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# Biodiversity of high-mountain woody plants in the Eastern Carpathians in Ukraine – continuation

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**Abstract:** The subalpine and alpine vegetation belts in the mountains are formed by plants adapted to harsh environmental conditions. In Central and Southern Europe, these types of vegetation have developed mainly in the Alps, the Pyrenees, the highest massifs of the Carpathians, and in the mountains of Balkan, Apennine, and Iberian Peninsulas. However, in the Eastern Carpathians in Ukraine, only a few massifs are sufficiently high for subalpine and alpine vegetation to develop. The aim of the present study was to verify the hypothesis that woody plant species frequently occurring in the subalpine and alpine vegetation belts in Ukraine, predominantly grow in the Chornohora, the Marmarosh-Chyvchyny ranges along the border with Romania, also in the Svydovets and Gorgany massifs. To test this hypothesis, we continued studies on the distribution of woody species. The results clearly indicate that the highest and most extensive mountain massifs of the Carpathians in Ukraine are the main centers of occurrence for subalpine and alpine species. Among the subalpine and alpine woody species are a few Carpathian endemics. Prevail the Central European mountain species, and arctic-alpine species reaching their southernmost, or at least near-southern distribution limits. Subalpine and alpine woody species in Ukraine are very rare and valuable components of the Ukrainian vascular flora. Alpine vegetation with typically alpine woody species is restricted to only the highest peaks of the Chornohora, Svydovets, Chyvchyny, and Gorgany mountains and is at risk of extinction due to climate change. This threat mainly concerns species known from only a single locality.

**Keywords:** arctic-alpine plants, alpine plants, subalpine plants; Eastern Carpathians; phytogeography; ecology; plant conservation.

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## Introduction

This study is a continuation of previously published research and concerns the same area (Tasenkevich et al., 2023: Fig. 1), but focuses on additional 16 woody taxa with local occurrence centers in the high mountains, except of *Juniperus sabina*, which grows there in montane vegetation belt (Table 1).

There are very few areas on Earth with native flora and vegetation that have remained unchanged by human colonization, agriculture, and urbanization. Mountains are among the regions where plant cover

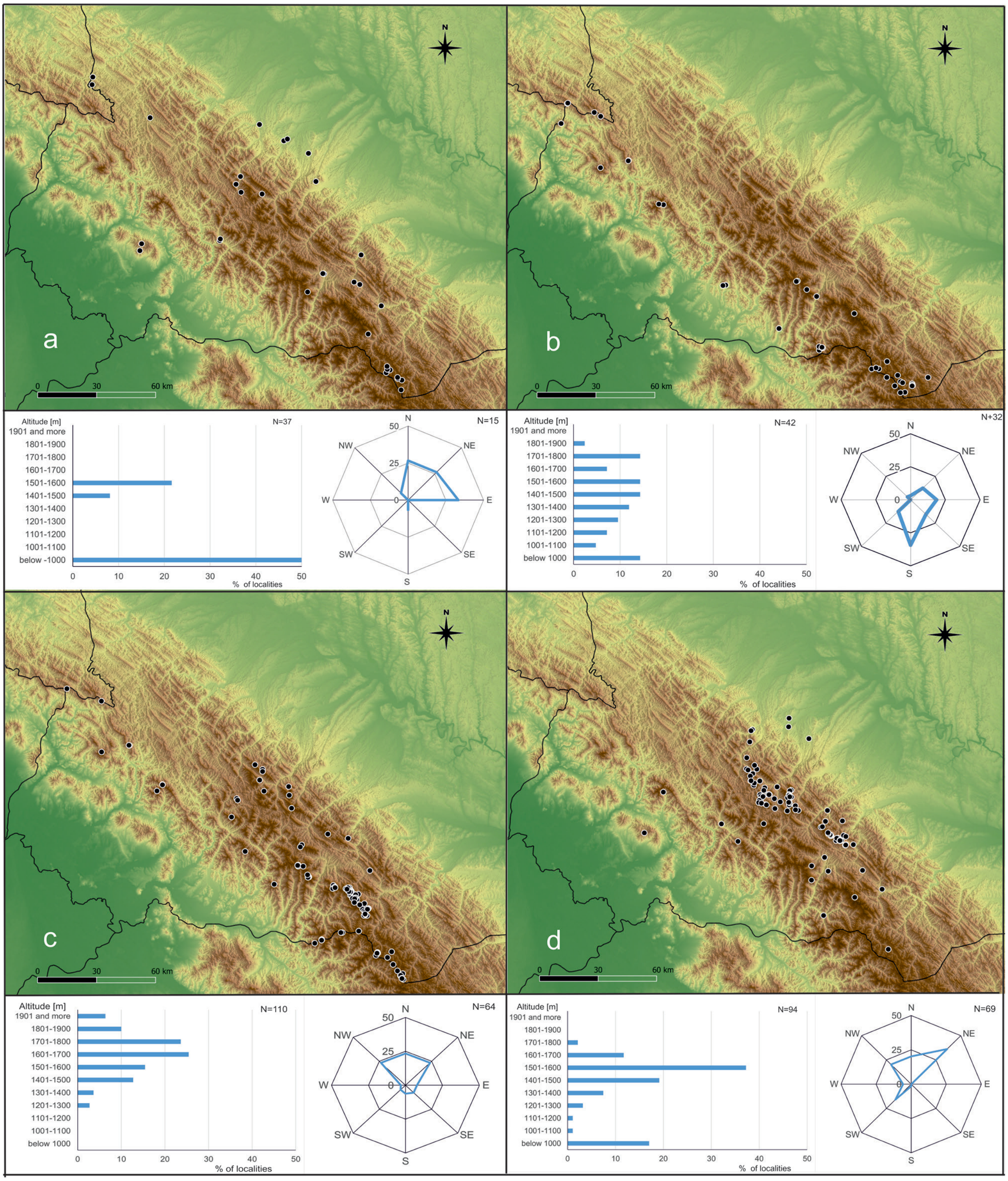



Fig. 1. Geographic distribution, altitudinal range, and exposition of localities of (a) *Andromeda polifolia*, (b) *Cotoneaster integerrimus*, (c) *Empetrum hermaphroditum*, (d) *Empetrum nigrum*

Table 1. Studied species of woody mountain plants of the East Carpathians in Ukraine; names after International Plant Names Index (IPNI)

| Species | General range | Range type | Vertical distribution in Carpathians | Number of localities |
|---|---|---|---|---|
| *Andromeda polifolia* L. | CIRPOL | bor– disj – (sub-alp) | sub-mont – disj – sub-alp | 37 |
| *Cotoneaster integerrimus* Medik. | CEUR | mont – sub-alp | mont – sub-alp | 42 |
| *Empetrum hermaphroditum* Hagerup | CIRPOL | ar – disj – alp | sub-alp – alp | 110 |
| *Empetrum nigrum* L. | CIRPOL | bor – disj – sub-alp | mont – disj – sub-alp | 94 |
| *Genista tinctoria* L. subsp. *oligosperma* (Andrae) Soó | CARP | sub-alp | sub-alp | 2 |
| *Helianthemum nummularium* (L.) Mill. subsp. *grandiflorum* (Scop.) Schinz & Thell. | CEUR | sub-alp | sub-alp | 23 |
| *Juniperus sabina* L. | ALTALP | mont – sub-alp | mont | 1 |
| *Kalmia procumbens* (L.) Gift, Kron & P.F.Stevens | CIRPOL | ar – disj – alp | sub-alp – alp | 72 |
| *Linnaea borealis* L. | CIRPOL | bor – disj – (sub-alp) | sub-alp | 1 |
| *Pinus mugo* Turra | CEUR | sub-alp | sub-alp | 973 |
| *Rhododendron mytrifolium* Schott & Kotschy [=*R. kotshyi* Simonk.] | CARP – (BALK) | sub-alp | (mont) – sub-alp | 202 |
| *Rosa pendulina* L. | CEUR | mont – sub-alp | mont – sub-alp | 83 |
| *Salix lapponum* L. | EUROSIB | bor – disj – sub-alp | sub-alp | 2 |
| *Sorbus aucuparia* L. subsp. *glabrata* (Wimm. & Grab.) Hedl. | EUROP | ar – disj – sub-alp | sub-alp | 72 |
| *Spiraea chamaedryfolia* L. | EUROSIB | bor – sub-alp | mont – sub-alp | 117 |
| *Vaccinium microcarpum* (Turcz. ex Rupr.) Schmalh. [=*Oxycoccus microcarpus* Turcz. ex Rupr.] | CIRPOL | bor – ar – disj – (sub-alp) | mont – disj – sub-alp | 34 |

General range (after literature cited in the text): ALTALP – Altaj-Alpine; BALK – Balkan; CARP – Carpathian; CEUR – Central-European; CIRPOL – circumpolar; EUROP – European; EUROSIB – Euro-Sibirian.
Vegetation zone: alp – alpine vegetation belt in the mountains; ar – arctic zone; bor – boreal zone; disj – disjunction in general and/or vertical distribution; mont – montane vegetation belt in the mountains; sub-alp – subalpine vegetation belt in the mountains.

has undergone relatively minor changes. The highest mountain areas still harbor native and near-native floras in undisturbed locations (Körner, 2021). The richness of high-mountain floras in Central Europe and Asia results, among other factors, from climate changes during the Neogene and a high degree of habitat differentiation within small areas (Nagy et al., 2003; Ralska-Jasiewiczowa et al., 2004; Bradley, 2014; Kupryjanowicz et al., 2018; Raduła et al., 2021; Lang et al., 2023).

Currently, high-mountain plants (alpine and subalpine) are considered among the most interesting and valuable elements of European floras (e.g., Aeschiman et al., 2004; Gómez et al., 2020; Mirek et al., 2020a). At the same time, these plants are increasingly threatened by global climate change (e.g., Franzén & Molander, 2012; Pauli et al., 2012; Gottfried et al., 2014; Gómez et al., 2020). The potential upward shift of the upper forest line due to climate warming (e.g., Işık et al., 2024) could significantly reduce the area available for high-mountain vegetation, particularly in massifs that are not sufficiently high. This threat primarily concerns subalpine and alpine plant species in the Eastern Carpathians in Ukraine (Tasenkevich et al., 2023; Walas et al., 2023).

