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SPECIAL FEATURE

Ultramafic Ecosystems: Proceedings of the 9th International Conference on Serpentine Ecology

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Ultramafic vegetation and soils in the circumboreal region of the Northern Hemisphere

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Abstract The paper summarizes literature on climate, soil chemistry, vegetation and metal accumulation by plants found on ultramafic substrata in the circumboreal zone (sensu Takhtajan, Floristic regions of the world, 1986) of the Northern Hemisphere. We present a list of 50 endemic species and 18 ecotypes obligate to ultramafic soils from the circumboreal region of Holarctic, as well as 30 and 2 species of Ni and Zn hyperaccumulators, respectively. The number of both endemics and hyperaccumulators are markedly lower compared to that of the Mediterranean and tropical regions. The diversity of plant communities on ultramafics soils of the circumboral region is also described. The underlying causes for the differences of ultramafic flora between arctic, cold, cool temperate and Mediterranean and tropical regions are also discussed.

Keywords Ultramafic vegetation · Ultramafic soils · Obligate serpentinophytes · Edaphic endemism · Metal hyperaccumulation

Introduction

The uniqueness of vegetation growing on ultramafic (serpentine) soils has long been discussed (Brooks 1987; Baker et al. 1992; Roberts and Proctor 1992; Rajakaruna et al. 2009; Galey et al. 2017). The most thoroughly studied ultramafic vegetation are those of Mediterranean and tropical regions where the communities are characterized by low productivity and reduced floristic diversity compared to those on non-ultramafic soils (Pichi-Sermolli 1948; Harrison and Rajakaruna 2011). Ultramafic habitats of Mediterranean and tropical regions are home to unique plant communities (Galey et al. 2017), often rich in endemic species and subspecies as well as specific morphological and ecological forms (i.e. ecotypes; O'Dell and Rajakaruna 2011). Ultramafic soils are unique in harboring both basicolous and acidicolous species and the ultramafic flora often has a relatively xerophytic character and is dominated by certain families (Rune 1953).

Ultramafic rocks are widely distributed in the circumboreal region of the Northern Hemisphere and represented in the British Islands, Scandinavia, Central and Southern Europe, Ural Mountains, Altai, Chukotka, Hokkaido, Alaska, Northeast USA, northwestern US and adjacent Canada, and north- and southeastern Canada (Brooks 1987; Roberts and Proctor 1992). However, the literature on ultramafic vegetation and soil of this region is scant. This is a consequence of dispersed location, patchiness of exposed habitat, remoteness and poor accessibility of ultramafic massifs. The most thorough treatments available to date are of ultramafic vegetation in the Scandinavian region (Rune 1953; Rune and Westerberg 1992; Nyberg Berglund et al. 2004) and eastern North America (Rajakaruna et al. 2009). Some ultramafic communities in Britain (Proctor 1992), including the Lizard peninsula in England and outcrops in Anglesey, Wales (Proctor and Woodell 1971), Scotland (Steele 1955), Cornwall (Coombe and Frost 1956a, b) and Unst outcrop in Shetland (Spence 1957, 1958, 1959; Shewry and Peterson 1976; Carter et al. 1987) and Ireland (Brearley 2018) have also received some attention.

Studies in North America include those of the Alaska region, part of the Circum-Pacific orogenic belt, along the northern Pacific coast of USA (Alexander 2004; Alexander et al. 2007), the Appalachian Mountains of eastern North America (Rajakaruna et al. 2009; Burgess

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et al. 2015; Flinn et al. 2017), Southern British Columbia (Lewis and Bradfield 2004; Lewis et al. 2004), Gaspé Peninsula in Québec (Sirois and Grandtner 1992) and the Island of Newfoundland (Roberts and Proctor 1992) in Canada.

Ultramafic flora of Europe focus on ultramafic outcrops in the Balkan Peninsula (Tatić and Veljović 1992; Bani et al. 2010), and the North Caucasus (Drozdova et al. 2013; Alekseeva-Popova et al. 2015). Studies in the Eastern part of Eurasia include those in the ultramafic mountains occurring in the Polar region (Alekseeva-Popova 1970; Yurtzev et al. 2004; Proctor et al. 2005; Kholod 2007), Northern (Kulikov and Kirsanova 2012), Middle and Southern Urals (Teptina and Paukov 2012, 2015), Chukotka (Drozdova and Yurtzev 1995; Drozdova and Alekseeva-Popova 1999) and Japan (Mizuno and Nosaka 1992; Sakaguchi et al. 2017).

Scattered data and the wide range of climatic and orographic conditions do not give a complete picture of the peculiarities of ultramafic floras of arctic, cold and cool temperate climate; however, it is known that unlike those of regions with Mediterranean and tropical climate, they usually do not bear such distinct differences in comparison with their surrounding vegetation (Proctor 1999). They are additionally characterized by low endemism (Kruckeberg 2002) and relatively low number of hyperaccumulator species (Baker and Brooks 1989). In order to highlight the unique attributes of ultramafic vegetation in the circumboreal region, we present an overview of the literature on the ultramafic vegetation of the arctic, cold and cool temperate regions of the Northern Hemisphere.

Delimitation of the region

We have chosen three approaches for delimitation of the territory under consideration. The primary consideration is based on the floristic criteria used by Takhtajan (1986). This is used in order to demonstrate the floristic and genetic affinity of the flora of the territory. We follow the nomenclature of Takhtajan who used the term “circumboreal” for this region. Much of the Northern Hemisphere belongs to the Circumboreal floristic region of Holarctic which includes almost entire Russia except for the Far East south to the river Amur; northern Mongolia, Caucasus (except Talysh), Europe (except for the Mediterranean region), USA and Canada north to the oblique line, connecting New Scotland and Kenai Peninsula, Alaska and Aleutian Islands.

The second step was the delimitation of vegetational types within the circumboreal region and defining borders including similar types on both continents. The outlined region includes the Arctic deserts to broadleaf forests or mixed forests in continental regions (Adams 2007).

Table 1 The climate of the circumboreal region

Climate groups (according to the Köppen climate classification)	Vegetation zone	Mean annual temperature (°C)	Annual precipitation (mm)	Isotherm of July (°C)	Isotherm of January (°C)	Distribution
Oceanic temperate (Cfb) and subpolar (Cfc)	Temperate broadleaf forests	9.7–11.4	650–1200	11.3–18.4	3.6–7.7	England, Scotland, Wales, Svolvær, Lofoten, Nordland, Norway, Germany, British Columbia, Canada
Hemiboreal (Dfb)	Broadleaf, broadleaf–coniferous, birch–aspen forests or forest–steppes	3.0–6.8	430–688	17.0–20.8	− 15–0.3	Southern Canada, northeastern USA, southern Norway, Sweden, Southern Siberia, Latvia, Lithuania, Belarus, Estonia, coastal zone Finland
Subarctic (Boreal) (Dfc)	Taiga	− 5.4–2.8	488–605	11.5–18.7	− 19.5– − 7.6	Northeastern Russia, Scandinavia, Scottish Highlands, northern Kazakhstan, Mongolia, Japan, northeastern USA, Canada, Alaska
Polar (ET)	Tundra	− 12.8–0.6	115–503	4.9–13.5	− 30.2– − 10.1	Alaska, Canada, parts of Scandinavia, North of Kola Peninsula, Western Siberia, Iceland

The data from http://www.pogodaiklimat.ru for cities and settlements situated in the territory with corresponding climate group

