Published in "Nordic Journal of Botany 31(1): 122–128, 2013"
which should be cited to refer to this work.

Allopatric distribution, ecology and conservation status of the *Pilosella alpicola* group (Asteraceae)

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The *Pilosella alpicola* group comprises four morphologically distinct and geographically vicariant alpine taxa. We performed a thorough herbarium revision and literature survey to infer their distributional pattern(s). *Pilosella alpicola* s.s. occurs in the Alps in two disjunct areas: the Swiss Valais Alps and the Italian Dolomites. Historical records come also from the Austrian Alps (Gurktaler Alps and Hohe Tauern) and from one site from the Alpes Maritimes (Col de Larche), but the localities have not been recently confirmed. *Pilosella rhodopea*, a Balkan subendemic taxon, is quite widespread in Bulgaria (Stara planina Mts, Rila Mts and Pirin Mts), but is more rare in Albania, Greece and Macedonia. Interestingly, this species has also been recorded at two isolated sites in the Romanian southern Carpathians (the Căpăţînii and Cozia Mts). This occurrence underlines the floristic affinities of this part of the Carpathians to the Balkan flora. Only two localities of *P. serbica*, based on voucher specimens, have been recorded so far; Kopaonik Mts in Serbia and the Prokletije Mts in Montenegro. The records from other ranges are related to *P. rhodopea*. *Pilosella ullepitschii*, the detailed distribution of which has already been published, is a Carpathian endemic with its core area of distribution in the western Carpathians (Slovakia and Poland). Three isolated localities are also known in the eastern Carpathians (Nemira Mts) and one locality in the southern Carpathians (Bucegi Mts). The possible causes of disjunctions between and within species ranges are briefly discussed. Based on the distributional data, population sizes and ecology, we evaluate the conservation status of the *P. alpicola* taxa and propose their inclusion in national Red Lists.

Geographic separation leading to reproductive isolation and natural selection is one of the most important processes promoting speciation (Darwin 1859, Mayr 1942, Grant 1981, Briggs and Walters 1997). Fragmentation of a previously larger range and long distance dispersal are the main mechanisms involved in geographic isolation. The fragmented pattern of European alpine system (Ozenda 1995) with a huge variety of environmental conditions offers an excellent opportunity to study allopatric evolution and diversification of the mountain flora (Kadereit et al. 2004). Taxonomic revisions based on detailed knowledge of morphological, karyological and molecular variation including distribution patterns should represent the first step in inferring possible biogeographic scenarios and putative adaptive mechanisms involved in the speciation of closely related taxa.

The alpine *Pilosella alpicola* group (Asteraceae, Lactuceae) shows a disjunctive distributional pattern. It has been reported from the Alps, Carpathians and several Balkan mountain ranges (cf. Zahn 1930, Bräutigam 1992, Šingliarová and Mráz 2009). Recent biosystematic studies showed that this group includes four closely related, but geographically vicariant species: *P. alpicola* F. W. Schultz et Sch. Bip., *P. rhodopea* (Griseb.) Szeląg, *P. serbica* (F. W. Schultz et Sch. Bip.) Szeląg and *P. ullepitschii* (Błocki) Szeląg (Šingliarová and Mráz 2009, Šingliarová et al. 2011a). According to Zahn's and Szeląg's taxonomic concepts (Zahn 1930, Szeląg 2008), *Pilosella* sect. *Alpicollinae* includes, in addition to the *P. alpicola* s.l. taxa, also the diploid *P. breviscapa* (DC.) Soják (syn. *Hieracium candollei* Monn., nom. ileg.) from the Pyrenees and another diploid taxon with a very restricted range: *P. petraea* F. W. Schultz et Sch. Bip. (syn. *Hieracium heuffelii* Janka). However, our recent data do not support this circumscription, and both these taxa should be excluded from the section (Šingliarová et al. 2011a). While the detailed distribution has been published only for the Carpathian endemic *P. ullepitschii* (Šingliarová and Mráz 2009), thorough chorological data for the three remaining species are still missing. Therefore, the present study aims to fill this gap. On the basis of gained data on distribution, population sizes and ecology, we also intend to evaluate the conservation status of the *P. alpicola* taxa.