The aim of the present study is to verify the geographic and altitudinal distribution of 16 woody species, and subspecies that occur in the Eastern Carpathians in Ukraine, primarily in the subalpine and alpine vegetation belts. We hypothesized that the distribution of these plants in the Carpathians would be restricted to the highest and most massive mountain ranges, specifically the Chornohora, Svydovets, and Chyvchyny–Marmarosh Mountains. Additionally, we assumed that most of the analyzed taxa would occur on the north-facing slopes of these mountains, as observed in other subalpine and alpine species (Boratyński & Didukh, 2000, 2002; Tsaryk et al., 2006; Boratyński et al., 2006; Tasenkevich et al., 2023).

# Materials and Methods

## Species and data on their distribution

We analyzed high-mountain woody taxa that had not been examined in our previous study (Table 1). We also included species occurring in peat bogs in the lowlands north of the Carpathian Arc, such as *Salix lapponum* L., *Empetrum nigrum* L., *Andromeda polifolia* L., *Linnaea borealis* L., and *Vaccinium microcarpum* (Turcz. ex Rupr.) Schmalh., which in the mountains grow predominantly in the subalpine vegetation belt. Additionally, *Cotoneaster integerrimus* Medik., *Rosa pendulina* L., and *Spiraea chamaedryfolia* L., are known from a large number of localities at relatively low elevations in the Carpathians in Ukraine but have been the most frequently reported in the subalpine vegetation belt.

The species analyzed in this study have at least local areas of distribution in the subalpine and alpine vegetation belts of the Carpathians in Ukraine, despite some of them have broad geographic ranges covering lowland areas outside the mountains. The only exception is *Juniperus sabina*, which in the Eastern Carpathians does not cross the montane vegetation belt, but is diagnostic and constant species of EUNIS habitat S23 "Alpine and subalpine *Juniperus* scrub". Plant names follow International Plant Name Index (IPNI, 2024), and their validity was verified in Plants of the World Online (POWO, 2024).

The methods of analyses follow those described by Tasenkevich et al. (2023). Georeferenced data on the natural localities of specific taxa were obtained from herbarium materials preserved in KOR, CHER, KRA, KRAM, LW, LWS (formerly LWD), UU, and partially from KW, KWH, PRA, and WA (herbarium acronyms follow Index Herbariorum, https://sweetgum.nybg.org/science/ih/). Additional data sources included literature, the authors' field observations, and databases such as the Global Biodiversity Information Facility (GBIF, 2024) and the Ukrainian Biodiversity Information Network (UKRBIN). When geographic coordinates and site exposure were not reported in the original data, they were determined using Google Earth (Google Earth, 2023). For *Pinus mugo*, we additionally extracted data from Google Earth satellite images, which allowed precise identification of this species (Kluczek et al., 2023).

Our dataset includes more than 3,000 records with sufficiently precise localization and elevation data, most of which also have detected exposure and evaluated slope inclination. A separate locality was defined as differing from the nearest one by at least 150–180 m (approximately 0.001° in geographic coordinates) or, when coordinates were identical, by an altitude difference of 20–30 m. Further selection and removal of duplicate records reduced the dataset to 1,867 records (Table 1).

The geographic distribution of each taxon was mapped using QGIS 3.16 (*QGIS Development Team*, 2020). The vertical distribution of localities is presented in graphs as a percentage of occurrences within 100-meter elevation intervals. For exposure descriptions, we categorized localities by percentage across main and intermediate geographic directions. For species with fewer than 10 analyzed localities, their positions within altitudinal intervals and exposure categories were indicated by dots.

## Results and species characteristics

***Andromeda polifolia* L.** (Ericaceae) is an evergreen chamaephyte, growing no more than 10–20 cm tall, with slender, erect, and sparsely branched stems emerging from creeping rhizomes. The alternately arranged leaves are lanceolate with revolute margins, 1–5 cm long, dark green on the upper surface (purplish in winter), and silvery-glaucous beneath (Webb, 1972a; Jacquemart, 1998). The terminal, umbellate inflorescence is nodding and bears 1 to 4–6 flowers. The corollas are spherical to ovoid, urn-shaped, 5–8 mm long, white or pinkish, with five short, outward-curved tips (Lauber, 2019; Kriebel et al., 2022).

This species has a circumpolar distribution, occurring mainly in the boreal zone (Hultén & Fries, 1984; Jacquemart, 1998). It primarily grows on ombrotrophic raised mires, sometimes within fen plant communities, but rarely on acidic mineral soils with pH <6.8. At the southern limits of its geographic range in Europe, *A. polifolia* is confined to mountain peat bogs (e.g., Bentham, 1937; Anderson, 1959; Matuszkiewicz & Matuszkiewicz, 1975; Meusel et al., 1978). In Central and Southern Europe, it is considered a relict species from the glacial period (Dítě et al., 2018; Kırmacı et al., 2019). Fossil macro-remains of *A. polifolia* have been reported from the Miocene (Łańcucka-Środoniowa, 1979) and the Pleistocene (Jacquemart, 1998).

In Ukraine, *A. polifolia* is widespread in Polissia, where ombrotrophic raised mires cover significant areas (e.g., Tołpa, 1933; Kulczyński, 1939; Fitsailo et al., 2012; Karpyuk, 2014). In the Carpathians, it occurs only occasionally in peat bogs (Fig. 1a), at 600 m in the Bieszczady Mountains (Danylyuk, 2006; Bezusko et al., 2009; Pidgrebel'na, 2001), and within the Skolivski Beskydy National Park (Vorontsov & Pidgrebel'na, 2002; Milkina et al., 2011). On the northeastern macro-slopes of the Carpathians, several peat lands are known in the vicinities of Dolyna and Rozhnyativ, where *A. polifolia* occurs at elevations of ca 400 m (Środoń, 1937; Andrienko, 1968).

In the Gorgany region, several peat bogs host *A. polifolia* at elevations of up to 1,000 m (Krupa, 1885; Kozij, 1934; Bradis et al., 1969; Onyshchenko & Andrienko, 2015). On the southwestern macro-slopes of the Eastern Carpathians, raised peat bogs are found at elevations of up to ca 850 m (e.g., Komendar & Fodor, 1960; Vorontsov et al., 2011; Felbaba-Klushina, 2015). Following an altitudinal disjunction, *A. polifolia* grows in high-mountain peat bogs above or at the upper forest line. It has been detected on Mount Shuryn in the Chornohora range and on Mounts Lozdun, Mokryn, and Rotundul in the Chyvchyny Mountains (Pawłowski & Walas, 1949).

In the Eastern Carpathians in Ukraine, *A. polifolia* occurs in plant associations of the class *Oxycocco-Sphagnetea* Br.-Bl. et R.Tx. ex Westhoff et al. 1946, within the order *Sphagnetalia magellanici* Kästner et Flössner 1933. The associations *Sphagnetum magellanici* (Malcuit 1929) Kästner et Flössner 1933

(=*Andromedo polifoliae-Sphagnetum magellanici* Bogdanovskaja-Gienev 1928 em. Neuhäusl 1984), *Eriophoro vaginati-Sphagnetum recurvi* Hueck 1925, and *Sphagno-Pinetum sylvestris* Kobendza 1930 (=*Eriophoro vaginati-Pinetum sylvestris* Hueck 1931) belong to the alliance *Sphagnion magellanici* Kästner et Flössner 1933. The association *Empetro hermaphroditi-Sphagnetum fusci* Du Rietz 1926 (=*Empetro nigri-Sphagnetum fusci* Osvald 1923) belongs to the alliance *Oxycocco-Empetrion hermaphroditi* (Nordh. 1936) R.Tx. 1937 (Pawłowski & Walas, 1949; Valachovič, 2001; Malynovski & Kricsfalusy, 2002; Matuszkiewicz, 2008; Felbaba-Klushina, 2015; Onyshchenko & Andrienko, 2015; Konishchuk & Felbaba-Klushina, 2019).

***Cotoneaster integerrimus* Medik.** (Rosaceae) is an erect or spreading, much-branched, deciduous shrub, typically reaching 1–1.5 m in height, though often smaller (Browicz, 1959, 1991). Its leaves are suborbicular to broadly elliptic-ovate, greyish tomentose beneath, entire, and borne on short petioles. The flowers, approximately 8 mm in diameter, have a campanulate hypanthium and form corymbs of 2–5 (–7) flowers. The fruit is subglobose to ovoid, 6–7 mm in diameter, red. This species is distributed in the mountains of Central Europe (Kurtto et al., 2013). Previously reported from Scandinavia (e.g., Meusel et al., 1965; Hultén & Fries, 1986), but these records have been revised to refer to *C. scandinavicus* B. Hylmö (Hylmö & Fryer, 1999). The species also occurs in the Western and Central Asian mountains, extending to Mongolia and Korea (Browicz, 1991). In the northern foothills of the European mountains, it descends into lowland areas. Its occurrence is closely linked to basic substrates, primarily limestone and/or basaltic rocks, and soils derived from calcium-rich material (Browicz & Gostyńska, 1963; Browicz, 1991; Boratyński, 1991).

In the Eastern Carpathians in Ukraine, local populations of *C. integerrimus* are dispersed from the Eastern Bieszczady in the west (Chopyk, 1976; Tasenkevich & Stoyko, 2007), along the Vododilny and Poloniny ridges, and across the main peaks of the Svydovets, Marmarosh, Chornohora, and Chyvchyny Mts (Fig. 1b). The species is primarily reported from limestone rocks within the subalpine vegetation belt, reaching a maximum elevation of ca 1820–1845 m in the Chornohora (Zapałowicz, 1889), around 1750 m in the Marmarosh (Kobiv et al., 2017), and similar elevations in the Chyvchyny Mountains (Pawłowski & Walas, 1949). It prefers south-facing slopes. Below the subalpine vegetation belt, *C. integerrimus* grows on limestone cliffs and rock outcrops, extending into the montane and even submontane vegetation belts, reaching elevations as low as 550–650 m in Putilske Niskogirya and Ugolka (Tasenkevich, 1982).