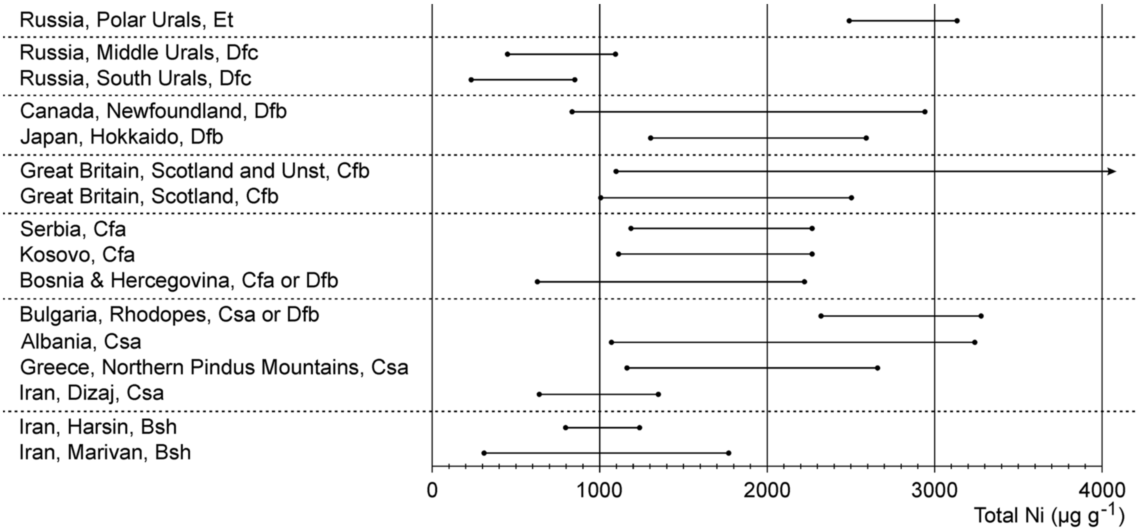

Fig. 1 Total Ni concentrations in ultramafic soils in particular localities of the Northern Hemisphere grouped according to Köppen climate classification (BSh—hot semi-arid climate, Cfa—humid subtropical climate, Cfb—temperate oceanic climate, Csa—hot-summer Mediterranean climate, Dfb—warm-summer humid continental climate, Dfc—subarctic climate, Et—tundra climate) Sources: Proctor and Woodell (1971), Proctor (1992), Roberts and Proctor (1992), Ghaderian et al. (2007a, b), Bani et al. (2009, 2010, 2013); Mizuno et al. (2009), Kataeva (2013), Tomović et al. (2013), Tumi (2013), Teptina and Paukov (2015) and Stamenković et al. (2017)

According to Köppen climate classification, the region under consideration covers areas with hemiboreal, boreal and polar climates (Peel et al. 2007). The climate of the territory is characterized by long and cold (below freezing point) winters, short and cool to warm summers, limited annual precipitation which exceeds evaporation and the absence of dry seasons. The warmest region under consideration is associated with cool temperate climate (Cfb and Cfc in the Köppen climate classification), whereas the coldest are subarctic (Dfc), extremely cold subarctic (Dfd) and polar (ET) climate. Intermediate conditions are characterized as humid continental climate (Dfb) (Table 1).

Elemental concentrations in ultramafic soils

Peculiarities of the climatic regime of the circumboreal region affect the processes of soil formation and chemical and physical characteristics of ultramafic soils. Ultramafic soils pose stressful conditions for plant growth. They are generally nutrient-poor (infertile), contain small amounts of most essential nutrients, such as nitrogen, potassium, phosphorus and calcium (Ca), and have high concentration of iron (Fe), magnesium (Mg), nickel (Ni), chromium (Cr) and cobalt (Co) (Proctor and Woodell 1975; Kruckeberg 1984; Brooks 1987; Roberts and Proctor 1992; Brady et al. 2005; Kazakou et al. 2008).

Skeletal soils on serpentinites are characterized by low plant nutrients, particularly phosphorus and potassium as reported for Great Britain (0.02%, Proctor and Woodell 1971). Potassium is also low in the soils of Newfoundland (0.03–0.39%, Roberts and Proctor 1992), Japan (0.02–4.7%, Mizuno et al. 2009), and Middle and Southern Urals (0.02–0.43%, Teptina and Paukov 2015). Low quantities of potassium are also reported in the Polar Urals (Proctor et al. 2005; Kataeva 2013), Chukotka (Drozdova and Yurtzev 1995; Drozdova and Alekseeva-Popova 1999), and North America (Alexander 2004). Unlike skeletal soils, ultramafic soils under a canopy of vegetation are distinct by having relatively higher concentrations of major nutrients (Proctor and Woodell 1971).

Ultramafic soils usually contain elevated concentrations of trace elements such as Ni, Co, and Cr, which are toxic to most plants. Ni concentrations in the circumboreal region commonly vary from 100–2600 μg g^{-1}, much lower compared to tropical regions which average 500–5000 μg g^{-1} (Reeves et al. 1996; Reeves and Baker 2000). Higher concentrations of total Ni were recorded in a few sites in Hokkaido (2590 μg g^{-1} Ni), Polar Urals (2830 μg g^{-1} Ni) and for skeletal soils in Newfoundland (3980 μg g^{-1} Ni). Exceptionally high concentrations were reported by Proctor (1992) and Carter et al. (1987) for Unst and Shetland ultramafic sites, respectively, in Great Britain (up to 9700 μg g^{-1} Ni).

Territories situated to the south of the circumboreal region similarly do not contain extremely high concentrations of total Ni. Examples include Albania 54–3579 μg g^{-1} (Shallari et al. 1998; Bani et al. 2010), Northern Greece (1160–2660 μg g^{-1}; Bani et al. 2010), Bulgaria (2333–3278 μg g^{-1}; Bani et al. 2010), and Iran (310–1775 μg g^{-1}; Ghaderian et al. 2007a, b) (Fig. 1). There is no particular trend for total Ni in ultramafic soils depending on latitude or climatic group, but may rather depend on the chemistry of underlying parental rocks.

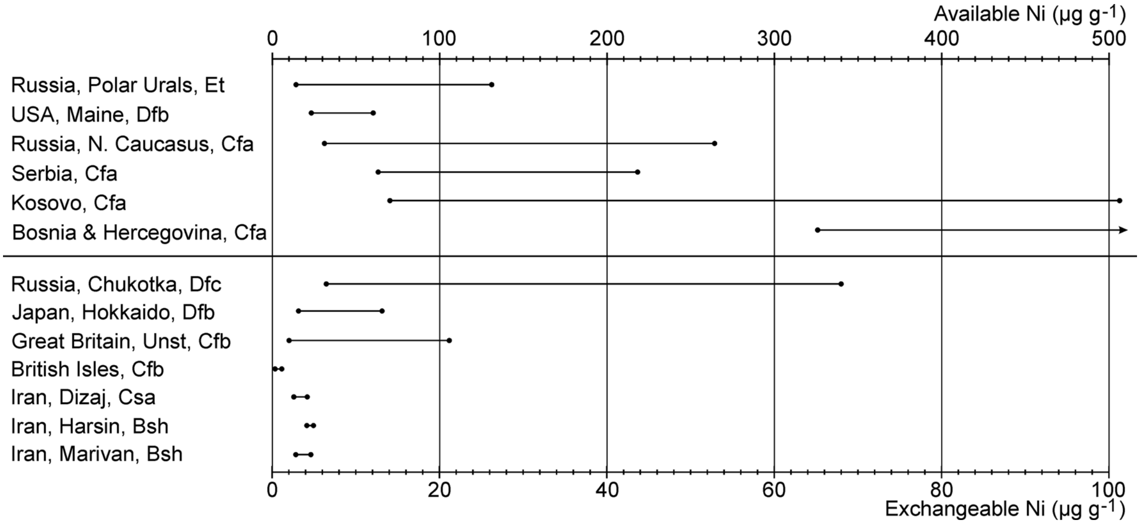

Fig. 2 Available and exchangeable Ni concentrations in ultramafic soils in particular localities of the Northern Hemisphere grouped according to Köppen climate classification Sources: Shewry and Peterson (1976), Carter et al. (1987), Garcia-Gonzalez and Clark (1989), Alekseeva-Popova and Drozdova (1996), Ghaderian et al. (Ghaderian et al. 2007a, b), Harris et al. (2007), Mizuno et al. (2009), Kataeva (2013), Tomović et al. (2013), Tumi (2013), Alekseeva-Popova et al. (2015) and Stamenković et al. (2017)

Data on available and exchangeable Ni in soils of different localities are not exhaustive to make a comprehensive conclusion on its dependence on climatic factors; however, soils in localities which belong to the circumboreal region contain less available and more exchangeable Ni compared to more southern sites situated in Iran or in the Mediterranean region (Fig. 2).

Content of other metals in soils of circumboreal zone is likewise highly variable and may reflect the peculiarities of chemical composition of ultramafic rocks. Chromium content in soils vary dramatically: 50–19,100 μg g^{-1} in Britain (Proctor 1992), 55–523 μg g^{-1} in the Southern and Middle Urals (Teptina and Paukov 2015) and 91–3865 μg g^{-1} in Albania (Shallari et al. 1998; Bani et al. 2010), 1110–2170 μg g^{-1} in Greece (Bani et al. 2010), 1785–3870 μg g^{-1} in Bulgaria (Bani et al. 2010), and 36–365 μg g^{-1} in Iran (Ghaderian et al. 2007a, b)

A ten-fold difference was found between the lowest and the highest concentrations of total Fe and Co in ultramafic soils between arctic, cold, cool temperate and Mediterranean regions. The northernmost localities contain less total Fe, Ca and Co (Figs. 3, 4). However, similarity of Fe and Co in ultramafic soils of Iran and Middle Urals may reflect its dependence on the features of underlying rocks.