Material and methods

This study is based on published data excerpted from national and regional floras, field keys and monographic works, and thorough revision of herbarium material originated from the following institutions: B, BP, BRA, BRNM, BRNU, CL, G, GRM, LW, SAV (including our collections), SB, SO, SOM, W, WU, Z. Mr Günter Gottschlich (Tübingen, Germany) kindly provided us the data from his collection (Go) and his revisions of the herbaria ROV, KL, PAD and TUB.

The distributional records were arranged from the west to the east within each geographic area. Samples with vague geographic localizations were listed at the end of the relevant geographic region. For distribution maps, approximate coordinates for localities based on herbarium specimens were obtained from tourist maps or using Google Earth (<www.google.com/earth/index.html>). In the list of revised herbarium specimens we use the following abbreviations: s.coll. = without the collector's name, s.d. = without date, s.n. = without specimen number (if the specimens are usually numbered in the particular herbarium). Unreadable data are replaced by '?'. Original determination is given only if it is somehow erroneous. In parts on ecology, the names of syntaxa without author names follow the nomenclature of Kliment et al. (2010). Estimation of conservation status of species in the *P. alpicola* group for the territories of particular countries follows the IUCN red list categories and criteria (IUCN 2001) and guidelines for using the IUCN red list categories and criteria (IUCN 2010).

Results and discussion

Pilosella alpicola F. W. Schultz & Sch. Bip.

(syn. *Hieracium alpicola* Steud. & Hochst.)

According to our study, the species occurs only in the Alps in two areas: the Valais Alps and the Italian Dolomites (Alpe di Siusi). In both regions it is distributed only very locally (Fig. 1A, Supplementary material Appendix 1; Fries 1862, Nägeli and Peter 1885, Zahn 1930, Hess et al. 1972, Zángheri 1976, Gottschlich and Pujatti 2002, Aeschimann et al. 2004). The two regions are separated by a nearly 300 km gap. In addition, two more than 100 year old records are known from the Austrian Alps. While the first record from Malnizter Tauern is based on a herbarium specimen (KL 26490), we did not find any voucher for the record from Mt Königstuhl in the Gurktaler Alps (Zahn 1930). Since the time of these records, the species has never been confirmed from the Austrian Alps. rFor that reason, the species has been considered missing and/or extinct in Austria (Hartl et al. 1992, Niklfeld and Schratt-Ehrendorfer 1999, Schuhwerk and Fischer 2003, Aeschimann et al. 2004). In the summer 2009, we visited both historical localities, but we did not find any plants corresponding to *P. alpicola*.

One literature record (Le Grand 1903) supported by herbarium specimen (GRM) exists from the Col de Larche (Alpes Maritimes, France). One plant of *P. alpicola* s.s. from the Col de Larche is mounted on the same sheet as five