As a companion species, *C. integerrimus* occurs in phytocenoses at higher elevations in the mountains. In the Svydovets, it is rarely found in the association *Cystopteridetum fragilis* Oberd. 1938, from the alliance *Cystopteridion* Richard 1972, class *Asplenietea trichomanis* (Br.-Bl. in Meier et Br.-Bl. 1934) Oberd. 1977 (Malynovski & Kricsfalushy, 2002). In the Chyvchyny Mountains, it occurs in the association *Festucetum saxatilis* Domin 1933 (Pawłowski & Walas, 1949). In the open *coenoses* of Ugolka, where *C. integerrimus* is found on limestone cliffs, relict remnants of the high-altitude association *Festucetum saxatilis* are evident.

***Empetrum hermaphroditum* Hagerup** (Ericaceae) is currently considered a synonym of *Empetrum nigrum* L. (POWO, 2024). However, due to morphological differences (e.g., Villar, 1993; Boratyński & Vera de la Puente, 1995; Boratyński & Didukh, 2000), distinct geographic distributions (Meusel et al., 1978; Hultén & Fries, 1986), differing site conditions (Didukh & Boratyński, 1999; Boratyński & Didukh, 2000), molecular distinctions (Li et al., 2002), and different chromosome numbers (Suda, 2002), we have opted to treat them as separate species.

Typical ***E. nigrum*** is a diploid (2n=26), dioecious, evergreen shrub forming dense mats. Its procumbent stem, extends up to 100–120 cm in length, is rooting and sparingly branched. The ericoid leaves are linear-oblong, (2.5)3–5 times as long as they are wide. The drupe is black, without staminal remnants at the base.

In Ukraine, *E. nigrum* has been reported from peat bogs in the northern part of the country and the Carpathians (Meusel et al., 1978). Its lowland and montane distribution areas are separated by a disjunction. In the Carpathians, this species occurs in peat bogs within the submontane and montane vegetation belts and, after an altitudinal disjunction, in the subalpine layer (Boratyński & Didukh, 2000, and references therein). The lowest Carpathian localities have been reported from below 500 m in a peat bogs complex near Dolina, while the highest at ca 1700 m on Mt. Doboshanka in the Gorgany (Fig. 1d).

In the peat bogs, the species grows in the plant communities of the class *Oxycocco-Sphagnetea* Br.-Bl. et Tx 1943, while in the subalpine zone, it forms tufts on the rocks among *Pinus mugo* thickets or enter communities of class *Loiseleurio procumbentis-Vaccinietea* Eggler ex Schubert 1960 (Konishchuk, & Felbaba-Klushina, 2019; Chorney & Iakushenko, 2019a). In the Gorgany and Chyvchyny mountains, it occurs frequently in the undergrowth vegetation of *Pinus mugo* thickets with dense cover of *Sphagnum* sp. (Sulma, 1929; Trampler, 1937; Pawłowski & Walas, 1949).

***Empetrum hermaphroditum*** is tetraploid (2n=52), monoecious, evergreen shrub forming clumps or dense mats, in high mountains frequently with *Vaccinium gaultherioides* Bigelow. Stem is no longer than

40–50 cm, ramified, decumbent to ascending, without roots. Leaves are elliptic-oblong, 2–4 as long as wide. Drupe is black, with remnants of stamens at base (Boratyński & Vera de la Puente, 1995).

*Empetrum hermaphroditum* is a circumpolar species (Hultén & Fries, 1986), in Europe, represents an arctic-alpine floristic element (Zając & Zając, 2009). In Ukraine, it occurs exclusively in the Carpathians, at elevations ranging from ca 1250–1300 m in the Bieszczady to around 2000 m in the Chornohora (Fig. 1c). It has also been reported from Ugolka (Fodor, 1974), though this record is considered highly questionable and requires careful field verification.

*Empetrum hermaphroditum* is a component of peat bog plant communities of the class *Oxycocco-Sphagnetea*, alliance *Oxycocco microcarpi-Empetrion hermaphroditi* Nordhagen ex Du Rietz 1954, and mainly the association *Empetro nigri (hermaphroditi)-Sphagnetum fusci* Osvald 1923 (Konishchuk & Felbaba-Klushina, 2019). Above the forest line, *E. hermaphroditum* is a component of plant communities of the class *Loiseleurio procumbentis-Vaccinietum*, the *Loiseleurio procumbentis-Vaccinion* alliance, and mainly the association *Empetro-Vaccinietum gaultherioides* Br.-Bl. in Br.-Bl. et Jenny 1926 corr. Grabherr 1993 (Chorney & Iakushenko, 2019a).

***Genista tinctoria* L. subsp. *oligosperma* (Andrae) Soó** (= *G. oligosperma* (Andrae) Simonk., *G. rupestris* Schur) (Fabaceae) is a mat-forming semi-shrub with short, upright flowering branches, 20 cm high (Schur, 1866; Morariu, 1957; Chopyk, 1976). It is endemic to the Eastern and Southern Carpathians (Pawłowski, 1970; Chopyk, 1976; Malynovski, 1980; Tasenkevich, 2003a, b; Kliment et al., 2016).

In the Ukrainian part of the Eastern Carpathians, *G. tinctoria* subsp. *oligosperma* is known only from the Marmarosh Mts (Deyl, 1934; 1940), from two localities on the south and south-east slopes of Mt. Pietros and Mt. Berlebaska, at 1600-1700 m a.s.l. (Fig. 2a), where it grows on white andesite rocks with not very deep, rocky soil (Deyl, 1940; Kobiv et al., 2017).

*Genista tinctoria* subsp. *oligosperma* enters two associations, *Carex sempervirens-Festuca supina* and *Carex sempervirens-Vaccinium myrtillus* with subass. *Vaccinium myrtillus-Thymus alpestris-Genista oligosperma* and *Festuca supina-Thymus alpestris* (Deyl, 1940), which can be attributed to *Caricetum sempervirentis* (Domin 1933) Pușcaru et al.1956 (Malynovski & Kricsfalusy, 2002).

In the Ukrainian part of the Eastern Carpathians, this plant was considered extinct in the wild (EW) (Kagalo, 2009), but it was rediscovered (Kobiv et al., 2017) and has since been classified as endangered (EN) (Onyshchenko et al., 2022).

***Helianthemum nummularium* (L.) Mill. subsp. *grandiflorum* (Scop.) Schinz & Thell.** [=*Helianthemum grandiflorum* (Scop.) DC.] (Cistaceae) is an evergreen subshrub 10-30 cm high. It is a high-mountain taxon with a native range covering mountains of South-West, South and Central Europe, Crimea, and Caucasus (Proctor & Heywood, 1968; Hrouda, 1990; Saule, 1991; Aeschimann et al., 2004; Takhtajan, 2012; Yena, 2012). It occurs in subalpine belt, in grassy and rocky habitats, and usually on basic, and dry substrates (Proctor & Heywood, 1968; Hrouda, 1990).

In Ukraine, *H. nummularium* subsp. *grandiflorum* is known from the most elevated part of the Carpathians, relatively often in the Chyvchyny Mts (Fig. 2b), between elevation 1410 m on Mt Lozdun, up to ca 1740 m on Mt Chyvchyn (Zapałowicz, 1889). It occurs in plant communities of the class *Elyno-Seslerietea* Br.-Bl., order *Seslerietalia caeruleae* Br.-Bl. in Br.-Bl. et Jenny 1926 (Pawłowski & Walas, 1949; Malynovski, 1980; Chorney & Iakushenko, 2019b), alliance *Festuco saxatilis-Seslerion bielzii* (Pawł. & Wal. 1949) Coldea 1984 (=*Festucion marmarossicae*), the association *Festucetum saxatilis* Domin 1933 (Coldea, 1984, 1991). In the Svydovets, *H. nummularium* subsp. *grandiflorum* occasionally grows on NE-oriented ledges, and calcium-rich flysch steep slopes of Dragobrat, Mala and Velyka Blyznytsia (Zapałowicz, 1889; Chopyk, 1976; Malynovski, 1980). On Dragobrat, *H. nummularium* subsp. *grandiflorum* is a companion species in association *Achilleo schurii-Dryadetum* (Beldie) Coldea 1984, of the alliance *Oxytropido-Elynion* Br.-Bl. 1949, class *Carici-rupestris-Kobresietea bellardii* Ohba 1974 (Coldea, 1984, 1991; Malynovski & Kricsfalushy, 2002).

One of the most interesting phenomena in the whole Carpathian range of *H. nummularium* subsp. *grandiflorum* is its occurrence on the Jurassic calcareous cliffs of the Ugolka (Fig. 2c). Here, it grows occasionally in open plant communities at elevation between 620 and 1050 m, on steep, southeast-facing ridges of calcareous rocks rising above the canopy of the beech forest (Tasenkevich, 1979, 1982). The Ugolka also hosts several high-mountain and endemic species, such as *Acinos alpinus* (L.) Moench. subsp. *baumgartenii* (Simonk.) Pawł., *Allium lusitanicum* Lam., *Cirsium erisithales* (Jacq.) Scop., *Festuca saxatilis* Schur, *Scabiosa lucida* Villars, *Sempervivum globiferum* subsp. *hirtum* (L.) ‘t Hart & B.Bleij, *Silene nutans* L. subsp. *dubia* (Herbich) Zapał., *Thymus pulcherrimus* Schur, *Phyteuma orbiculare* L. These species are characteristic for the subalpine association *Festucetum saxatilis* (Pawł. 1936) Pawł. & Wal. 1949, of the alliance *Festucion marmarossicae* Pawł. & Wal. 1949, the order *Seslerietalia variae* Br.-Bl. 1926, described as endemic to Chyvchyny Mts. (Pawłowski & Walas, 1949). The remnants of high-altitude flora in the Ugolsky massif confirm its refugial character for both, thermophilic and cold-hardy Pleistocene floras (Gladilin & Pashkevich, 1977; Bezusko & Tasenkevich, 1978).

***Juniperus sabina* L.** (Cupressaceae) is a dioecious shrub, usually low and spreading, 1–1.5 m height, forming dense clumps. Juvenile leaves acicular, adult scale-like, with specific odour when rubbed (e.g., Chopyk & Fedoronchuk, 2015; Farjon, 2017). Ripen cones are black or blackish and contain 2 (1–4) seeds (Mazur et al., 2021).