Generally reduced Ca is another distinguishing feature of ultramafic soils, as emphasized in studies of Proctor and Woodell (1971) and others (Rajakaruna et al. 2009; Galey et al. 2017). It is generally less than 1% (often with a Ca:Mg molar quotient of < 1), however, Ca concentrations may vary from very low (0.11% in Albania) to fairly high (7% in Britain). Conversely, Mg is prevalent in all ultramafic soils of circumboreal region, including 0.8–5.4% in the Southern and Middle Urals (Teptina and Paukov 2015), 0.16–0.17% in Maine (Pope et al. 2010), 11–26% in Japan (Mizuno et al. 2009), 13–19% in Bulgaria (Bani et al. 2010), and 10–16% in Iran (Ghaderian et al. 2007a, b).

Vegetation

The flora of the region under consideration is extremely heterogeneous, often resulting from extreme localisation, climate, orography and other abiotic and biotic factors. Even in regions with the same climate there is a significant heterogeneity with respect to ultramafic associated vegetation (Rune 1953; Proctor 2003).

In the global scale, vegetation communities of ultramafic soils vary from wet bogs and different types of forests to steppe and open, outcrop communities. Within the circumboreal region, the features of ultramafic vegetation are determined by geology, climate and relief. Rune (1953) noted that the vegetation of ultramafics, even within a small region such as Northern Sweden, is not uniform, varying from grasslands and forests to open, rock outcrop communities.

Despite numerous studies on the significant contrast of vegetation between ultramafic and non-ultramafic sites in regions with Mediterranean and tropical climates (reviewed in Kruckeberg 1992; Roberts and Proctor 1992; Galey et al. 2017), such differences in vegetation of ultramafics in arctic, cold and cool temperate regions are not well known. Plant communities on the ultramafic outcrops in Britain and Shetland essentially do not have any soil-specific features (Coombe and Frost 1956a, b; Spence and Millar 1963; Spence 1970). A weak contrast in the structure and species composition on ultramafic and granite outcrops of Deer Isles, Maine was, however, noted (Pope et al. 2010). On developed soils on flatlands, vegetation is often represented by zonal communities,

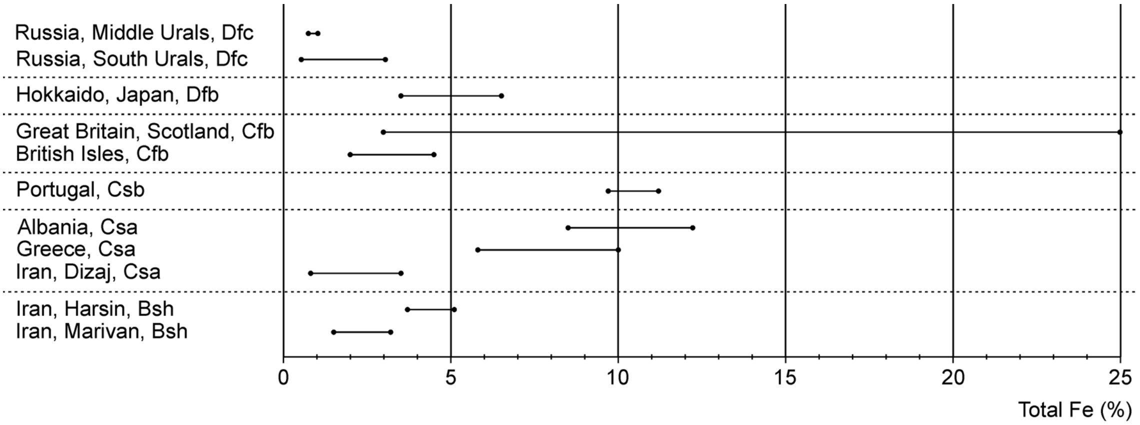

Fig. 3 Total Fe concentrations in ultramafic soils in particular localities of the Northern Hemisphere grouped according to Köppen climate classification. Sources are the same as in Figs. 1 and 2

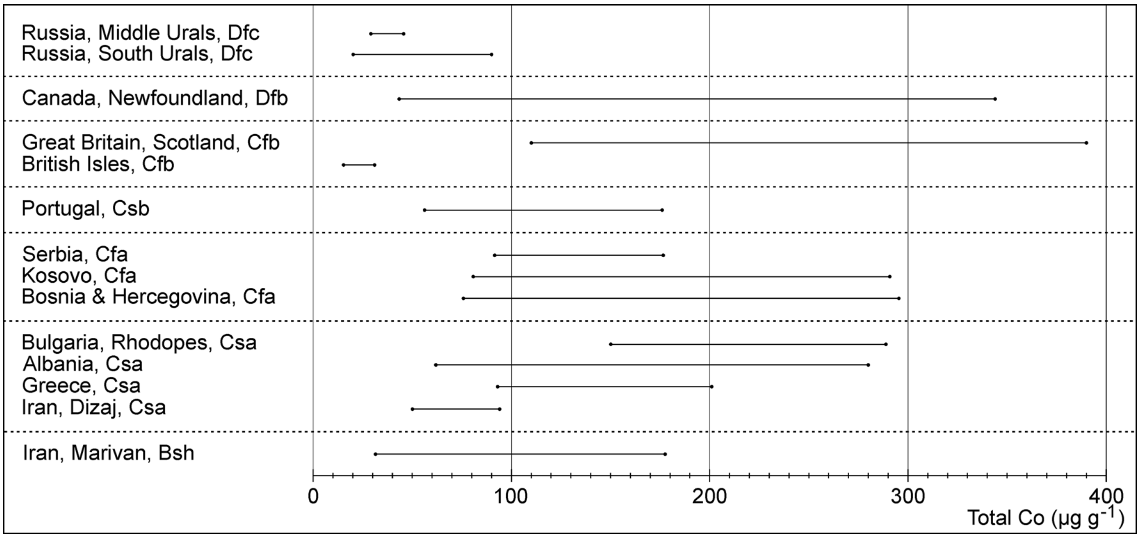

Fig. 4 Total Co concentrations in ultramafic soils in particular localities of the Northern Hemisphere grouped according to Köppen climate classification. Sources are the same as in Figs. 1 and 2

devoid of unique features, as in the Urals Mountains (Teptina and Paukov 2012) and in the Czech Republic (Chytrý 2012).

On undeveloped soils, which are formed on slopes, summits of mountains and river banks, the influence of underlying rocks is greater. Rune (1953) notes the presence of sharp division between ultramafic and non-ultramafic vegetation of coastal districts in Norway and on Mt. Albert in Québec (Rune 1954). Chitrý (2012) reports a marked shift of *Fagus sylvatica*- and *Carpinus betulus*-dominated communities by *Pinus sylvestris* or *Quercus petraea* forests on shallow ultramafic soils.

Syntaxonomical revision of plant communities on ultramafic bedrocks allows describing unique, often endemic ultramafic associations (Roberts and Proctor 1992; Stevanović et al. 2003; Alexander et al. 2007). Numerous phytosociological studies have been conducted for ultramafic vegetation of Mediterranean region of California (Rivas-Martínez 1997; Rodríguez-Rojo et al. 2001a, b; Sánchez-Mata et al. 2004; Sánchez-Mata and Rodríguez-Rojo 2016).

Comparatively little data exist on the diversity of ultramafic communities in cool temperate sites of the Balkan region. Several associations, which belong to the endemic order *Halacsyetalia sendtneri*, were discribed from the eastern and central part of ultramafic grasslands of western Balkans (Ritter-Studnička 1970) and from the south-eastern part of Kosovo (Blečić et al. 1969; Jovanović et al. 1992; Millaku et al. 2011). The associations from Kosovo belong to alliance *Centaureo–Bromion fibrosi*. Thorough investigations of ultramafic grasslands in Bulgaria and similar communities of regional countries have resulted in one new endemic association, *Onosmo pavlovae–Festucetum dalmaticae*, which is included in *Alyssion heldreichii* alliance occuring on ultramafic outcrops in northern Greece (Janišová et al. 2011; Vassilev et al. 2011; Tzonev et al. 2013).