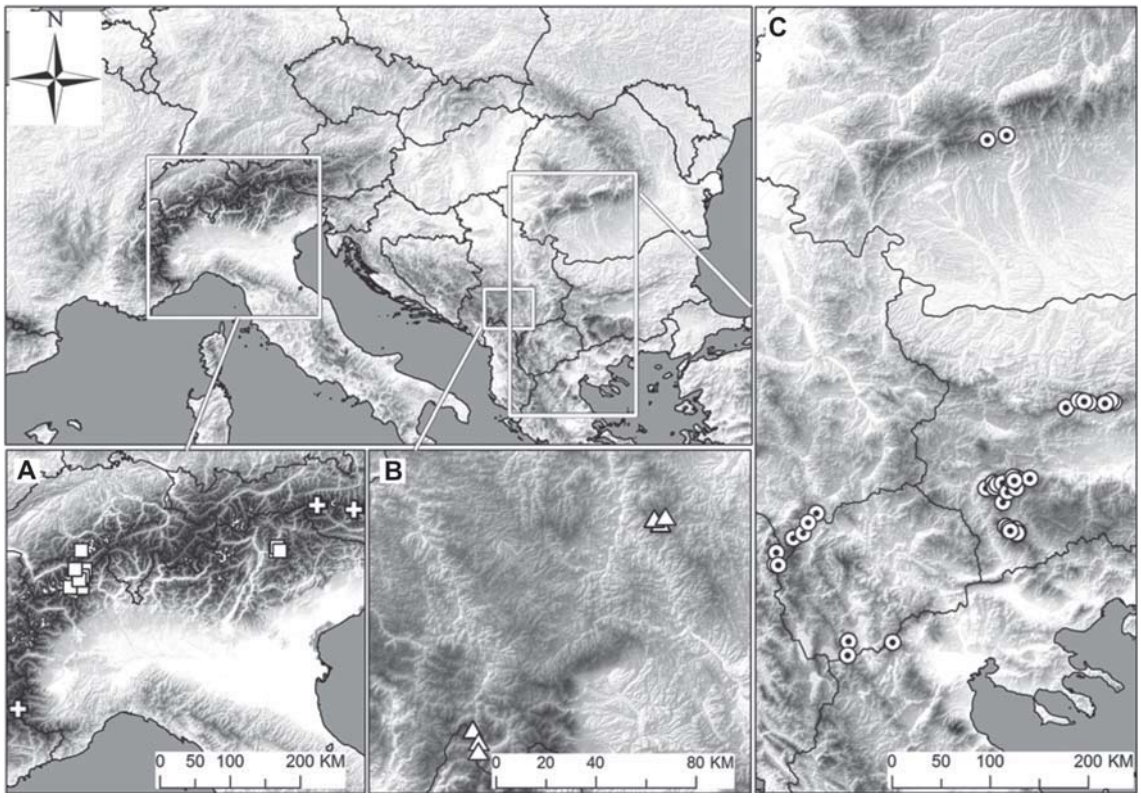

Figure 1. Distribution of the three taxa belonging to the *Pilosella alpicola* group: (A) *P. alpicola* s.s., crosses represent doubtful localities, (B) *P. serbica*, (C) *P. rhodopea*. Distribution of the fourth taxon *P. ullepitschii* was published in Šingliarová and Mráz (2009).

other collections of *P. alpicola* from the Valais Alps, collected by Wolf in 1897. Due to the long distance of the locality from the core area situated in the Valais Alps, the unusual substrate (calcareous bedrock) and strange circumstances of the herbarium sheet, we cannot exclude the possibility that specimens were mislabelled during herbarium mounting. Moreover, nobody has confirmed this record since 1897 and the species has not been included in the French checklist of vascular plants (Kerguélen 1993). Taking these facts into account, we consider this record doubtful.

The plants from the Valais Alps are tetraploids, while the plants from the Italian Dolomites are pentaploid (Šingliarová et al. 2011a). Disjunct distribution of cytotypes, different multi-locus allozyme pattern and small morphological differences suggest a polytopic origin of this allopolyploid taxon arosen from hybridization between the two putative parental taxa *P. rhodopea* and *P. glacialis* (Reyn. ex Lachen.) F. W. Schultz & Sch. Bip. (Šingliarová et al. 2011a, 2011b). According to castration and isolation experiments and flow cytometric seed screening analysis, the tetra- and pentaploids of *P. alpicola* reproduce apomictically (Šingliarová et al. 2011a). Interestingly, this mode of reproduction, considered as very advantageous for colonizing new habitats (Vandel 1928, Bierzychudek 1985, Asker and Jerling 1992), did not contribute to the range expansion as observed in many other apomictic taxa (Bayer 1990, Urbani 2002, van Dijk 2003, Thompson and Whitton 2006, Mráz et al. 2008, 2009). This may suggest either the existence of some effective selection mechanism(s) that prevent the expansion of the range of *P. alpicola* and/or that the taxon is young and has not had sufficient time to spread further. A similar pattern has been observed in apomictic *Erigeron trifidus*, a hybridogeneous species between two polyploid *Erigeron* taxa, forming only restricted and disjunct populations (Burke and Bain 2008).