Two varieties, the typical one and *J. sabina* var. *balkanensis* R. P. Adams et A. N. Tashev, were described, revealing clear molecular but inconspicuous morphological differences (Adams et al., 2016; Mazur et al., 2021). Individuals of *J. sabina* from the Ukrainian Eastern Carpathians have not been verified until

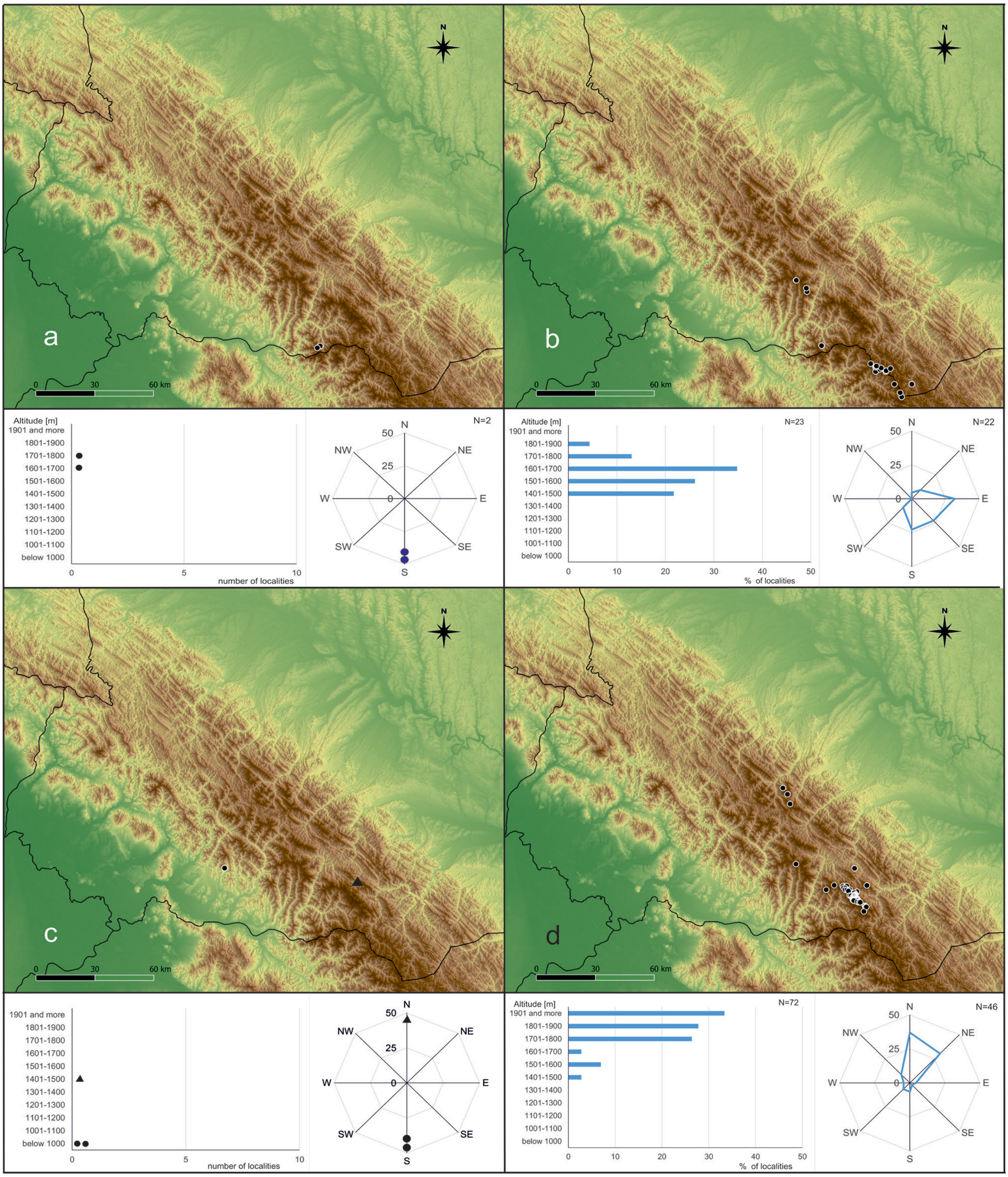



Fig. 2. Geographic distribution, altitudinal range, and exposition of localities of (a) *Genista tinctoria* subsp. *oligosperma*, (b) *Helianthemum nummularium* subsp. *grandiflorum*, (c) *Juniperus sabina* (dots) and *Linnaea borealis* (triangle), (d) *Kalmia procumbens*

now as concern their taxonomic status, but other West- and East-Carpathian populations was stated as *J. sabina* var. *sabina* (Jadwiszczak et al., 2023). Savin juniper is a frost and drought-resistant and light-demanding (Bannister & Neuner, 2001; Jadwiszczak et al., 2023), subcontinental, Altai-Alpine species (Zając & Zając, 2009). It occurs in the mountains of Southern and Central Europe, at altitudes between 500 and 2300 m, and its geographic range is strongly disjunct (Jalas & Suominen, 1973; Bobrov, 1979; Zając & Zając, 2009).

In the Alps, *J. sabina* is found from montane to the subalpine vegetation belts, in the shrubby plant communities classified as a suballiance *Berberido-Juniperenion sabinae* Theurillat 1995 (Theurillat et al., 1995). In the Western Carpathians, it is known only from the Pieniny Mountains (e.g., Smólski, 1937; Jasičová, 1966; Browicz & Gostyńska-Jakuszewska, 1968) where it is considered a Tertiary relict (e.g., Zarzycki, 1976; Wróbel et al., 2014; Jadwiszczak et al., 2023, 2024). It grows there on the limestone rocks, in the association *Dendranthemo-Seslerietum variae* Grodzińska & Jasiewicz 1979 (Dzwonko & Grodzińska, 1979) and in the open forests of *Pinus sylvestris* L. (Jasičová, 1966; Wróbel et al., 2014).

In the Eastern Carpathians within Ukrainian territory, *J. sabina* was found in 1960, in the Ugolka Massif (Stoyko, 1960; Tasenkevich, 1982; Stoyko et al., 2004). The Ugolka is a narrow, rugged ridge of Jurassic limestones, forming a continuation of the West Carpathian Pieniny Klippen Belt (Shlapinskyi et al., 2017; Golonka et al., 2022). On the southern cliffs of Hrebin's ridge, from the side of the village of Velyka Ugolka, at an altitude of 790-820 m (Fig. 2c), seven separate groups of *J. sabina* have been detected. Each group consist of 4–5 prostrate shrubs approximately 1 m in height. The largest group extends for 5–6 m.

The east and west side of these rocky outcrops are occupied by *Phyllitido-Aceretum* Moor 1952. Consequently, the plant community containing *J. sabina* is difficult to classify due to the mixture of xerophytic and mesophytic species, typical of low elevations, such as *Actaea europaea* (Schipcz.) J.Compton, *Asplenium scolopendrium* L., *Galium transcarpaticum* Stojko & Tasenk., *Iris graminea* L., *Melica transsilvanica* Schur, *Rhamnus cathartica* L., *Sesleria heufleriana* Schur, *Taxus baccata* L., and *Tilia platyphyllos* Scop., as well as high-altitude species including for example *Cotoneaster integerrimus* Medik., *Festuca saxatilis* Schur, *Saxifraga paniculata* Mill., *Scabiosa lucida* Vill. subsp. *barbata* Nyár., *Sempervivum globiferum* L. subsp. *preissianum* (Domin) M.Werner, and *Trisetum alpestre* (Host.) P. Beauv.

In Europe, *Juniperus sabina* has been assessed as Least Concern (LC) (Farjon, 2013). However, it is considered Endangered (EN) in Poland (Wróbel et al., 2014), Slovakia (Turis et al., 2014), and Romania (Tasenkevich, 2003b), and Critically Endangered (CR) in Bulgaria (Peev et al., 2015). It is not included in the Red Book of Ukraine, mainly due to its relative abundance in the Crimea (Didukh, 1992, 2009), but in Ugolka it is protected within the Carpathian Biosphere Reserve (Tasenkevich, 1982).

***Kalmia procumbens* (L.) Gift, Kron & P.F.Stevens** [=*Loiseleuria procumbens* (L.) Loisel.] (Ericaeae) is an evergreen, prostrate shrub, frequently creeping to the ground, particularly in the harsh environment of high elevations. It is an arctic-alpine, circumpolar, amphi-Atlantic plant (Hultén, 1971, 1973; Meusel et al., 1978; Hultén & Fries, 1986). In the mountains of Central Europe, it reaches its southernmost localities, where it is a cold-adapted glacial relic (Abeli et al., 2018; Dítě et al., 2018; Walas et al., 2023), though it can withstand temperatures even exceeding 50 °C (Buchner et al., 2013). In the mountains, it occurs primarily on the rocky ridges (Gómez et al., 2020; Löffler & Pape, 2020).

In the Carpathians within Ukrainian territory, *K. procumbens* occurs only in the Chornohora and rarely in the Gorgany, in the alpine and subalpine vegetation belts. It grows from 1500 m to the highest peaks, exceeding 2000 m (Fig. 2d), though it likely does not yet reach its potential altitudinal limit (Boratyński & Didukh, 2002; Walas et al., 2023). It occupies open, often rocky sites, growing among *Pinus mugo* thickets and above them. Here, it forms plant communities of the class *Loiseleurio procumbentis-Vaccinietea* Eggler ex Schubert 1960, and occurs primarily in the association *Loiseleurio-Cetrarietum* Br.-Bl. et al. 1939 of the alliance *Loiseleurio procumbentis-Vaccinion* Br.-Bl. in Br.-Bl. et Jenny 1926 (Chorney & Iakushenko, 2019a).

Due to climate change, *K. procumbens* is expected to lose most of its potential habitats in the Eastern Carpathians of Ukraine by 2080 (Walas et al., 2023).