Table 2 Endemic taxa reported for the region

Taxon	Family	Status	References	Distribution
Adiantum pedatum subsp. *calderi* Cody (currently considered as *A. aleuticum* (Ruprecht) Paris)	Pteridaceae	Endemic, mostly obligate to ultramafics in eastern N America	Cody (1983), Gawler (1983) and Lewis and Bradfield (2003)	Maine, Vermont, California, Washington, USA; Quebec, Newfoundland, Canada
Adiantum viridimontanum C. A. Paris	Pteridaceae	Endemic, obligate to ultramafics	Paris (1991) and Harris and Rajakaruna (2009)	E North America
Anchusa leucantha Selvi and Bigazzi (sometimes treated as a synonym of the *A. officinalis* subsp. *leucantha* Boiss.)	Boraginaceae	Endemic, obligate to ultramafics	Cecchi and Selvi (2009) and Tan et al. (2013)	SE Albania, S former Yugoslav Republic, Macedonia and N Greece
Aristolochia merxmuelleri Greuter and E. Mayer	Aristolochiaceae	Endemic, obligate to ultramafics	Mayer and Greuter (1985)	Kosovo
Aspidotis densa (Brack.) Lellinger	Pteridaceae	Endemic, obligate to ultramafics	Harris and Rajakaruna (2009)	from British Columbia to California to Wyoming, Quebec
Asplenium adiantum-nigrum L.	Aspleniaceae	Locally adapted ecotypes	Sleep (1985)	Scotland, Europe, North America
Aster albanicus Degen.	Asteraceae	Endemic, obligate to ultramafics	Krasniqi et al. (2008)	Serbia, Albania
Bornmuellera dieckii Degen	Brassicaceae	Paleoendemic, obligate to ultramafics	Mayer and Greuter (1985), Niketić (1994), Stevanović et al. (2003) and Tomović et al.(2014)	W, C Serbia, N Albania, N Macedonia
Cerastium alpinum L. var. *ophiticola*	Caryophyllaceae	Locally adapted ecotypes	Raymond (1955)	Canada, Québec
Cerastium alpinum L. var. *serpentinicola* (sometimes treated as a synonym of the *C. alpinum* L.)	Caryophyllaceae	Locally adapted ecotypes	Rune (1953) and Nyberg Berglund et al. (2001)	Fennoscandia
Cerastium alsinifolium Tausch	Caryophyllaceae	Neoendemic, obligate to ultramafics	Vit et al. (2014)	W Bohemia, Czech Republic
Cerastium arvense f. *serpentini* Novák	Caryophyllaceae	Locally adapted ecotypes	Novák (1928)	Bohemia, E, C Europe
Cerastium arvense var. *ophiticola* Raymond (sometimes treated as a synonym of the *C. arvense* subsp. *strictum* Gaudin.)	Caryophyllaceae	Locally adapted ecotypes	Raymond (1955) and Flora of North America (efloras.org)	S Québec, Canada
Cerastium caespitosum f. *serpentini* F. A. Novák (sometimes treated as a synonym of the *C. fontanum* subsp. *vulgare* (Hartm.) Greuter and Burdet)	Caryophyllaceae	Locally adapted ecotypes	Novák (1927)	Czech Republic
Cerastium fontanum Baumg. subsp. *scoticum* Jalas e Sell	Caryophyllaceae	Endemic, obligate to ultramafics	Nagy and Proctor (1997)	Meikle Kilrannoch, Angus, United Kingdom

Table 2 continued

Taxon	Family	Status	References	Distribution
Cerastium holosteoides subsp. *serpentini* (F. A. Novák) J. Dostál (sometimes treated as a synonym of the *C. fontanum* subsp. *vulgare* (Hartm.) Greuter and Burdet)	Caryophyllaceae	Locally adapted ecotypes	Dostál (1984)	Czech Republic
Cerastium malyi (T. Georgiev) Niketić subsp. *serpentini* (Novák) Niketić	Caryophyllaceae	Endemic, obligate to ultramafics	Tomović et al. (2014)	W, C, SW Serbia; Kosovo
Cerastium neoscardicum Niketić	Caryophyllaceae	Endemic, obligate to ultramafics	Mayer and Greuter (1985), Niketić (1994), Marin and Tatić (2001), Vasié and Diklié (2001), Stevanović et al. (2003)	Balkans
Cerastium nigrescens (H. C. Watson) Edmondston ex H. C. Watson	Caryophyllaceae	Endemic, obligate to ultramafics	Scott and Palmer (1987), Stace (1997) and Brysting (2008)	Shetland
Cerastium smolikanum Hartvig	Caryophyllaceae	Endemic, obligate to ultramafics	Niketić (1994), Marin and Tatić (2001) and Stevanović et al. (2003)	Balkans
Cerastium utriense Barberis	Caryophyllaceae	Endemic, obligate to ultramafics	Marsili et al. (2009)	NW Italy
Cerastium velutinum Rafinesque var. *villosissimum* (Pennell) J. K. Morton (*C. arvense* var. *villosissimum* Pennell)	Caryophyllaceae	Endemic, obligate to ultramafics	Tyndall and Hull (1999), Gustafson et al. (2003), Morton (2004) and Rajakaruna et al. (2009)	E North America
Cerastium vourinense Moschl and Rech. f.	Caryophyllaceae	Endemic, obligate to ultramafics	Niketić (1994), Marin and Tatic (2001) and Stevanović et al. (2003)	Balkans
Cerastium vulgatum var. *kajanense* Kotil. and Veera Salmi (sometimes treated as a synonym of the *C. fontanum* subsp. *vulgare* (Hartm.) Greuter and Burdet)	Caryophyllaceae	Locally adapted ecotypes	Kotilanen and Salmi (1950) and Rune (1953)	Norway, N Sweeden
Cerastium vulgatum L. var. *serpentini* (Novák) Gartner (sometimes treated as a synonym of the *C. fontanum* subsp. *vulgare* (Hartm.) Greuter and Burdet)	Caryophyllaceae	Locally adapted ecotypes	Kotilanen and Salmi (1950) and Rune (1953)	Norway
Drymocallis malacophila (Borbás) Kurtto	Rosaceae	Paleoendemic, obligate to ultramafics	Stevanović et al. (2003) and Tomović et al. (2014)	W, C Serbia, N Albania, N Macedonia
Eryngium serbicum Pančić	Apiaceae	Paleoendemic, obligate to ultramafics	Stevanović et al. (2003) and Tomović et al. (2014)	W, C Serbia, N Albania, N Macedonia
Euphorbia glabriflora Vis.	Euphorbiaceae	Paleoendemic, obligate to ultramafics	Stevanović et al. (2003) and Tomović et al. (2014)	W, C Serbia, N Albania, N Macedonia
Euphorbia serpentini Novák	Euphorbiaceae	Endemic, obligate to ultramafics	Tomović et al. (2014)	W Serbia

Table 2 continued

Taxon	Family	Status	References	Distribution
Fumana bonapartei Maire and Petitm.	Cistaceae	Paleoendemic, obligate to ultramafics	Stevanović et al. (2003) and Tomović et al. (2014)	W, C Serbia, N Albania, N Macedonia
Gypsophila spergulifolia Griseb.	Caryophyllaceae	Paleoendemic, obligate to ultramafics	Stevanović et al. (2003) and Tomović et al. (2014)	W, C Serbia, N Albania, N Macedonia, Metohija
Halacsya sendtneri (Boiss.) Dörfl.	Boraginaceae	Paleoendemic, obligate to ultramafics	Stevanović et al. (2003) and Tomović et al. (2014)	W, C Serbia, N Albania, N Macedonia, Kosovo, Metohija
Haplophyllum boisserianum Vis. and Pančić	Rutaceae	Paleoendemic, obligate to ultramafics	Stevanović et al. (2003)	W, C Serbia, N Albania, N Macedonia
Japonolirion osense Nakai	Petrosaviaceae	Endemic, obligate to ultramafics, relict	Tomović et al. (2014)	Japan
Juniperus communis L. subsp. *communis*	Cupressaceae	Locally adapted ecotypes	Proctor (1992)	Great Britain
Knautia pseudolongifolia (Szabó) Żmuda (former *K. arvensis* subsp. *pseudolongifolia*)	Caprifoliaceae	Endemic, obligate to ultramafics, postglacial relict	Štepánek (1989) and Kaplan (1998)	Czech Republic
Knautia serpentinicola Smejkal ex Kolář, Z. Kaplan, J. Suda et Štech (former *K. arvensis* subsp. *serpentinicola*)	Caprifoliaceae	Endemic, obligate to ultramafics, postglacial relict	Štepánek (1989), Kaplan (1998) and Kolár et al. (2015)	Czech Republic
Lilium japonicum var. *abeanum* (Honda) Kitam (sometimes treated as a synonym of *L. japonicum* Thunb.)	Liliaceae	Endemic, obligate to ultramafics	Kitamura and Momotani (1952) and Kawase et al. (2010)	Japan
Melandrium rubrum Garcke var. *serpentini* (sometimes treated as a synonym of *Silene dioica* (L.) Clairv.)	Caryophyllaceae	Locally adapted ecotypes	Kruckeberg (2002)	Scandinavia
Melandrium rubrum Garcke var. *serpentinicola* (sometimes treated as a synonym of *Silene dioica* (L.) Clairv.)	Caryophyllaceae	Locally adapted ecotypes	Rune (1953)	N Sweden
Melandrium rubrum Garcke var. *smithii* (sometimes treated as a synonym of *Silene dioica* (L.) Clairv.)	Caryophyllaceae	Locally adapted ecotypes	Rune (1953)	N Sweden
Minuartia marcescens (Fernald) House	Caryophyllaceae	Endemic, obligate to ultramafics	Harris and Rajakaruna (2009)	E North America
Minuartia smejkalii Dvořáková (sometimes treated as a synonym of *M. verna* (L.) Hiern. subsp. *verna*)	Caryophyllaceae	Neoendemic, obligate to ultramafics	Dvoráková 1988	W Bohemia, Czech Republic
Minuartia verna (L.) Hiern. subsp. *verna*	Caryophyllaceae	Locally adapted ecotypes	Proctor (1992)	Great Britain
Onosma elegantissima Rech. f. and Goulimy	Boraginaceae	Endemic, obligate to ultramafics	Stevanović et al. (2003) and Cecchi and Selvi (2009)	Balkans
Onosma euboica Rech. f.	Boraginaceae	Endemic, obligate to ultramafics	Stevanović et al. (2003) and Cecchi and Selvi (2009)	Balkans
Onosma kittanae Strid	Boraginaceae	Endemic, obligate to ultramafics	Stevanović et al. (2003) and Cecchi and Selvi (2009)	Balkans

