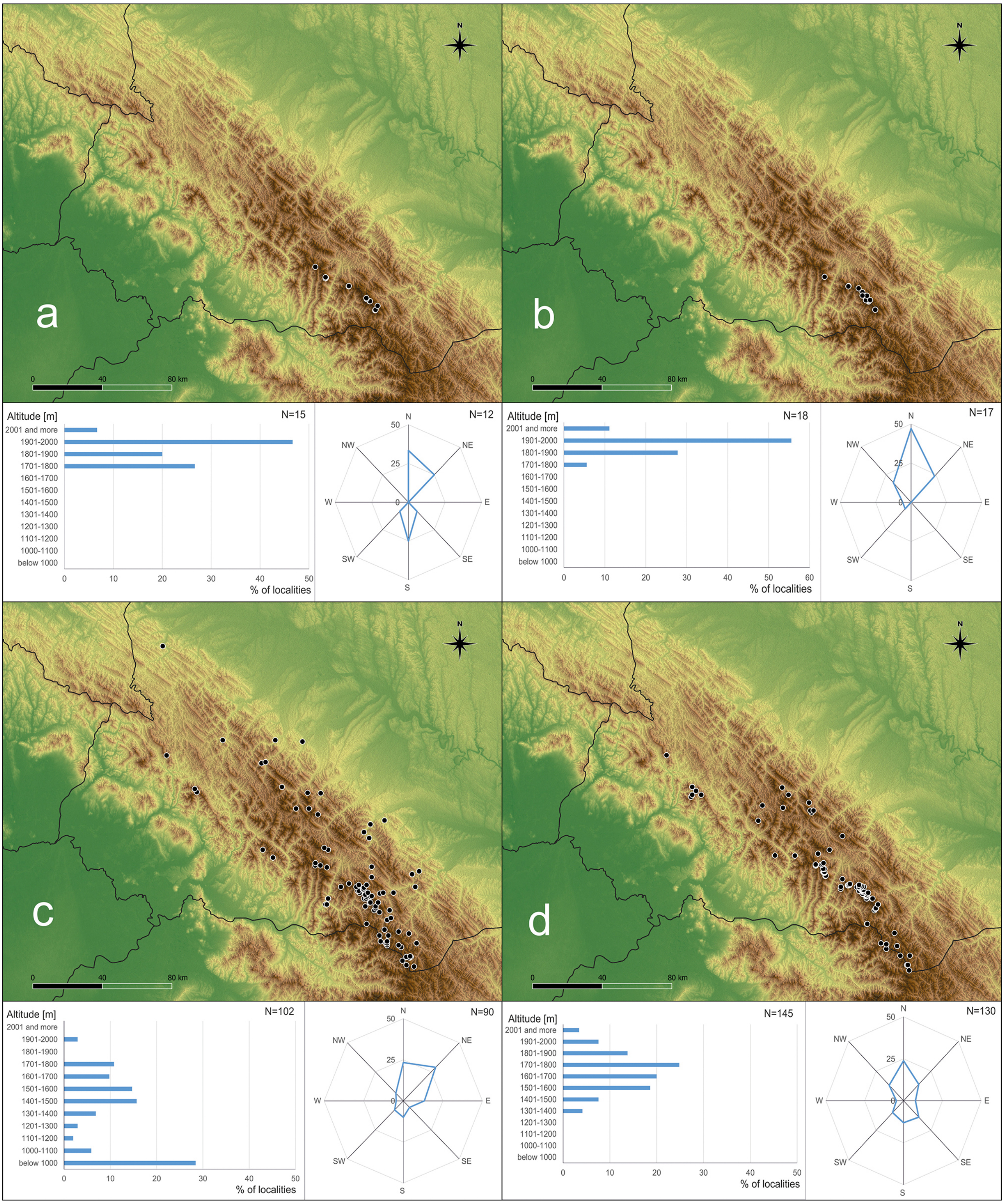

Fig. 5. Geographic distribution, altitudinal range and exposition of localities of (a) *Salix retusa*, (b) *Salix kitaibeliana*, (c) *Salix silesiaca*, (d) *Vaccinium gaultherioides*

mountains it is known only from the Chornohora and Svydovets (Fig. 5b).