***Linnaea borealis* L.** (Caprifoliaceae) is a creeping to the ground, small shrub with very thin shoots, rooting in nodes. Its upright flowering shoots bear two slightly zygomorphic, sympetalous, pendent, white to pinkish flowers. It is the only species in the genus *Linnaea*, and is divided into three varieties: the typical *L. borealis* var. *borealis*, the American *L. borealis* var. *americana* (J. Forbes) Rehder, and the Pacific and Greenland variety *L. borealis* var. *longiflora* Torr. (Landrein & Farjon, 2019). In Europe, only typical variety is known. It has a circumpolar geographic range, in the boreal and subarctic zones (Landrein & Farjon, 2019), with southernmost localities reported from the subalpine vegetation belt of the Alps (Aeschimann et al., 2004; Landrein & Farjon, 2019), the Sudetes, and the Carpathians (Hultén & Fries, 1986; Landrein & Farjon, 2019). There, *L. borealis* is considered a relic of the glacial period (Browicz &

Gostyńska-Jakuszewska, 1966; Tsaryk & Andrienko, 2009; Landrein & Farjon, 2019).

In the Carpathians, *L. borealis* is known from only single localities in Ukraine and Romania (Sanda et al., 2003). In Ukraine, it has a unique locality in cirque Tsybulnyk (Fig. 2c), on the foot of northeastern slope of Pozhyzhevska Mt., at elevation 1435–1440 m (Koziy, 1954). Initially, its population occupied 120 m$^2$, but after the avalanche in 1984, it was fragmented into six plots with a total area of 10.4 m$^2$ (Tsaryk & Malynovski, 1995; Burlaka, 2016). This site is significant in terms of historical phytogeography and plant conservation, and is protected within the strict reserve zone of the Carpathian National Nature Park. *Linnaea borealis* is listed in the VU category in the Red Book of Ukraine (Tsaryk & Andrienko, 2009).

***Pinus mugo*** **Turra** (Pinaceae) is a variable taxon sometimes considered as a complex species (Christensen, 1987a, 1987b; Christensen & Dar, 1997). The taxonomic status of the taxa included within the complex remain debated (e.g., Boratyńska et al., 2015; Dzialuk et al., 2017; Zaborowska et al., 2020; Boratyńska et al., 2021 and references therein). The typical *P. mugo* occurs in the eastern part of the complex range, mainly in the Eastern and Southern Carpathians (Boratyńska et al., 2015; Dzialuk et al., 2017). It is a large shrub with stems lying on the ground, but with apical parts raised up to even 2–3 m. It forms dense thickets in the subalpine vegetation belt, from the forest line up to the 2700 m in the Abruzzian Apennines and Rila Mts (Boratyńska et al., 2005; Tsaryk et al., 2006, and references therein).

In Ukraine, *P. mugo* is common in the Chornohora, Gorgany, Chyvchyny and Marmarosh Mountains, regardless the slope exposure or inclination (Fig. 3a). The single specimen of *P. mugo* was also reported from Polonyna Rivna (Charkevicz, 1951). Historically, it was more widespread in other Carpathian mountain ranges, but its populations have been significantly reduced due to human activity (e.g., Vincenz, 1936; Kontny, 1938). On the northern slopes, *P. mugo* descends to an elevation of 1200 m, occasionally reaching as low as 1100 m (Sulma, 1929; Trampler, 1937). The lowest recorded localities are in peat bogs, where it has been found at ca 700 m. In some peat bogs, tree-like specimens with asymmetric cones, resembling *P. uliginosa* Neumann, have been observed (Trampler, 1937; Jasińska et al., 2009; Boratyńska et al., 2010). However, this issue requires further study.

In the Eastern Cartpathians in Ukraine, *P. mugo* dominates in the subalpine vegetation belt forming shrubby communities of the class *Roso pendulinae-Pinetea mugo* Theurillat in Theurillat et al. 1995, the order *Junipero-Pinetalia mugo* Boşcaiu 1971, the alliance *Pinion mugo* Pawłowski et al. 1928, for which is a diagnostic species (Boşcaiu, 1971; Chorney & Iakushenko, 2019c). To the mentioned alliance are included *Adenostylo alliariae-Pinetum mugo* (Sillinger 1933) Šoltésova 1974, *Driopterido dilatatae-Pinetum mugo* Unar in Unar et al. 1985, and *Rhododendro myrtifolii-Pinetum mugo* Borza 1959. However, classifying *P. mugo* communities described from the Gorgany by T. Sulma (1929) and T. Trampler (1937), as well as from the Chyvchyny by B. Pawłowski & J. Walas (1949) as *Mughetum carpaticum*, remains problematic. Within the forest vegetation belt, *P. mugo* occurs also in the peat bog vegetation, being one of the important components of association *Vaccinio uliginosi-Pinetum mugo* Lutz 1956 of the class *Oxycocco-Sphagnetea* Br.-Bl. et Tx. ex Westhoff, Dijk et Paschier 1946, order *Sphagnetalia medii* Kästner et Flössne, alliance *Sphagnion medii* Kästner et Flössner 1933 (Konishchuk & Felbaba-Klushina, 2019).

***Rhododendron myrtifolium*** **Schott & Kotschy** (= *R. kotschyi* Simonk.) (Ericaceae) is a small, evergreen shrub, usually not exceeding 40 cm in height, with elliptic leaves and pink flowers arranged in upright racemes (e.g., Popova, 1972; Danylyk, 2009). Specimens with white flowers have also been reported from Chornohora (Waldon & Didukh, 2004). Leaves are lepidote beneath, light green when young, becoming brownish at the end of vegetation period and brown in the subsequent year. The species occurs in the Eastern and Southern Carpathians, and in the mountains of the Balkan Peninsula (Boratyński et al., 2006; Lewandowska et al., 2023, and references therein).

In the Eastern Carpathians on the Ukrainian territory, *R. myrtifolium* primarily occurs in the Chornohora, Chyvchyny and Marmarosh, and on dispersed localities in other the most elevated mountain massifs (Fig. 3b). It occupies the subalpine vegetation belt entering the meadow communities and *Pinus mugo* thickets, but on the northern slopes going down even to about 1100 m, entering the upper forest belt. It generally prefers northern exposures of the slopes and the moist sites, as bases of the rocks and the slope concavities (Fig. 3b).

*Rhododendron myrtifolium* is a component of grassy associations, such as *Primulo-Caricetum curvulae* (Br.-Bl. 1926) Oberd. 1957 of the alliance *Caricion curvulae* Br.-Bl. 1925, order *Caricetalia curvulae* Br.-Bl. in Br.-Bl. et Jenny 1926, class *Juncetea trifidi* Hadač in Klika et Hadač 1944 (Chorney et al., 2019b), association *Hyperico alpigeni-Calamagrostietosum villosae* Pawłowski et Walas 1949 of the alliance *Calamagrostion villosae* Pawłowski et al. 1928, order *Calamagrostietalia villosae* Pewłowski et al. 1928, class *Mulgedio-Aconitetea* Hadač et Klika in Klika et Hadač 1944 (Chorney et al., 2019a). It grows most frequently in shrubby plant communities of the classes *Roso pendulinae-Pinetea mugho* Theurillat in Theurillat et al. 1995 and *Loiseleurio procumbentis-Vaccinietea* Eggler ex Schubert 1960 (Chorney & Jakushenko, 2019a, c). To the first class belongs the association *Rhododendro myrtifolii-Pinetum mugo* Borza 1959 of the alliance *Pinion mugo* Pawłowski et al. 1928, the order *Junipero-Pinetalia mugo* Boşcaiu 1971, to the second are included associations *Junco trifidi-Rhododendretum kotschyi* Resmeriţa 1978 of the alliance *Rhododendrion myrtifolii* Foucault ex Theurillat et Mucina in Mucina et al. 2016, and *Loiseleurio-Cetrarietum* Br.-Bl. et al. 1939 and *Empetro-Vaccinietum gaultherioidis* Br.-Bl. in Br.-Bl. et Jenny 1926 corr. Grabherr 1993 of the alliance *Loiseleurio procumbentis-Vaccinion* Br.-Bl. in Br.-Bl. et Jenny 1926, the order *Rhododendro*

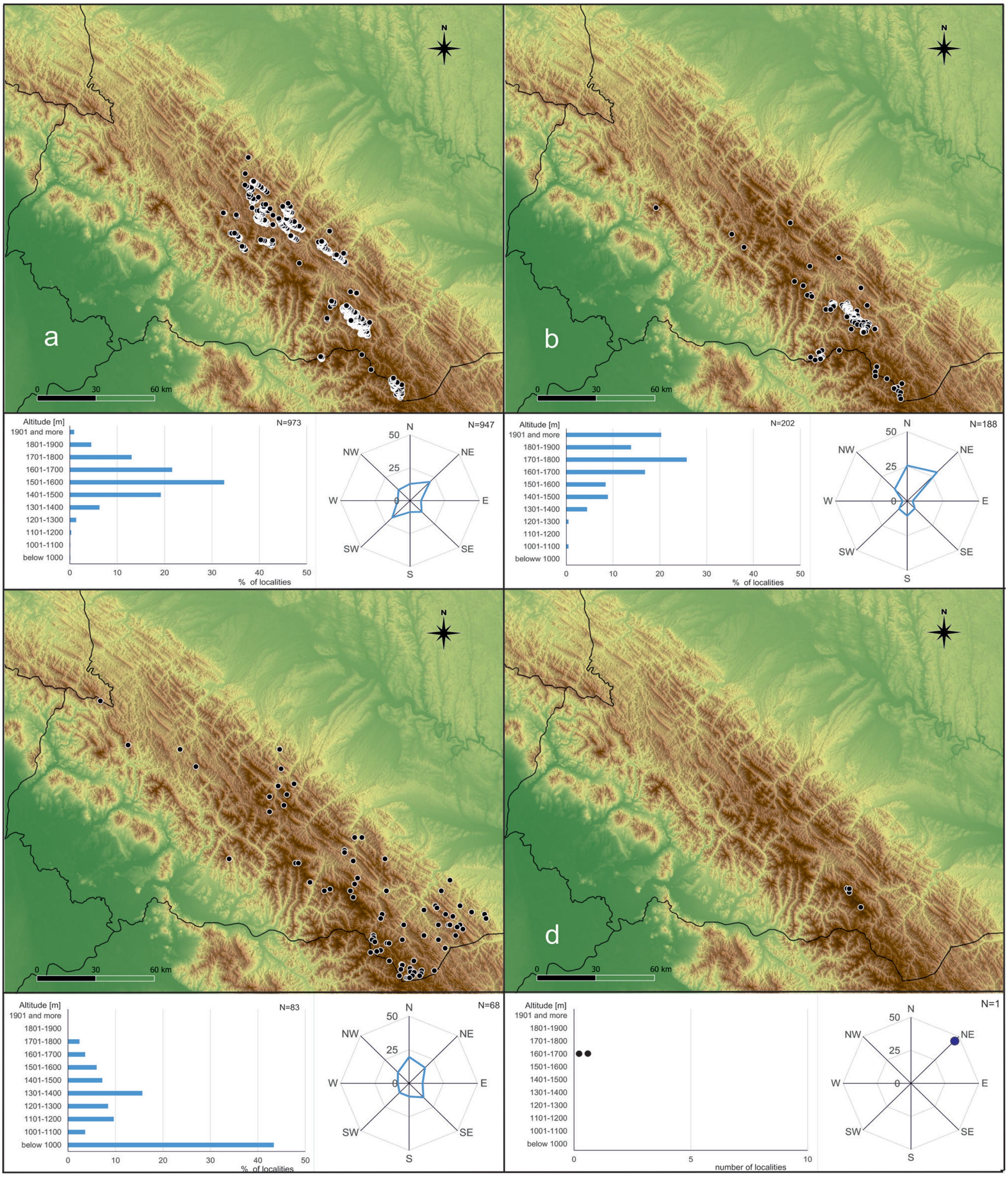



Fig. 3. Geographic distribution, altitudinal range, and exposition of localities of (a) *Pinus mugo*, (b) *Rhododendron myrtifolium*, (c) *Rosa pendulina*, (d) *Salix lapponum*