Table 2 continued

Taxon	Family	Status	References	Distribution
Onosma pygmaea H. Riedl	Boraginaceae	Endemic, obligate to ultramafics	Stevanović et al. (2003) and Cecchi and Selvi (2009)	Balkans
Onosma stridii Teppner	Boraginaceae	Endemic, obligate to ultramafics	Stevanović et al. (2003) and Cecchi and Selvi (2009)	Balkans
Oxytropis deflexa subsp. *norwegica* (sometimes treated as a synonym of the *O. deflexa* (Pall.) DC.)	Fabaceae	Alpine-northern boreal endemic, obligate to ultramafics	Dahl (1998)	N Norway, NE, Altai Mountains, Russia
Packera serpenticola (L.) A. Löve and D. Löve	Asteraceae	Endemic, obligate to ultramafics	Boufford et al. (2014)	Clay County, N Carolina, USA
Paramoltkia doerfleri (Wettst.) Greuter and Burdet	Boraginaceae	Paleoendemic, obligate to ultramafics	Stevanović et al. (2003) and Tomović et al. (2014)	W, C Serbia, N Albania, N Macedonia
Peltaria emarginata (Boiss.) Hausskn. (former *Leptoplax emarginata* (Boiss.) O.E. Schulz	Brassicaceae	Endemic, obligate to ultramafics	Stevanović et al. (2003)	N Greece
Plantago maritima	Plantaginaceae	Locally adapted ecotypes	Proctor (1992)	Great Britain
Polygala doerjleri Hayek	Polygalaceae	Endemic, obligate to ultramafics	Tomović et al. (2014)	Kosovo, Metohija
Potentilla visianii Pančić	Rosaceae	Paleoendemic, obligate to ultramafics	Stevanović et al. (2003) and Tomović et al. (2014)	W, C Serbia, N Albania, N Macedonia
Rumex acetosa L. var. *serpentinicola*	Polygonaceae	Locally adapted ecotypes	Rune (1953)	Norway
Lychnis alpina L. var. *serpentinicola*	Caryophyllaceae	Locally adapted ecotypes	Rune (1953)	Norway
Sanquisorba albanica Andraszovsky	Rosaceae	Paleoendemic, obligate to ultramafics	Niketić (1994), Mayer and Greuter (1985), Tomović et al. (2014) and Stevanović et al. (2003)	W, C Serbia, N Albania, N Macedonia, Kosovo, Metohija
Saponaria intermedia Simmler	Caryophyllaceae	Paleoendemic, obligate to ultramafics	Niketić (1994), Mayer and Greuter (1985), Stevanović et al. (2003) and Tomović et al. (2014)	W, C Serbia, N Albania, N Macedonia, Kosovo, Metohija
Sempervivum kosaninii Praeger	Crassulaceae	Endemic, obligate to ultramafics	Niketić (1994), Mayer and Greuter (1985), Tomović et al. (2014) and Stevanović et al. (2003) and Tomović et al. (2014)	Kosovo, Metohija
Stipa mayeri Martinovský	Poaceae	Endemic, obligate to ultramafics	Niketić (1994), Mayer and Greuter (1985), Tomović et al. (2014), Stevanović et al. (2003) and Tomović et al. (2014)	Kosovo, Metohija
Symphyotrichum rhiannon Weakley and Govus	Asteraceae	Endemic, obligate to ultramafics	Harris and Rajakaruna (2009)	E North America
Tulipa serbica Tatić and Krivošej		Endemic, obligate to ultramafics	Niketić (1994), Mayer and Greuter (1985), Tomović et al. (2014), 1997) and Stevanović et al. (2003)	Kosovo

Table 2 continued

Taxon	Family	Status	References	Distribution
Veronica andrasovszkyi Jávorka	Plantaginaceae	Endemic, obligate to ultramafics	Vasić and Diklić (2001)	Serbia, Albania
Veronica scardica Gris.	Plantaginaceae	Endemic, obligate to ultramafics	Fischer et al. (1984) and Vasić and Diklić (2001)	NE Serbia, Albania
Viola dukadjinica Becker and Košanin	Violaceae	Endemic, obligate to ultramafics	Yurtsev et al. (2001) and Tomović et al. (2014)	Serbia, Albania, Kosovo
Viscaria alpina var. *serpentinicola* Rune (sometimes treated as a synonym of the *Silene suecica* (Lodd.) Greuter and Burdet / *Silene dioica* subsp. *dioica* / *Lychnis alpina* L. var. *serpentinicola* (Rune) P. Kallio and Y. Mäkinen)	Caryophyllaceae	Locally adapted ecotypes	Rune (1953)	N Sweden

Ultramafic vegetation of rocks and screes in the Czech Republic was assigned to the class *Asplenietea trichomanis*, order *Asplenion cuneifolii* (Chytrý 2012) and the class *Asplenietea trichomanis*, alliance *Cystopteridion* (Vicherek 1970). Chasmophitic vegetation of ultramafic cliffs was included in the alliance *Asplenion serpentini*. Communities of dry ultramafic grasslands included in the alliance *Asplenio cuneifolii–Armerion serpentini* (Chytrý and Tichý 2003). Similarly, in Serbia, 19 associations were described on ultramafic soils and scree slopes (Jovanović et al. 1986; Lakušić and Sabovljević 2005), which were assigned to the alliance *Centaureo–Bromion fibrosi* and order *Halacsyetalia sendtneri*. One of these associations, *Stipetum novakii*, occurs on open rocky ultramafic grasslands in Brdjani Gorge (Kabaš et al. 2013).

On ultramafic outcrops of the Middle Urals, one association (*Pulsatillo uralensis–Helictotrichetum desertorum*) with two subassociations (*P. u.–H. d. calamagrostietosum arundinaceae*, *P. u.–H. d. calamagrostietosum epigeii*) were described (Teptina et al. 2018). The communities were assigned to the alliance *Helictotricho desertorum–Orostachyion spinosae*, of the order *Helictotricho-Stipetalia*, and class *Festuco-Brometea*.

Ultramafic pine forests were assigned to the class *Erico-Pinetea* and alliance *Erico-Pinion* (Chytrý and Tichý 2003). Pine forests on ultramafics at lower altitudes in central Bohemia and south-western Moravia *Sesleria caerulea* are assigned to the class Erico-Pinetea and alliance *Erico carneae–Pinion* (Chytrý 2012).

Geoedaphic factors determine the composition of flora of ultramafic substrates worldwide (Rajakaruna and Boyd 2008). The unique character of ultramafic flora has been repeatedly emphasized by researchers in both tropical and temperate regions (Robinson et al. 1997; Reeves et al. 1999; Van der Ent et al. 2015; Galey et al. 2017). Ultramafic flora of tropical regions, especially on islands, is characterized by a high level of endemism, often reaching 90% (Anacker 2011).