Salix silesiaca is a shrub reachinh up to 3 m high, occurring in the Sudetes, Carpathians, and mountains of the Balkan Peninsula (Jalas & Suominen, 1976; Zieliński, 1976c; Rivers, 2017). It is a pioneer species of cold, frequently unstable sites and grows on the banks of streams, on avalanche tracks, in glacial cirques, on slope springs, in the subalpine shrub formations, and sometimes also on roads escarpments. In the Carpathians in Ukraine, it occurs quite frequently in the montane, but the most common in the subalpine vegetation belts, between 1400 and 1800 m (Fig. 5c). However, the lowest localities are in the sub-montane vegetation belt, where the species downs to an elevation of 500 or even less, as in the Tisa river valley (Zapałowicz, 1889). The most elevated localities of *S. silesiaca* attain 2000 m in the Chornohora. Silesian willow is a diagnostic species of the high mountain shrub association *Salici silesiacae-Betuletum carpaticae* Rejmánek et al. 1971 from alliance *Salicion silesiacae* Rejmánek et al. 1971, described from Sudetes (Kočí, 2007). This association has not been identified in the Ukrainian Carpathians, but thickets dominated by *S. silesiaca* are found in all massifs in the upper mountain and subalpine belts, mainly along the stream banks, on rocky places, and mountain tracks.

Vaccinium gaultheroides is one of several taxa forming *V. uliginosum* L. complex (Alsos et al., 2005). It distinguishes from the typical *V. uliginosum* L. by a relatively low high of the shrubs not exceed 15 cm, and small leaves and fruits (Young, 1970; Popova, 1972; Jacquemart, 1996). In contrast, typical *V. uliginosum* is characterized by a height to 80–120 cm and two times larger leaves. However, these differences are only partly genetically conditioned (Alsos et al., 2005). Nevertheless, the form of low shrub with small leaves occurs mainly in the Arctic in the North and in the highest mountains in the South, also in the mountains of Central Europe (Hultén & Fries, 1986). It was lately accepted as a separate species, occurring in the subalpine and alpine zones of the Carpathians (Mosyakin & Fedoronchuk, 1999; Mirek, 2020; Mirek et al., 2020). In Ukraine, it grows quite frequently on the shallow, stony soils developed from acid bedrock, in the entire Carpathian arc, from the East Bieszczady to the Chyvchyny Mts., at elevations from 1500 to 2000 m (Fig. 5d). The lowest localities were found at 1250 m on Kinchyk Bukovsky (Kińczyk Bukowski) in the Bieszczady (Winnicki & Zemanek, 2009) and 1300 m on Sheshul in the Chornohora (Malynovski & Kricsfalusy, 2002), the most elevated on about 2050 m at the top of Hoverla (Zapałowicz, 1889). *Vaccinium gaultheroides* is one of the dominant species, along with *Vaccinium myrtillus* L. and *Empetrum hermaphroditum* Hagerup, in the association *Empetro-Vaccinietum gaultheroides* Br.-Bl. in Br.-Bl. et Jenny 1926 corr. Grabherr 1993. On the slopes of all exposures where the *Empetro-Vaccinietum gaultheroides* is developped, the above-ground cover is dominated by Arctic-Alpine lichen *Cetraria islandica* (L.) Ach. with an admixture of *Cladonia rangiferina* (L.) Weber and mosses *Thammolia vermicularis* (Sw.) Schaer., *Polytrichum alpinum* (Hedw.) G.L.Sm., and *Rhytidiadelphus triquetrus* (Hedw.) Warnst. (Malynovski & Kricsfalusy, 2002).