There is an obvious difference in population size between the populations from the Valais Alps and those from the Italian Dolomites. While the populations in the Valais Alps (Simplon pass and Mt Monte Moro) consist of tens of thousands of individuals covering relatively large more or less continuous areas, the three populations known in the Dolomites (Alpe di Siusi) are substantially smaller and more fragmented (B. Šingliarová and P. Mráz pers. obs.). On the plateau of Mt Puflatch the species grows in small patches (some tens to some hundreds of individuals) on embossed places with more skeletal soils forming mosaic-like structures surrounded by large surfaces of heavily grazed (cattle and horses) and mowed meadows. Populations at the foothills of Mt Schlern and in the Val Duron are even less rich in individuals, forming only a few patches in disturbed places. The total estimated population size in the Italian Dolomites does not exceed 4000–5000 individuals. The distribution of the acidophilous *P. alpicola* s.s. in the Italian Dolomites is restricted to outcrops of porphyre bedrock (large-grained granitic igneous rock) representing only small isolated islands in the predominating calcareous bedrock. Unsuitable geological and soil conditions certainly prevent the species from spreading further to adjacent areas. In addition to abiotic constraints, we observed that plants at the flowering stage suffer from a strong fungal or viral infection, inducing stem withering. As a consequence, most of the plants did not produce any seeds at Mt Schlern and Mt Puflatch sites during the summers 2008 and 2009 (B. Šingliarová pers. obs.). However, the seed production at Mt Puflatch in 2010 was normal (P. Mráz pers. obs.). Moreover, the locality on Mt Puflatch has recently (summer 2009) been severely damaged by the building of a cabin lift (B. Šingliarová pers. obs.).

Literature data

Besides the localities based on herbarium vouchers (see Supplementary material Appendix 1), there are literature data without specimens originating from Switzerland (Illalp, Bellalui, Saflischtal and Mettental; cf. Zahn 1930), Italy (Ossola and Bormiese, cf. Fiori 1925–1929, Pignatti 1982), and very broadly defined regions in France ('Basses Alpes, Savoyen', cf. Hess et al. 1972). All Swiss localities come from the Valais Alps, which is the distribution center for *P. alpicola* s.s. As far as Italy is concerned, although we did not see any specimens from the Italian part of Valais Alps, the occurrence of the species in the region of Ossola seems very likely, because this part is adjacent to the Simplon Pass, where the taxon is quite common. Region Bormiese is situated in the central part of the Italian Alps from which no other record is known and the closest confirmed occurrence is in the Dolomites, near Bolzano ca 100 km away. While the locality Basses Alpes may refer to the aforementioned doubtful record from the Col de Larche, the record from Savoy (Hess et al. 1972) is not supported by any specimen or other literature record.

Ecology

Pilosella alpicola grows on alpine grassland and in dwarf-shrub communities (1900–2800 m a.s.l.) on acid bedrock (most commonly granite, rarely porphyre). As no information on particular plant communities exists (Pascal Vittoz pers. comm.), we have performed one relevé at the Simplon Pass in Valais Alps and a list of co-occurring species at Mt Puflatsch in the Italian Dolomites. There, *P. alpicola* can be found in the communities of the 'Juncion trifidi' alliance. Occurrence of species such *Luzula spicata*, *Pulsatilla vernalis* or *Botrychium lunaria* also indicate the close relationship to the plant communities of the 'Carici rupestris–Kobresietea bellardii' class, that very often form mosaics of small patches.