In comparison with floras on other rock types, ultramafic vegetation, even in higher latitudes, differs by fairly low species diversity and abundance. For example, the ultramafic flora of Norway and Finland (Rune 1953, 1954) includes a small number of species and individuals. Similarly, impoverished species diversity and abundance were documented in the Polar Urals (Igoshina 1966) where the flora of ultramafic massif Rai-Iz is species poor in comparison to the flora of schist massif Yar-Keu. Comparative studies of plant diversity on ultramafic soils of Rai-Iz and Voikaro-Syninsky ultramafic massifs and acidic soils of Big Paipudinskiy massif in tundra zone of the Polar Urals have also showed low diversity of species on ultramafic soils (Alekseeva-Popova 1970; Yurtsev et al. 2001). In the Southern Urals, lower plant species diversity on ultramafic rocks (Sugomakskiy ultramafic massif) was observed in comparison with the species diversity of Vishnevogorskiy sienite massif (Teptina and Paukov 2012).

The cover and abundance of plants are mainly determined by the nature of the soil. Shallow ultramafic soils usually have extremely sparse vegetation. Proctor and Woodell (1971) note poor composition of the debris flora in Scotland, but note relatively high abundance of heath communities on ultramafics, which occur on more developed soils. Likewise, diversity of plants on well developed ultramafic soils in the Middle Urals is similar to that on other substrates (Teptina and Paukov 2012).

The flora of ultramafics in northern Eurasia is distinguished by the presence of Caryophyllaceae (Rune 1953; Teptina and Paukov 2012), a family that is characteristic of Holarctic floras (Malyshev 1972) and typical for petrophytic communities on initial successional stages on rock substrates (Rune 1953; Kinzel 1982). One characteristic feature of boreal serpentinite floras is the absence of distinct families and genera (Yurtsev et al. 2001; Teptina and Paukov 2012). For example, the ultramafic flora of the Southern Urals is often devoid of members of Fabaceae, mainly the genera *Astragalus* and *Oxytropis*.

Ultramafic ecotypes and endemic taxa

Ultramafic soils provide a favourable environment for the origin of new taxa and can be considered as "islands" sharply demarcated by distinct edaphic conditions. Adaptations of plant populations to such unique conditions and their further divergence in isolation lead to the formation of ecologically, physiologically and morphologically distinct populations which can be considered as different taxa, i.e., forms, varieties, ecotypes, subspecies and species endemic to ultramafic soils (Rajakaruna 2018).

Morphological differences between populations of plants on ultramafic and non-ultramafic soils appear in the form of *serpentinomorphoses*. They are often described as stenophyllism, glabrescence, glaucescence and nanism (Rune 1953; Kruckeberg 2002). The existence of ultramafic races has been repeatedly noted by many researchers (Novák 1928; Rune 1953; Kruckeberg 2002; O'Dell and Rajakaruna 2011). For instance, physiological and morphological races of plants have been documented on British ultramafics (Proctor and Woodell 1971; Proctor 1992), including *Asplenium adiantum-nigrum* L. (Aspleniaceae), *Juniperus communis* L. (Cupressaceae), and *Minuartia verna* (L.) Hiern. (Caryophyllaceae). Additionally, Proctor (1992) reported several races of species, which differ ecologically or even morphologically, including *Plantago maritima* L. (Plantaginaceae), *Rubus saxatilis* L. (Rosaceae), *Rumex acetosa* L. (Polygonaceae) (on the Keen of Hamar, Shetland), *Minuartia verna* (L.) Hiern. subsp. *verna*, and *Juniperus communis* L. subsp. *communis* (on the 'Rock Heath'). Some ultramafic-associated varieties have also been described from ultramafics in Norway (e.g., *Rumex acetosa* L. var. *serpentinicola*, *Lychnis alpina* L. var. *serpentinicola* and *Cerastium alpinum* L. var. *serpentinicola* (Caryophyllaceae)) (Rune 1953), Canada, Québec (e.g., *Cerastium arvense* var. *ophiticola*) (Raymond 1955), Finland and Moravia (e.g., *Cerastium vulgatum* L. var. *serpentini* (Novák) Gartner) (Kotilanen and Salmi 1950), Scandinavia [e.g, *Melandrium rubrum* Garcke var. *serpentini* (Caryophyllaceae)] (Kruckeberg 2002). Investigation of ultramafic and non-ultramafic populations of *Cerastium alpinum* L. in Sweden and Finland (Nyberg Berglund and Westerbergh 2001; Nyberg Berglund et al. 2001, 2004) revealed differences in serpentine tolerance within the species and independent and multiple evolution of serpentine-tolerant populations (Table 2).

The main taxonomic problem associated with the numerous geoedaphic variants, subspecies and species, which were distinguished in the past, was that they were based only on information about occurrence on specific (ultramafic) bedrocks or their distinct morphological features. Many of these taxa need to be genetically examined to confirm if they are "good taxa."

Numerous ultramafic floras of the world are characterized by a high level of endemism (Brooks 1987). This is particularly true for tropical and subtropical regions, where ultramafic soils are inhabited by a large number of endemic plant taxa, many of which have limited distribution and are often endangered (Skinner and Pavlik

Fig. 5 Endemic species: **a** *Adiantum viridimontanum* C. A. Paris (eastern North America), **b** *Alyssum litvinovii* Knjaz. (Southern Urals, Russia)

Table 3 Hyperaccumulator species reported for the region

Species	Distribution	Ni concentrations (μg g^{-1})	References
Alyssum alpestre L. (currently *Odontarrhena alpestris* (L.) Ledeb.)	Central and western Alps of France, Germany, Switzerland	3640	Brooks et al. (1979)
Alyssum bertolonii Desv. subsp. *scutarinum* E. I. Nyàràdy	Albania	6984–8567	Bani et al. (2013)
	East of Prizren, former Yugoslavia	10200	Mengoni et al. (2003)
Alyssum markgrafii O. E. Schulz ex Markgraf	Albania	1113–12625	Shallari et al. (1998)
		3731–8089	Bani et al. (2013)
Alyssum montanum L.	Serbia	549–13160	Tumi (2013)
Alyssum murale Waldst. & Kit. (currently *Odontarrhena muralis* (Waldst. & Kit.) Endl.)	Northern Caucasus, Russia	4300–12130	Alekseeva-Popova et al. (2015)
	Bosnia and Herzegovina	10552	Stamenkovic et al. (2017)
	Albania	420–8463	Shallari et al. (1998)
		4973–10354	Bani et al. (2013)
	Serbia	946–13160	Tumi (2013)
	Armenia	> 10% 15%	Doksopulo (1961)
Alyssum obovatum (C. A. Mey.) Turcz. (currently *Odontarrhena obovata* C. A. Mey.)	Russia	1–4597	Brooks and Radford (1978); Brooks et al. (1979)
	Russia (originally identified and recorded as *A. fitcherianum*)	1026	Brooks and Radford (1978); Brooks et al. (1979)
	Alaska, USA, Yukon, Canada (originally identified and recorded as *A. americanum* Green)	11–381	Brooks et al. (1979)
	Southern Chukotka, Russia	926–1308	Brooks et al. (1979)
	Southern Chukotka, Russia	1200	Alekseeva-Popova et al. (1995)
	Polar Urals, Russia	2491	Proctor et al. (2005)
	Polar Urals, Russia	1000–4500	Alekseeva-Popova and Drozdova (2013)
	Middle Urals, Russia	728–1740	Teptina and Paukov (2015)
	Southern Urals, Russia	1110–6008	Teptina and Paukov (2015)
Alyssum saxatile L. (currently *Aurinia saxatilis* (L.) Desv.)	Albania	1300	Bani et al. (2013)
Arenaria humifusa Wahlenb.	Western Newfoundland, Canada	2330	Roberts and Proctor (1992)
Arenaria marcescens (Fernald) House	Western Newfoundland, Canada	2365	Roberts and Proctor (1992)
Armeria maritima (Mill.) Willd.	Island of Unst, Keen of Hamar, Scotland	1370	Shewry and Peterson (1976)
	Island of Unst, Dalepark, Scotland	3199	Shewry and Peterson (1976)
Bornmuellera baldaccii subsp. *markgrafii* O. E. Schulz	Albania	12115	Bani et al. (2013)
Calluna vulgaris (L.) Hull	Island of Unst, Keen of Hamar, Scotland	1599	Shewry and Peterson (1976)
	Island of Unst, Greenhill Serpentine, Scotland	1923	Shewry and Peterson (1976)
Cerastium holosteoides Fr. (probably *C. nigrescens*)	Island of Unst, Greenhill Serpentine, Scotland	1662	Shewry and Peterson (1976)