Discussion

Most of the high mountain woody plants in the Carpathians in Ukraine occur in the Chornohora, Chyvchyny, Svydovets, and Marmarosh mountains, and in the most elevated massifs of the Gorgany. This finding confirmed our hypothesis and earlier studies on the distribution of high mountain plants in the East Carpathians. Occurrence in such a centres of distribution demonstrated the Central-European mountain species as *Pinus mugo* (Tsaryk et al., 2006) and *Rhododendron myrtifolium* (Boratyński et al., 2006) and the Arctic-Alpine taxa, as *Empetrum hermaphroditum* Hagerup (Boratyński & Didukh, 2000) and *Kalmia procumbens* (L.) Gift, Kron & P.F.Stevens ex Galasso, Banfi & F.Conti (Boratyński & Didukh, 2002). The localities of other high mountain species were reported mostly from the Chornohora, Svydovets, and Chyvchyny. *Cotoneaster integerrimus* Medicus, species subalpine in Central and Southern Europe, occurs in the East Carpathians in Ukraine in these three mountain chains and additionally on single localities in the Bieszczady, Polonyna Krasna and Gorgany (Pawłowski & Walas, 1949; Tasenkevich, 1979; Tasenkevich & Stoyko, 2007; Kobiv et al., 2017). *Salix reticulata* L. was found in one locality in the Svydovec (Malynovski & Kricsfalusy, 2002; Mirek, 2020). *Genista tinctoria* subsp. *oligosperma* (Andrae) Soó, endemic to the Carpathians (IPNI, 2022), was reported from two localities in the Marmarosh (Deyl, 1940), *Helianthemum nummularium* (L.) Mill. subsp. *grandiflorum* (Scop.) Schinz & Thell., the species of the mountains of Central and Southern Europe (POWO, 2022), in Ukraine was found only in the Svydovets, Marmarosh, and Polonyna Krasna (Pawłowski & Walas, 1949; Tasenkevich, 1982; Malynovski & Kricsfalusy, 2002). The Arcto-Alpine *Sorbus aucuparia* L. subsp. *glabrata* (Wimm. & Grab.) Hedl., common in the Tatras (Pawłowski, 1956), in the Ukrainian Carpathians occurs in the Chornohora, Svydovets, Chyvchyny, Marmaros, and Gorgany, singly also in the East Bieszczady (Pawłowski & Walas, 1949; Malynovski & Kricsfalusy, 2002; Stoyko et al., 2007). Similarly, the Euro-Siberian *Spiraea chamaedryfolia* L., the high mountain at their south-westernmost localities, grows only in the Chyvchyny and Marmaros (Pawłowski & Walas, 1949; Mirek, 2020). Additionally, the southernmost localities of the northern, peat-bog species as *Andromeda polifolia* L., *Vaccinium microcarpum* (Turcz. ex Rupr.) Schmalh. and *Salix lapponum* L. have been found only in the Chornohora and Chyvchyny (Pawłowski & Walas, 1949; Malynovski & Kricsfalusy, 2002; Pryadko, 2009). From 29 species of trees and shrubs, revealing subalpine and alpine character in the Ukrainian Carpathians, 13 represent Central European, mountain floristic elements, 12 Arctic-Alpine, and four the Euro-Siberian floristic elements.

The Carpathians are included in the list of global biodiversity hot spots as one of the world's key Palaearctic montane ecoregions (Webster et al., 2001) and recognized as one of the World's endemism centre (Kier et al., 2009). However, the East Carpathians in Ukraine has a rather restricted group of endemic plants comprising 125 taxa, 49 of which are of subspecies rank (Tasenkevich, 2003), and without woody plants. Within the Carpathians, the main centres of endemism are recognized in the Tatras, the Făgăraș, and Retezat, the only Carpathian massifs with elevations exceeding an altitude of 2500 m. These three mountain ridges act as islands of alpine and subalpine floras. All the other massifs, even with the highest peaks over 2000 m, the altitude of the lower line of the alpine vegetation belt, does not form extensive centres of subalpine and alpine plants (Ronikier, 2011).

In the Ukrainian territory, the Chornohora, Svydovets, Marmaros, and Chyvchyny mountains are the regions with the highest number of localities of high mountain woody plants. Such a concentration of alpine and subalpine species in these mountain massifs results from their highest elevation and massiveness. The relatively high elevation and extended scope of mountains modify the local climate (Romer, 1909; Nagy et al., 2003; Körner, 2003;) and form suitable conditions for cold-adapted plants and the plant communities (Pawłowski, 1937a, b; Środoń, 1948; Malynovski & Kricsfalushy, 2000, 2002).