*ferruginei-Vaccinietalia* Br.-Bl. in Br.-Bl. et Jenny 1926. In Ukraine, *R. myrtifolium* is a protected species (Danylyk, 2009).

***Rosa pendulina* L.** (Rosaceae) is a straight shrub up to ca 1.5 m. It is a Central-European mountain species, in the northern parts of geographic range going down to submontane vegetation belt. In the Carpathians it is frequent but occurs mainly in form of dispersed single specimens, up to subalpine vegetation belt.

In the Carpathians in Ukrainian territory, *R. pendulina* is present in all mountain ranges (Fig. 3c), from submontane to subalpine vegetation belts. However, the highest concentration of occurrences is near the upper forest line and in the subalpine belt. In the submontane and montane vegetation belts, it is dispersed along the streams, and in the subalpine vegetation is more frequent in moist places. The most elevated localities of *R. pendulina* were reported from altitudes of ca 1740-1750 m in Chornohora and Chyvchyny Mts.

*Rosa pendulina* is a diagnostic species of the order *Adenostyletalia alliariae* Br.-Bl. 1930, of the class *Mulgedio-Aconitetea* Hadač et Klika in Klika et Hadač 1944 (=*Betulo-Adenostyletea* Br.-Bl. et Tx 1943 *pro parte*). It is also a diagnostic species of the association *Calamagrostio-Spiraeetum chamaedrifoliae* Resmeriță et Crűsös 1966 of the alliance *Calamagrostion arundinaceae* (Luquet 1926) Oberd. 1957 (Chorney et al., 2019a). In the subalpine layer, it is a diagnostic species of the alliance *Salicion silesiacae* Rejtmánek et al. 1971 of the order *Alnetalia viridis* Rübel ex Karner et Willner in Willner et Grabherr 2007 of the class *Betulo carpaticae-Alnetea viridis* Rejtmánek ex Boeuf, Theurillat, Willner, Mucina et Simler in Boeuf et al. 2014 (Chorney & Iakushenko, 2019d), and enters plant communities from the class *Roso pendulinae-Pinetea mugo* Theurillat in Theurillat et al. 1995.

***Salix lapponum* L.** (Salicaceae) is a dioecious shrub with crooked branches, straight up to ca 1 m. It is an Euro-Siberian species (Meusel et al., 1965; Zając & Zając, 2009), occurring in Arctic and boreal zones (Hultén & Fries, 1986), in the latter mainly on peat bogs, as a glacial relic. In southern part of their geographic range, *S. lapponum* grows in the mountains, in Europe from the Pyrenees in the west to the Carpathians in the east, and in the Vitosha and Rila mountains in southern Balkan Peninsula, where it reaches elevations of 2600 m (Boratyński, 1987; Chmelař & Koblížek, 1990; Gostyńska-Jakuszewska, 1992; Assyov et al., 2002). In the Alps and Tatras (West Carpathians), *S. lapponum* is replaced by its close relative *S. helvetica* Vill. (Jalas & Suominen, 1976). Although *S. helvetica* has been reported from the Eastern Carpathians in Ukraine (Mirek et al., 2020a), studies of herbarium specimens have confirmed only the presence of *S. lapponum*.

In Ukraine, *S. lapponum* is frequent in the peat bogs of the northern part of the country (Andrienko, 1980; Pogorzelec, 2003). Following a distributional disjunction, it reappears in the Carpathians, where it has been recorded in a few localities (Fig. 3d), including glacial cirques below Breskul (Zapałowicz, 1889) and Turkul. At the bottom of these cirques, *Sphagnum* spp. accumulate water creating favorable conditions for Lapland willow. These sites are protected in the strict reserve zone in the Carpathian National Nature Park. *Salix lapponum* is considered to be a glacial relic and is classified as vulnerable (VU) (Pryadko, 2009).

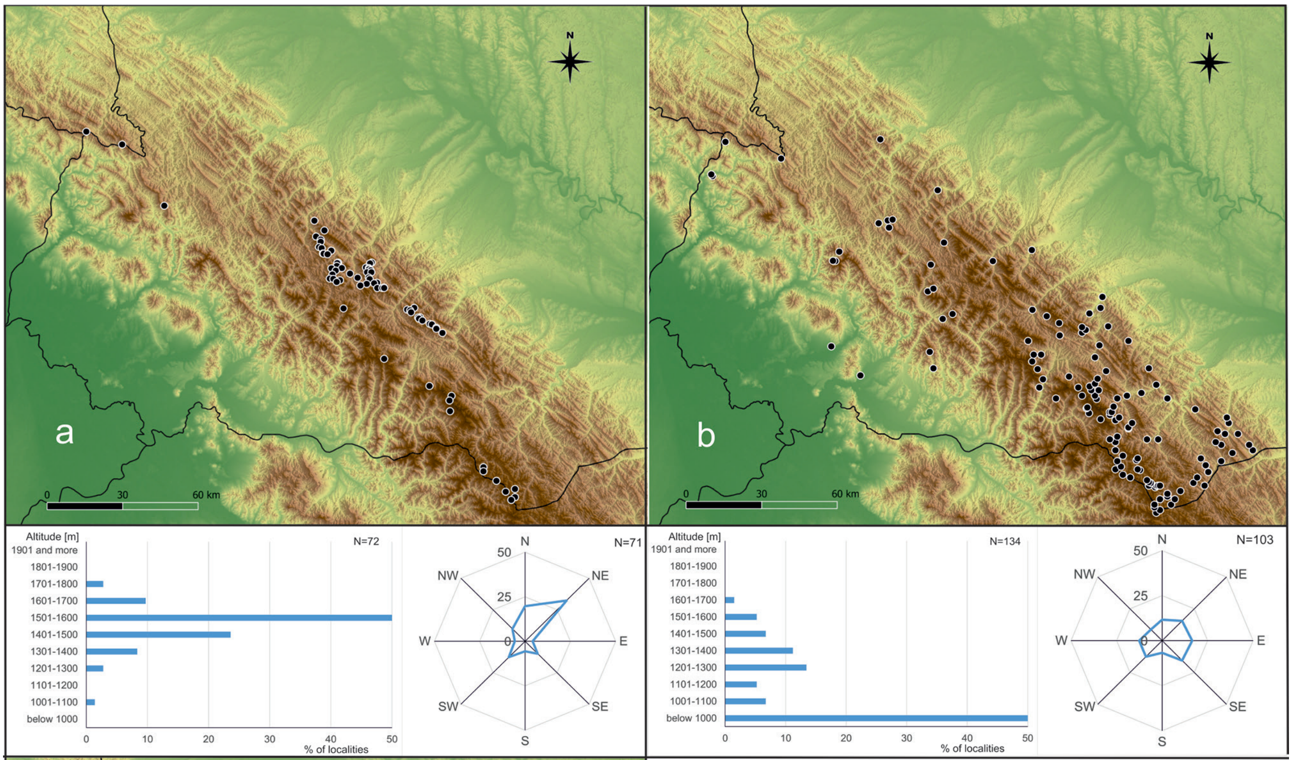
***Sorbus aucuparia* L. subsp. *glabrata* (Wimm. & Grab.) Hedl.** (Rosaceae) is a tree up to about 8 m high, with glabrous (or subglabrous) inflorescence axis and leaflets; the latter sometimes sparsely hairy (Warburg & Kárpáti, 1968). It is an arctic (subarctic) -alpine species (Warburg & Kárpáti, 1968; Zając & Zając, 2009). In the mountains of Central Europe, it is known mostly from the subalpine vegetation belt (Hultén & Fries, 1986), but its geographic distribution remains poorly understood (Zając & Zając, 2001). In the Carpathians, it is known from the most elevated massifs, primarily in the Western (Májovský, 1992), southern part of the Eastern, and from several localities in the Southern Carpathians (Mirek et al., 2020a).

In the Ukrainian part of the Eastern Carpathians, *S. aucuparia* subsp. *glabrata* occurs in the Chornohora, Gorgany, and Chyvchyny, and in dispersed localities across the Svydovets, Bieszczady and Borzhava (Fig. 4b). It is generally found at elevations above 1300 m, with minimum at ca 1100 m in the Bieszczady, up to more than 1700 m in the Chyvchyny and even 1750 m in the Chornohora, with prevailing localities at altitudes between 1500 and 1600 m (Fig. 4b). This species is a component of *Pinus mugo* and *Alnus alnobetula* (Ehrh.) K. Koch thickets and is also found in *Picea abies* forests, particularly at the upper forest line.