Table 3 continued

Species	Distribution	Ni concentrations (μg g^{-1})	References
Cerastium nigrescens (H. C. Watson) Edmondston ex H. C. Watson	Island of Unst, Keen of Hamar, Scotland	1266	Shewry and Peterson (1976)
Noccaea alpestris (Jacq.) Kerguélen (former *Thlaspi alpestre* Jacq.)	Central Europe	4000	Severne and Brooks (1972)
Noccaea aptera (Velen.) F.K.Meyer	former Yugoslav Republic	13600	Brooks (1983)
Noccaea borealis F. K. Mey. (former *Thlaspi cocheiariforme* DC)	Polar Urals, Russia	1400	Proctor et al. (2005)
Noccaea caerulescens (J. Presl & C. Presl) F. K. Mey.	Ayrshire, Scotland (now extinct)	> 1000	Proctor et al. (2005)
Noccaea japonica (H. Boissieu) F. K. Mey. (former *Thlaspi japonicum* H. Boiss)	Hokkaido, Japan	1299 820–1955	Mizuno et al. (2009); Reeves (1988)
Noccaea kovatsii (Heuff.) F. K. Mey.	Serbia	3082–3379	Tumi (2013)
Noccaea praecox (Wulfen) F. K. Mey.	Serbia	756–9244	Tumi (2013)
Noccaea thlaspidioides (Pall.) F. K. Mey.	Southern Urals, Russia	159–232	Teptina and Paukov (2015)
Packera paupercula (Michx.) Á. Löve & D.Löve. (former *Senecio pauperculus* Michx.)	Western Newfoundland, Canada	1903	Roberts and Proctor (1992)
Peltaria emarginata (Boiss.) Hausskn.	Greece	4800–34400	Reeves et al. (1980)
Sagina sp.	Island of Unst, Keen of Hamar, Scotland	1236	Shewry and Peterson (1976)
	Island of Unst, Greenhill Serpentine, Scotland	2407	Shewry and Peterson (1976)
Silene acaulis (L.) Jacq.	Island of Unst, Keen of Hamar, Scotland	1906	Shewry and Peterson (1976)
Solidago hispida Muhl. ex Willd.	Western Newfoundland, Canada	1023	Roberts and Proctor (1992)
Thymus praecox subsp. *britannicus* (Ronniger) Holub. (former *Th. drucei* Ronniger)	Island of Unst, Keen of Hamar, Scotland	1362	Shewry and Peterson (1976)
Thlaspi sylvium Gaudin (former *Th. alpinum* var. *sylvium* Gaudin Kerguélen)	Valle d'Aosta, Italy, along the Swiss border	10000	Reeves and Brooks (1983); Verger (1992)
Thlaspi goesingense Halácsy	Bruck an der Mur (Steiermark), Bernstein (Burgenland), Austria	6380–9010 4960–12400	Reeves and Baker (1984)
		Zn concentrations (μg g^{-1})	
Thlaspi goesingense Halácsy	Bruck an der Mur (Steiermark), Bernstein (Burgenland), Austria	170–1580 281–1800	Reeves and Baker (1984)
Thlaspi sylvium Gaudin (former *Th. alpinum* var. *sylvium* Gaudin Kerguélen)	Valle d'Aosta, Italy, and along the Swiss border	100–3000	Reeves and Baker (1984)

1994; Galey et al. 2017). Approximately 3000 endemic taxa restricted to ultramafic soils are known, however, many of them occur in tropical and subtropical regions (Brooks 1987; Anacker 2011; Galey et al. 2017). The level of endemism of ultramafic floras of the southern Mediterranean regions such as California is also extremely high (Kruckeberg 2002; Safford et al. 2005; Alexander et al. 2007), and is also strongly manifested on island floras (New Caledonia, Cuba, Borneo: Borhidi 1992; Jaffré 1992; Galey et al. 2017).

Low levels of endemism have often been reported in ultramafic floras of the arctic, cold and cool temperate zone. The only endemic species in the United Kingdom—*Cerastium nigrescens* (H. C. Watson) Edmondston ex H. C. Watson is known from few ultramafic habitats in Scotland (Dennes 1845; Watson 1860; Brooks 1998). Further treatments permit use of the name *C. nigrescens* not only for Shetland populations but also for other Scottish and Scandinavian ones (Brummitt et al. 1987).

Endemics have not been recorded on serpentinites in the Polar Urals (Proctor et al. 2005). Yurtsev et al. (2001) also noted that new taxa in the rank of species and subspecies do not occur in the ultramafic flora of the Polar Urals. Further, in the Southern and Middle Urals, new species and subspecies endemic to ultramafic substrate have yet to be described (Teptina and Paukov 2012).

In other circumboreal regions the number of endemic taxa obligate to ultramafic soils is not high. Rajakaruna et al. (2009), Harris and Rajakaruna (2009), and Boufford et al. (2014) report several ultramafic endemics for eastern North America, including *Adiantum viridimontanum* C. A. Paris (Pteridaceae) (Fig. 5), *Minuartia marcescens* (Fernald) House (Caryophyllaceae), *Symphyotrichum rhiannon* Weakley and Govus (Asteraceae), and *Packera serpenticola* (L.) A. Löve and D. Löve (Asteraceae). There are some perennial endemics on the ultramafics within *Cerastium* in Balkan region (e.g., *Cerastium alsinifolium* Tausch, *C. neoscardicum* Niketić, *C. smolikanum* Hartvig), North America (*C. velutinum* Rafinesque var. *villosissimum* (Pennell) J. K. Morton) and on the British Isles (*C. fontanum* Baumg. subsp. *scoticum* Jalas and Sell).

The origin of neoendemics in the northern floras is often associated with polyploidy (Stebbins 1984). Polyploid forms have competitive advantages in extreme environments and is often typical for genera such as *Alyssum* and *Cerastium*. Comprehensive morphological, cytological, genetic and ecological analyses support the existence of two new endemic species restricted to ultramafic outcrops in the Czech Republic (Kaplan 1998; Kolář et al. 2015). Similarly, diploid and tetraploid species of *Knautia serpentinicola* Smejkal ex Kolář, Z. Kaplan, J. Suda et Štech (Caprifoliaceae) have been described in ultramafic areas in the Czech Republic and Germany. The diploid *K. pseudolongifolia* (Szabó) Żmuda is known from only one site in Krkonoše Mountains (Kolář et al. 2015). Another two neoendemic species, *Cerastium alsinifolium* Tausch and *Minuartia smejkalii* Dvořáková (Chitrý 2012), are known from Western Bohemia. *Adiantum viridimontanum*, endemic to ultramafic soils in Maine, Vermont, and Québec, is also considered to be an allotetraploid hybrid between *A. aleuticum* (Ruprecht) Paris and *A. pedatum* L. (Harris and Rajakaruna 2009).

Hyperaccumulation of trace elements

Ultramafic outcrops are home to over 500 species of Ni-hyperaccumulating plants, the majority of which are found in Mediterranean and tropical climates (Berazaín et al. 2007; Gall and Rajakaruna 2013; Sánchez-Mata et al. 2013). Many of these hyperaccumulating plants belong to seven territories—New Caledonia, Western Australia, southern Europe and Asia Minor, The Malay Archipelago, Cuba, western United States and Zimbabwe (Reeves 1970; Baker and Brooks 1989; Galey et al. 2017). In regions with arctic, cold and cool climates, the number of such species is not high. Ultramafic flora of cold regions is characterized by atypically low level of hyperaccumulator species (Table 3). Some ultramafic floras do not include such species at all; for instance, Proctor (1992) noted the absence of Ni-hyperaccumulating plants on ultramafic outcrops of Britain. The arctic and boreal regions affected by the glaciation events during the Pleistocene do not appear to harbor hyperaccumulator species (Brooks 1983, Baker and Brooks 1989); perhaps due to the lack of time for the evolution of such traits or reduced selection for hyperaccumulation.