Interestingly, most of the subalpine and alpine woody species grow on the northern slopes, frequently strongly inclined. Such orographic conditions were also underlined for *Empetrum hermaphroditum* (Boratyński & Didukh, 2000), *Kalmia procumbens* (Boratyński & Didukh, 2020), *Rhododendron myrtifolium* (Boratyński et al., 2006; Sosnovsky et al., 2021) and *Pinus mugo* (Tsaryk et al., 2006). The prevalence of northern expositions of the localities of subalpine and alpine woody plants could result from generally colder, not so continental thermal and more humid conditions of the northern slopes compared to the southern one (Körner, 2003; Kobiv, 2018; Sosnovsky et al., 2021). Independence of exposition revealed only *Juniperus communis* var. *saxatilis* and *Vaccinium gaultherioides*. The localities of these two species occur in similar percentages in the northerly and southerly exposed places. This could result from their tolerance to high diurnal amplitudes of temperature, winter low temperatures, and irregular precipitation during the vegetation period and winter (Carrer et al., 2019).

The north or close to north expositions of the localities of the subalpine and alpine plants could also result from the relatively not very high elevations of the East Carpathians in Ukraine, with only fragmentary formed alpine vegetation belt, without the nival belt (Zapałowicz, 1889; Mirek, 1989; Cherepanyn, 2017; Sosnovsky et al. 2021). The lowest localities of the high mountain plants are generally in the northern or close to the northern expositions and in the valleys with restricted direct insolation and frequent temperature inversion (Boratyński & Didukh, 2000, 2002; Nagy et al., 2003; Holtmeier, 2003; Tsaryk et al., 2006). Thus, the prevalence of the northern expositions of most of the subalpine and alpine species could indicate their relic character from the cold period of the end of the last glacial and the first period of the Holocene. The area covered by alpine vegetation during the last glacial, especially during the last glacial maximum was much broader and extended than currently, due to a downward displacement of vegetation belts resulting from the depression of permanent snow (Ronikier, 2011: Fig. 2). This was also well proved by macro remnants of *Dryas octopetala* from these periods (Tralau, 1963; Noryśkiewicz et al., 2004) and pollen of this species and *Pinus cembra* (Obidowicz et al., 2004). Following this idea, we can suspect that even the highest mountain ridges in the East Carpathians in Ukraine do not provide optimal climatic conditions for the alpine plants but are sufficient for the subalpine species.

The ongoing climate changes with growing temperatures and prolonged periods of water deficit (Alsos et al., 2009; Niskanen et al., 2019; Barredo et al., 2020) influence the vertical distribution of organisms in the mountains. Climate change concerns also the high mountain plants in the Carpathians in Ukraine (Kobiv, 2017; Cherepanyn, 2019). Considering, that only a few peaks exceed the Ukrainian Carpathians an altitude of 2000 m and forming the conditions suitable for the alpine plants and the alpine vegetation belt, the rarest and most valuable woody components of the Ukrainian flora shall be treated as strongly endangered. The highest threat concerns the species known from a single or only e few localities, such as *Dryas octopetala*, *Salix alpina* and *S. reticulata*, however, these species occur more frequently in the neighbouring Rodna Mountains in Romania, which attain an altitude of about 2300 m (Ronikier, 2011; Mráz & Ronikier, 2016).

Strongly threatened are more frequent species, such as *Salix retusa*, *S. kitaibeliana*, *S. hastata*, *S. herbacea*, *S. bicolor*, also *Rhododendron myrtifolium*, *Kalmia procumbens*. These species are known from several localities each, dispersed in the Chornohora, Svydovets, Chyvchyny, and Marmarosh, predominantly on the northern steep slopes. Mentioned orographic conditions moderate the influence of the highest temperatures (Körner, 2003; Nagy et al., 2003), but these could not be sufficient at least for some number of their localities, especially in the case of the scenario of the highest warming level. The group of strongly endangered shall be also included *Lonicera caerulea* and *Prunus padus* subsp. *borealis*.

Conclusion

The high mountain woody species occur in the Ukrainian parts of the East Carpathians mainly in the largest mountain massifs, the Chornohora, Svydovets, Chyvchyny, Marmarosh, and to a lesser extent, also in the Gorgany. The vertical distribution and predominant occurrence on the northern or close to northern expositions of most of the subalpine and alpine species indicate their demands for the relatively high level of humidity of the soil and high level of precipitation. These conditions point to the relic character of most of the analysed species, which originate from the glacial periods of the Pleistocene. Most of the taxa, which have centres of their distribution in the alpine and sub-alpine vegetation belts of the East Carpathians in the Ukraine territory are valuable but threatened elements of the Ukrainian flora.

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