***Spiraea chamaedryfolia*** L. (=*S. ulmifilia* Scop.) (Rosaceae) is a variable species, with two varieties and/or subspecies distinguished, treated lately as synonyms of *S. chamaedryfolia* (e.g., Dostál, 1968; Mosyakin & Fedoronchuk, 1999; Kurtto et al., 2004; Mirek et al., 2020b). This is a deciduous, densely branched shrub up to 1.5–2 m high. It has generally glabrous, elliptical to rhombic-elliptical leaves, 4–7 cm long (Pawłowski, 1955; Dostál, 1968; Ziman, 1999). In Europe, this species is native to the Eastern Alps, Eastern and Southern Carpathians, and mountains of the Balkan Peninsula (Jovanovič, 1972; Ozenda & Borrel, 2003; Kurtto et al., 2004; Chopyk & Fedoronchuk, 2015). Outside the Europe, it occurs in the mountains of Central Asia (Meusel et al., 1965; Sokolov et al., 1980).

The northernmost known localities of *S. chamaedryfolia* L. are in the Ukrainian Carpathians (Kurtto et al., 2004). The species is known from all parts of the Ukrainian Carpathians (Fig. 4c), from the Bieszczady on the west up to the Marmarosh and Chyvchyny Mountains on the east (Chopyk, 1976; Ziman, 1999; Chorney et all, 2012; Chopyk & Fedoronchuk, 2015). The species primarily inhabits rocky sites, open forest clearings, forest edges, and enters shrubby communities along the stream banks. It is widespread between 400 and 1715 m a.s.l. (Pawłowski, 1955; Zapałowicz, 1889), particularly in the upper forest and in the subalpine zone.

*Spiraea chamaedryfolia* grows at the edges of coniferous and mixed forests and in *Alnus alnobetula* (Ehrh.) K.Koch and *Pinus mugo* Turra thickets. In montane tall grasslands of the class *Mulgedio-Aconitetea* Hadač et Klika in Klika 1948 (Kočí, 2007), of the



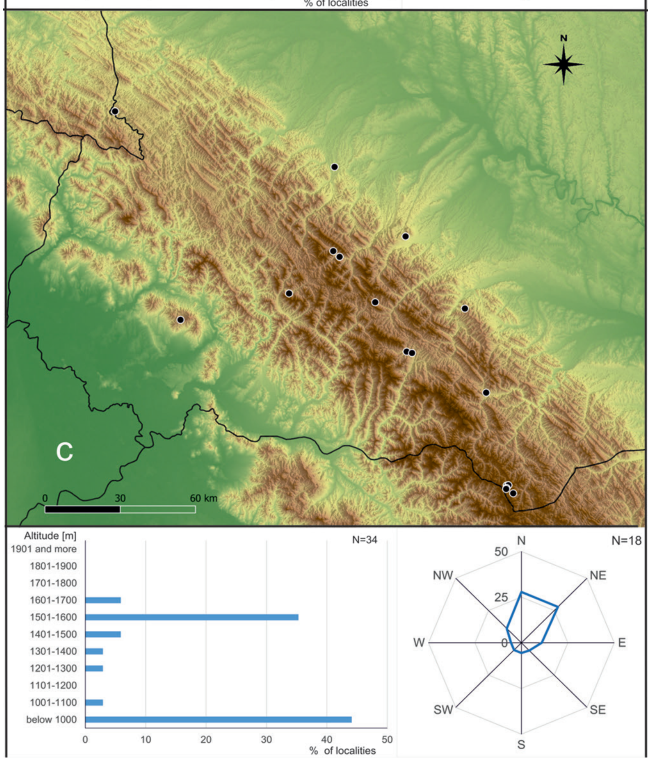




Fig. 4. Geographic distribution, altitudinal range, and exposition of localities of (a) *Sorbus aucuparia* subsp. *glabrata*, (b) *Spiraea chamaedryfolia*, (c) *Vaccinium microcarpum*

alliance *Calamagrostion arundinaceae* (Luquet 1926) Oberd. 1957, it is one of the main components of the association *Calamagrostio-Spiraeetum chamaedrifoliae* Resmeriţă et Crüsös 1966, which is endemic to the Eastern Carpathians, and develops on the strongly inclined, north-facing flysh rock debris (Iakushenko, 2007; Chorney et al., 2019a). This species is also present in plant communities of the alliance *Adenostylion alliariae* Br.-Bl. 1925, the associations *Ranunculo platanifolii-Adenostyletum alliariae* (Krajina 1933) Dubravcová in Mucina et Maglocký 1985 and *Pulmonario-Alnetum viridis* Pawł. et Wal. 1949, of the alliance *Calamagrostion villosae* Pawł. 1928, the association *Vaccinio myrtilli-Pinetum mugo* Sill. 1933, and even in the *Festucetum saxatilis* Domin 1933 of the alliance *Festuco saxatilis-Seslerion bielzii* (Pawłowski et Walas 1949) Coldea 1984.

***Vaccinium microcarpum* (Turcz. ex Rupr.) Schmalh.** [=*Oxycoccus microcarpus* Turcz. ex Rupr.] (Ericaceae) is an evergreen creeping chamaephyte with recumbent, thin (almost filiform), branched, 10-30 cm long shoots, and upright flowering shoots rising to 5 cm. Its leaves are 2 – 6 × 1 – 2.5 mm, often widest at base, triangular-ovate, dark green above whitish beneath (Webb, 1972; Van der Kloet, 1983; Jacquemart, 1997). The pedicels, usually the bracteoles and the calyx, are glabrous. Flowers are pink and solitary. The fruits are lemon-shaped, ellipsoid or pyriform, 5 – 8 mm across (Webb, 1972; Stace, 1991). The species has a chromosome number of 2n=24, and whole plant is generally smaller than its closely related *V. oxycoccos* L., whith 2n=48 (Hummer et al., 2015).

*Vaccinium microcarpum* is a circumpolar, predominantly boreal plant. At the southern limit of geographic range in Central Europe and Eastern Asia, it enters the subalpine vegetation belt (Hultén & Fries, 1986; Boratyński, 1991). In Ukraine, this species occurs frequently on the rising peat bogs in the northern part of the country. In the Carpathians, it grows in dispersed localities on the peat bogs at submontane and montane vegetation belts, and after an altitudinal disjunction, reappears in the subalpine vegetation belt, there mainly in the most elevated massifs. The highest localities of *V. microcarpum* were found at about 1700 m in the Chornohora (Fig. 4d).

*Vaccinium microcarpum* is a diagnostic species of the class *Oxycocco-Sphagnetea* Br.-Bl. et Tx. ex Westhoff, Dijk et Pashier 1946, the raised peat bogs, and among them is characteristic for alliance *Oxycocco microcarpi-Empetrion hermaphroditi* Nordhagen ex Du Rietz 1954, the oligotrophic peat bogs developed in the subalpine vegetation belt of the mountains in Central Europe and Scandinavia (Matuszkiewicz, 2008; Konishchuk & Felbaba-Klushina, 2019). It is also a component of the association *Caricetum chordorrhizae* Paul et Lutz 1941 of the alliance *Stygio-Caricion limosae* Hordhagen 1943, the order *Scheuchzerietalia palustris* Nordhagen et Tx. 1937, the class *Scheuchzerio palustris-Caricetae fuscae* Tx. 1937 (Felbaba-Klushina & Konishchuk, 2019). *Vaccinium microcarpum* is considered a glacial relic and is classified as vulnerable (VU) in the Red Book of Ukraine (Andrienko, 2009).

## Discussion

In the Carpathians of Ukraine, only the Chornohora, Svydovets, Chyvchyny, Marmarosh and partly Gorgany mountain ranges have sufficiently well-developed subalpine vegetation. Furthermore, only the highest parts of these massifs contain small fragments of alpine vegetation (e.g., Zapałowicz, 1889; Środoń, 1948; Chopyk, 1976; Kotov & Chopik, 1976; Malynovski, 1980; Holubets et al., 1988; Malynovski et al., 2002; Nersteruk, 2003; Stoica et al., 2017; Tasenkevich et al., 2023). The Chornohora, along with the aforementioned massifs, harbors localities of all analyzed species and contains most of Ukraine's subalpine and alpine flora, regardless of their biogeographic element (Tasenkevich et al., 2023).

The taxa analysed in this study, represent several geographic elements (after Hultén & Fries, 1986; Kong & Watts, 1999; Zając M & Zając, 2009; but see also Finnie et al., 2007; Tkach et al., 2008). The prevailing group consists of species with broad circumpolar geographic ranges (Hultén, 1971), also classified as circumboreal (Zając & Zając, 2009). Among these, the species with boreal main range in the Carpathians attain southernmost or close to the southernmost localities only entering the sub-alpine vegetation belt. A typical example of such species is *Linnaea borealis*, known from the Eastern Carpathians from the only locality in Chornohora.

Species with circumpolar geographic distribution include species broadly occurring in the boreal zone. Some of them enter the sub-arctic and southern part of Arctic zone, and after disjunction appear in the mountains at the southern parts of their geographic ranges in Eurpe. The circumpolar group of species includes also *Andromeda polifolia*, *Empetrum nigrum* and *Vaccinium microcarpum*. These species are relatively common on the lowland peat bogs to the north, not far from of the Carpathians arch. These three species are also present in the peat bogs at the bases and in the lower montane vegetation belt of the Carpathians, and after break in vertical range, they reappear on the peat bogs in the subalpine vegetation belt.

The remaining species with circumpolar geographic ranges are associated with Arctic zone in the north and with the alpine and subalpine vegetation belts in the mountains to the south. This group includes *Empetrum hermaphroditum*, and *Kalmia procumbens*. In the Eastern Carpathians of Ukraine, these species occur primarily in the highest mountain massifs, predominantly within alpine and subalpine vegetation belts of the Chornohora, Svydovets and Chyvchyny.

In the Eastern Carpathians, the species representing the circumpolar floristic element are considered relics from the glacial periods. This is supported by fossil evidence from the areas between high mountain massifs in the south and the Arctic zone in the north (Tralau, 1963; Hultén & Fries, 1986; Birks, 2008). Molecular studies have confirmed this hypothesis at least for some species (e.g., Alsos et al., 2005).