Only genera *Alyssum* and *Noccaea*, which belong to Brassicaceae, are able to hyperaccumulate Ni in the circumboreal regions (Brooks and Radford 1978; Reeves and Brooks 1983). Nickel hyperaccumulation has been reported in *Alyssum obovatum* (C. A. Mey.) Turcz. in the Polar Urals (1000–4500 μg g^{-1}) (Alekseeva-Popova et al. 1995; Proctor et al. 2005), Middle and Southern Urals (818–6003 μg g^{-1}) (Teptina and Paukov 2015) and Chukotka (926–1308 μg g^{-1}) (Drozdova and Yurtzev 1995; Drozdova and Alekseeva-Popova 1999). *Alyssum obovatum* is also known as a Ni hyperaccumulator in Alaska, USA and Canada (Brooks and Radford 1978; Brooks et al. 1979), although recent studies have not been undertaken to confirm these earlier findings.

Further to the south, the number of hyperaccumulator *Alyssum* species rise. Several other species from *Alyssum* have been reported as strong hyperaccumulators of Ni, such as *Alyssum murale* Waldst. and Kit. in the Northern Caucasus (Drozdova et al. 2013; Alekseeva-Popova et al. 2015), Bosnia and Herzegovina (Stamenković et al. 2017), Armenia (Doksopulo 1961) and Albania (Shallari et al. 1998) and *Alyssum markgrafii* O. E. Schulz ex Markgraf in Albania (Shallari et al. 1998).

The members of the genus *Noccaea* (Brassicaceae) are also characterized by their ability to accumulate Ni, as shown in *Noccaea japonica* (H. Boissieu) F. K. Mey. in Hokkaido, Japan (Mizuno et al. 2009), *N. borealis* F. K. Mey. in the Polar Urals (Alekseeva-Popova et al. 1995; Proctor et al. 2005; Al-Shehbaz 2014) and *N. thlaspidioides* (Pall.) F. K. Mey. in the Middle and Southern Urals (Teptina and Paukov 2015).

Some species from circumboreal region are also capable of hyperaccumulating Zn. For instance, *Alyssum gehamense* Halácsy in the Northern Caucasus (Drozdova et al. 2013), *Noccaea caerulescens* (J. Presl and C. Presl) F. K. Mey. in central Europe (Reeves and Brooks 1983) and *Noccaea borealis* in the Polar Urals have all been documented as accumulating Zn, but not reaching the hyperaccumulator threshold (Proctor et al. 2005).

Few species from families other than the Brassicaceae have been documented as hyperaccumulators of Ni, particularly members of Caryophyllaceae—*Arenaria marcesens* (Fernald) House in Western Newfoundland, *Cerastium holosteoides* Fr., *C. nigrescens* (H. C. Watson) Edmondston ex H. C. Watson, *Sagina* sp., *Silene acaulis* (L.) Jacq. and Plumbaginaceae—*Armeria maritima* (Mill.) Willd. in the Unst island (Shewry and Peterson 1976; Roberts and Proctor 1992). The records of Ni hyperaccumulation by members of other families, particularly *Calluna vulgaris* (L.) Hill. (Ericaceae) in the island of Unst (Shewry and Peterson 1976) and *Solidago hispida* Muhl. ex Willd. (Asteraceae) in western Newfoundland (Roberts and Proctor 1992) need to be verified.

Discussion

The question of why northern plant communities on ultramafic rocks often lack high levels of species endemism and are largely devoid of hyperaccumulators have long-intrigued serpentine ecologists. There are few explanations posed for why territories with arctic, cold and cool temperate climates are poor or devoid of obligate serpentinophytes and hyperaccumulators. The degree of endemism, in the opinion of Proctor (2003), depends on historical reasons, including climate, rather than purely on edaphic factors. These include recent glaciation and the ratio of precipitation and evaporation (Rune 1953; Proctor 1992). The last glaciation, which covered the territory of modern Canada, reached Black Sea and peaks of the Northern Urals (Baker and Brooks 1989; Kulikov et al. 2013), severely impacting colonization and subsequent evolution of plants. The endemic flora of these territories, which arose after the glaciers had retreated, can be considered as neoendemics (Kruckeberg 1986; Rajakaruna 2004; Anacker 2011). The flora of the Middle and Northern Urals has 88 (5.5% of total diversity) endemic species. Most of these plants are petrophytes and erosiophyles tolerant to open habitats and have evolved after the retreat of the last glacier (Kulikov et al. 2013), however, none of them is known as endemic to ultramafic soils. Tolerance to open (bare) habitats may be a prerequisite to formation of obligate serpentinophytes (Armbruster 2014; Cacho and Strauss 2014) and it is likely that in the northern latitudes this process is currently in its early stages, where subspecies, ecotypes, or races differing in edaphic tolerance or in their ability to hyperaccumulate Ni have yet to evolve as full-fledged species (Brummitt et al. 1987; Nyberg Berglund et al. 2004; Brysting 2008; Teptina and Paukov 2015). Territories in the Holarctic which have never been frozen bear high numbers of these species—at least 215 ultramafic endemic taxa are known in California, and the Mediterranean region is likewise rich in endemics (Anacker 2011). The only obligate serpentinophyte *Alyssum litvinovii* Knjaz. (Fig. 5b) is currently known from the Southern Urals but in the territory outside the circumboreal region (Knjasev 2011). Arid territories of Holarctic which have never been affected by glaciation processes may therefore represent a unique opportunity to discover new taxa which may qualify as obligate to ultramafic soils. These territories may include Mugodzhary mountains in Kazakhstan, Caucasus and Altai and are all worthy of intense field exploration.

Unlike in the tropics, where hyperaccumulation is known in many unrelated families, the hyperaccumulators in the northern territories belong mostly to Brassicaceae. The adaptive significance of metal hyperaccumulation has been discussed in detail (see Boyd 2014 for a discussion), pointing to elemental defense as a primary selecting agent in the evolution of metal hyperaccumulation. Some evidence suggests that some metals, including Ni, are physiologically essential for serpentinicolous plants (Ghasemi et al. 2014). Nickel may act as an osmoticum during drought stress (Baker and Walker 1990; Boyd 1998; Martens and Boyd 2002) or enhance reproductive fitness via increased flowering (Ghasemi et al. 2014). The high amounts of Ni may also act as defense from herbivores (Reeves et al. 1981; Ernst 1987; Boyd 2012). While the same factors hypothesized as driving the evolution of metal hyperaccumulation should apply wherever there are plants on ultramafic soils, the lack of time for the evolution of this trait (due to recent glaciation in the circumboreal regions) and reduced intensity of herbivore and pathogen damage (compared to warmer regions) may contribute to fewer hyperaccumulators in the northern climates.

One of the more adverse conditions on ultramafic soils is a constant lack of moisture, high insolation and a significant temperature drop on the soil surface (Proctor and Woodell 1975; Kruckeberg 1984; Brooks 1987; Brady et al. 2005). In the regions with arctic, cool and cold temperate climate, hyperaccumulators occur on shallow skeletal ultramafic soils, where there are significant periods of water deficiency or drought (Roberts and Proctor 1992; Hughes et al. 2001). Therefore, drought stress could likely drive the evolution of this trait and is worthy of examination via experimental studies. Interestingly, the number of hyperaccumulators rises southwards and, in continental regions, with the highest numbers found in the most arid regions. The species with wide latitudinal distribution in Holarctic such as *Alyssum obovatum*, which occurs in Eurasia, Canada and Alaska, may be useful in understanding this pattern.

The second reason may be the difference in the amounts of metals and their bioavailability in soils in circumboreal and tropical regions. Utramafic soils in Cuba and Brazil contain much higher Ni than any ultramafic soil of the Holarctic (Reeves et al. 1999, 2007). However, the cause and effect of reduced Ni in soil are difficult to demonstrate as there are only weak trends in the concentrations of metals in ultramafic soils in different climatic zones of the Holarctic (Figs. 1, 2, 3, 4). Further, it is difficult to find strong correlations between soil metal concentration and metal accumulation rates by plants. Additional work with unified protocols for determination of metals both in soils and plants (Reeves and Kruckeberg 2018) should help in understanding if there are differences in metal availability in soils of circumboreal regions compared to those of more southern regions.

In conclusion, we stress three possible reasons for the lack of high levels of diversity and endemism in the ultramafic flora in the Circumboreal region and the reduced levels of metal hyperaccumulation observed among the region's plants: (1) the brief growth period post glaciation (< 12,000 years) has not been adequate for the evolution of full-fledged species obligately endemic to ultramafic soils, (2) water stress and other stressors, including herbivory, hypothesized to drive the evolution of hyperaccumulation, are not as severe compared to those of more warmer climates, (3) low concentration of total/bioavailable metals in soils due to reduced weathering of parent material due to climatic factors and the time available for soil formation due to recent glaciation. These factors may act separately or in concert, leading to the distinct patterns of plant diversity and metal accumulation so far documented on ultramafic soils of the circumboreal region.

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