Locality 1: Switzerland, Valais, Simplon Pass, western slopes of Mt Hübschhorn, 46°14.76′N, 008°02.681′E, 2290 m a.s.l., 7 Aug 2010, 2 × 2 m, west exposure, 30% slope, vegetation cover 60%, granite substrate, skeletal soil.

Relevé: *Juncus trifidus* 3, *Pilosella alpicola* s.s. 3, *Trifolium alpinum* 2, lichenes 1, Musci 1, *Pulsatilla vernalis* 1, *Antennaria dioica* +, *Avenula versicolor* +, *Botrychium lunaria* +, *Empetrum hermaphroditum* +, *Hieracium glanduliferum* +, *Lotus alpinum* +, *Luzula* cf. *spicata* +, *Minuartia* sp. +, *Phyteuma hemisphaericum* +, *Saxifraga bryoides* +, *Sedum atratum* +, *Sempervivum arachnoideum* +, *Sempervivum montanum* +, *Senecio carniolicus* +, *Vaccinium vitis-idaea* +, *Veronica bellidioides* +.

Locality 2: Italy, Dolomites, Mt Puflatsch, the plateau on the summit area, 46°33.131′N, 011°37.172′E, 2119 m a.s.l., 10 Aug 2010, northeast exposure, porphyry substrate, skeletal soil.

Dominant species*: Carex sempervirens*, *Loiseleuria procumbens*, *Vaccinium gaultherioides*;
Other species: *Agrostis rupestris*, *Antennaria dioica*, *Campanula scheuzeri*, *Hieracium piliferum*, *Minuartia* sp., *Phyteuma hemisphaericum*, *Pilosella alpicola*, *Pulsatilla vernalis*, *Trifolium alpinum*, *Vaccinium vitis-idaea*, *Saxifraga paniculata*.

Pilosella rhodopea (Griseb.) Szeląg

Pilosella rhodopea is the most widely distributed species of the *P. alpicola* group. It has been confirmed in the Korab Mts (Albania), the Shar planina and Baba Mts (Macedonia), the Voras Mts (Greece/Macedonia), and in the Căpăţînii and Cozia Mts in the Romanian Carpathians (Fig. 1C, Supplementary material Appendix 1; Zahn 1930, Nyárády 1955, 1965, Pawłowski 1963, Popescu et al. 1970, Šingliarová and Mráz 2009). However, the majority of localities have been recorded in Bulgaria, where it occurs in the following mountain ranges: the Rila Mts, the Pirin Mts and the central part of the Stara planina Mts.

Pilosella rhodopea has also been reported from the Rhodope Mts, namely from Čepelare (Urumov in Zahn 1930). We were, however, not able to find any relevant voucher to this unique record. Čepelare is quite low (1750 m a.s.l.) without an alpine belt and therefore we consider this record as questionable. The taxon was described by Grisebach (1853) from type locality: "Rhodope regio superior". Because the name Rhodope/Rhodopes has been used in the past in a broader sense encompassing also the Rila and Pirin Mts (see the original labels given in the part of herbarium revision), the species might have been described from these mountain ranges where its presence has been proven.

Pilosella rhodopea is a karyologically variable species, ranging from diploid to pentaploid ploidy level. All cytotypes have been shown to reproduce sexually, without obvious reproductive barriers and without any morphological and genetic differentiation (Šingliarová et al. 2011a, 2011b). These facts suggest that *P. rhodopea* polyploids have arisen by autopolyploidization (Šingliarová et al. 2011a, 2011b).

The recent distributional pattern of *P. rhodopea* indicates that its former range during presumably more favourable cold periods was much larger and extended more northwards. A close biogeographical connection between high mountain biota of Bulgarian mountains and the southern Carpathians has previously been reported (Reed et al. 2004, Varga and Schmitt 2008, Schmitt 2009). A distributional pattern similar to that of the *P. alpicola* group is known for *Hieracium* sect. *Cernua* (*Hieracium* s.s.) (Szeląg 2006, Ronikier and Szeląg 2008). Genetic links between these areas have also been suggested for other alpine species (Puşcaş et al. 2008).