The most interesting and particularly valuable are species endemic for analysed area (e.g., Breman et al., 2020). However, there are no woody taxa endemic to the Ukrainian part of the Eastern Carpathians. Among the taxa analysed in this study, only two can be considered as endemic to the entire Carpathians. *Genista tinctoria* subsp. *oligosperma* is a subalpine plant known only from the Carpathians, while *Rhododendron myrtifolium* has its occurrence centre in the Eastern and Southern Carpathians, but after a break in geographic range, it appears also in the mountains of the Balkan Peninsula (Lewandowska et al., 2023). The relatively low number of endemic taxa in the Carpathians (e.g., Pawłowski, 1970; Ronikier, 2011; Tasenkevich, 2013, 2014; Kliment et al., 2016) may result, among other factors, from the relatively young age of the Carpathians flora (Nagy et al., 2003; Mráz & Ronikier, 2016; Stoica et al., 2017).

Among predominantly subalpine woody plants in the Eastern Carpathians of Ukraine, we analyzed four taxa with a Central-European geographic range: *Cotoneaster integerrimus*, *Rosa pendulina*, *Pinus mugo* and *Helianthemum nummularium* subsp. *grandiflorum*. *Cotoneaster integerrimus* and *R. pendulina* have a broad vertical distribution (e.g., Boratyński, 1991; Gómez et al., 2020). In the Eastern Carpathians in Ukraine, these two species occur from the submontane and montane to the subalpine vegetation belts, but with the relatively highest number of localities in the latter. In contrast, *P. mugo* and *H. nummularium* subsp *grandiflorum* occur predominantly in the subalpine vegetation belt.

*Salix lapponum* and *Spiraea chamaedryfolia* can be classified as Eurosiberian species with relatively broad geographic ranges. The former is mostly found in the northern and central regions, while the latter in the southern parts of the Eurosiberian province (Jalas & Suominen, 1976; Hultén & Fries, 1986; Boratyński, 1991; Kurtto et al., 2004).

*Juniperus sabina* represents one of the most interesting geographic elements of the Ukrainian flora. Its entire geographic range is extensive, streching from the Iberian Peninsula in the west to the Altai Mountains in the east (Hultén & Fries, 1986; Zając & Zając, 2009; Adams, 2014), but highly disjunct. Sabinian juniper is considered an Altai-Alpine floristic element (Zając & Zając, 2009), and is regarded as tertiary relic (Dorofeev, 1963; Jadwiszczak et al., 2023, 2024 and references therein). In the Carpathians, it occurs only in scattered localities (Mirek et al., 2020a), typically on calcareous rocks. In the Eastern Carpathians of Ukraine, its localities resemble those described from the Pieniny Mountains near the Polish-Slovak border (compare: Wróbel et al., 2014; Tasenkevich, 1982).

*Sorbus aucuparia* subsp. *glabrata* is classified as a high mountain woody plant. Its geographic range is poorly understood, mainly due to its debated taxonomic rank and the lack of distinction in floristic studies. It has an European distribution, divided into the northern Arctic, and southern mountain subalpine parts (Hultén & Fries, 1986; Májovský, 1992; Mirek et al., 2020a). In Europe, it represents a group of taxa with arctic-alpine distribution. Among the species analyzed in this study, into this geographic category fall also *Empetrum hermaphroditum*, and *Kalmia procumbens* (Zając & Zając, 2009; Cherepanyn, 2017).

Peat bog species such as *Andromeda polifolia*, *Empetrum nigrum*, *Linnaea borealis*, *Salix lapponum*, and *Vaccinium microcarpum* are relatively common in the peat bogs of northern Ukraine (Meusel et al., 1965, 1978; Hultén & Fries, 1986). They persist in subalpine mires as relics of the last glacial period. In Ukraine, most of their localities are found in Polissia (e.g., Kulczyński, 1939), with some also occurring in peat bogs at submontane and montane elevations in the Carpathians (Kozij, 1934). These species are also present, though less frequently, in the subalpine vegetation belt. A similar vertical distribution pattern for peat bog species has been observed in the Eastern Carpathians of Romania (e.g., Danci, 2016) and in the Sudetes (Boratyński, 1991).

Among the originally peat bog taxa in the Eastern Carpathians of Ukraine, *Linnaea borealis* and *Salix lapponum* are known from only a single localities in the Chornohora, with small populations (Andrienko, 1980; Burlaka, 2016). *Andromeda polifolia* and *Vaccinium microcarpum* have most of their Carpathian localities in submontane peat bogs but are relatively common in subalpine ones (e.g., Pawłowski & Walas, 1948; Malynovski & Kricsfalusy, 2002). *Empetrum nigrum* in the Carpathians is not restricted to peat bogs; it also occurs frequently in subalpine *Pinus mugo* communities, particularly in moss- and *Sphagnum*-dominated habitats in the Gorgany and Chyvchyny Mountains (e.g., Sulma, 1929; Pawłowski, 1937b; Trampler, 1937; Boratyński & Didukh, 2000; Malynovski & Kricsfalusy, 2002).

Summarizing the data on peat bog species, their occurrence in the mountains is of relic nature from the glacial periods. This conclusion is supported by subfossil and fossil records from regions between their northern and southern occurrences (e.g., Tralau, 1963; Łańcucka-Środoniowa, 1979; Hultén & Fries, 1986; Jacquemart, 1997, 1998; Skrede et al., 2006).

The habitat preferences of particular species in the mountains of Central Europe are closely related to their thermal requirements (Winkler et al., 2016). Taxa that are common in the subalpine and alpine vegetation belts, occur independently of the geographic exposure of their localities (e.g. Tasenkevich et al., 2023). However, some species exhibit a preference for southern slopes at the upper limits of their occurrence (e.g., Boratyński, 1991; Holtmeir, 2003). Among the taxa analyzed in this study, only *Pinus mugo*, *Rosa pendulina*, and *Spiraea chamaedryfolia* have localities distributed more or less independently of slope exposure. Most of the remaining taxa exhibit a preference for north-facing slopes. These include *Empetrum hermaphroditum*, *Empetrum nigrum*, *Linnaea borealis*, *Kalmia procumbens*, *Rhododendron myrtifolium*, *Salix lapponum*, and *Sorbus aucuparia* subsp. *glabrata*. The same preference is also observed in the peat bog species *Andromeda polifolia* and *Vaccinium microcarpum*, though these two species predominantly grow in flat or only slightly inclined areas of mires.

There are significant differences in the availability of direct solar radiation and, consequently, in temperature with its daily amplitude, and humidity between the northern and southern slopes in the mountains of Central Europe (e.g. Holtmeier, 2003), including the Eastern Carpathians. Generally, the south-facing slopes receive more insolation, and consequently have higher temperatures, longer vegetation period and earlier snowmelt than northern ones (e.g. Środoń, 1948; Nagy et al., 2003; Holtmeier, 2003; Ronikier, 2011; Winkler et al., 2016; Drewnik et al., 2016; Błażejczyk & Skrynyk, 2019; Löffler & Pape, 2020; Körner, 2021; Owczarek et al., 2024). For that reason, the north- and north-east - facing slopes form more suitable site conditions for most of subalpine and alpine, Pleistocene relict plants, than slopes of south- and south-western exposures.

Another group of taxa, including *Cotoneaster integerrimus*, *Juniperus sabina*, *Genista tinctoria* subsp. *oligosperma*, and *Helianthemum nummularium* subsp. *grandiflorum*, are predominantly found on south-facing or near south-facing slopes. Notably, all these taxa grow on calcium-rich sites or in fissures of limestone rocks, often on steep inclines.

Species with natural geographic ranges restricted to subalpine and alpine vegetation belts are generally highly vulnerable to environmental changes (e.g., Engler et al., 2011; Pauli et al., 2012; Niskanen et al., 2019; Barredo et al., 2020). In recent decades, climate change has emerged as the primary threat to such plants, with rising temperatures, reduced precipitation, and altered precipitation patterns posing significant risks (Kobiv, 2017, 2018; Rixen & Wipf, 2017; Winnicki, 2017).

In the Carpathians, potential ecological niche loss or significant reductions have already been detected for *Kalmia procumbens* (Walas et al., 2023) and, in the Romanian Carpathians, for *Leontopodium alpinum* Colm. (Maghiar et al., 2020). Similar projections have been made for several boreal tree species (e.g., Dyderski et al., 2018). Geographic analyses of high mountain woody species in the Ukrainian Carpathians have also highlighted their potential vulnerability (Tasenkevich et al., 2023). However, the negative effects of climate change in the mountain locations may be mitigated by local microsite conditions (Opedal et al., 2014).

Future climate change scenarios suggest rising temperatures and the migration of cold-adapted species, such as glacial relics, to higher elevations. However, in some areas, this vertical range shift may not be feasible, particularly if the mountain region lacks sufficient altitudinal range or if the temperature increase occurs too rapidly (Spinoni et al., 2015). The very high risk of extinction concerns the peat-bog species from the submontane and montane zones, but also from the subalpine vegetation belt. Identifying potential climate refugia for arctic-alpine and peat-bog plants is therefore crucial for their preservation in European mountain ecosystems.

Beyond climate change, human influence poses an additional and significant threat to high mountain flora, subalpine and alpine vegetation, and mountain peat bog species in the Eastern Carpathians of Ukraine. The cessation of traditional land use, the upward shift of trees and shrubs due to warming, and mass tourism are frequently cited as major threats to high mountain plant cover (e.g., Pauli et al., 2012; Ross et al., 2012; Didukh et al., 2017; Czortek et al., 2018; Zeidler et al., 2023). These processes contribute to biodiversity loss and may lead to the extinction of some of the most valuable elements of the Ukrainian Eastern Carpathian flora (Cherepanyn, 2019; Tasenkevich et al., 2023).

## Conclusion

The data presented in this study, along with the findings published by Tasenkevich et al. (2023), provide a comprehensive account of the occurrence of woody subalpine and alpine plants in the Carpathians of Ukraine. High mountain woody species in the Ukrainian parts of the Eastern Carpathians are significant and valuable components of the regional flora, occurring predominantly in the highest and most extensive mountain massifs. The predominance of subalpine and alpine species on north- or near-north-facing slopes suggests that these taxa are more tolerant to low temperature and present higher humidity requirements for both soil and air conditions. However, species that prefer south-facing slopes may have a different origin, potentially unrelated to Pleistocene glaciations. Subalpine and alpine taxa represent valuable yet highly threatened elements of the Eastern Carpathian flora. Their conservation is essential to maintaining the region's biodiversity, particularly in light of ongoing climatic and anthropogenic pressures.

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