Literature data

Reports on the occurrence of *P. alpicola* s.l. has also been published for Mt Varnous (Baba Mts) and Mt Tzena (Voras Mts) in Greece (Buttler 1991), which are part of the massif that continues northwards into the Macedonian Baba Mts, where the presence of *P. rhodopea* has been confirmed. According to Buttler (1991) both glandular and eglandular morphotypes grow sympatrically at these localities. This might suggest a co-occurrence of *P. rhodopea* and *P. serbica* in these Greek localities. However, according to morphological observations and karyological analyses (Šingliarová unpubl.) only *P. rhodopea* grows in Voras Mts (Mt Kajmakčalan).

Ecology

The typical habitats of *Pilosella rhodopea* are subalpine and alpine meadows and screes on acid bedrock (granite) at 1800–2800 m a.s.l. In the Balkans *P. rhodopea* has been reported from alpine communities belonging to the associations 'Agrostio–Seslerietum comosae' Horvat et al. 1937 and 'Carici-Festucetum riloensis' Horvat et al. 1937 (Pawłowski 1963, Roussakova 2000, Velev and Apostolova 2009). The occurrence of this taxon in the Cozia Mts is interesting because of the low altitude (1600 m a.s.l.) and the absence of a true alpine or subalpine belt. There, *P. rhodopea* occupies the crevices in steep rock cliffs (built from crystaline schist) and secondary grasslands near the summit belonging to the association 'Bruckenthalieto–Vaccinietum' Nyárády 1955 (Nyárády 1955). The presence of several endemic and relict taxa (e.g. *Lycopodium tristachyum* Pursh., *Leontopodium alpinum* Cass., *Daphne blagayana* Freyer, *Lilium carniolicum* subsp. *jankae* (A. Kern.) Asch. & Graebn., *Galium baillonii* Brândză, *Silene dinarica* Spreng.) indicates a relict character of this locality (Nyárády 1955, Popescu et al. 1970). The second known locality of *P. rhodopea* in the southern Carpathians, the Zmeuretu saddle, is ecologically more typical (alpine grasslands on acid bedrock at ca 2000 m a.s.l.). Nevertheless, despite our four visits in 2007–2011 we did not refind the species.

Pilosella serbica (F. W. Schultz & Sch. Bip.) Szeląg

Pilosella serbica has the most restricted distributional range of the taxa in the *Pilosella alpicola* group (Fig. 1B, Supplementary material Appendix 1). According to the present revision, based on voucher specimens, this diploid sexual taxon occurs only in the Kopaonik Mts (southern Serbia) and Prokletije Mts (Montenegro, on the border to Kosovo). The previously reported occurrences of *P. serbica* in Bulgaria (Zahn 1930) and Albanian Korab Mts (Zahn 1930, Szeląg and Illnicki 2011) was not confirmed by our study. On the contrary, only *P. rhodopea* was found there. Our data show that *P. rhodopea* and *P. serbica* are vicariant. The variety of records of the species might, to some extent, be a consequence of the long-lasting inaccessibility of the high mountains in former Yugoslavia (often representing state borders in a politically unstable region).

Literature data

In Kopaonik Mts *Pilosella serbica* grows at least on three peaks situated very close to each other – Mt Suvo Rudište (Šingliarová et al. 2011a), Mt Karaman (Szeląg et al. 2007) and locality Krčmar (northeast slope of Mt Pančićev vrh, herbarium specimen, Supplementary material Appendix 1).

Zahn (1930) reported also other records from the Komovi Mts in Montenegro, Mt Peristeri (Mt Varnous, Greece) and Mt Tesoron near the town of Saloniki (Greece). However, we did not find herbarium vouchers from these mountain ranges.

Ecology

In the Kopaonik Mts, *P. serbica* grows on subalpine and alpine meadows in the highest altitudes of the range 1850–2000 m a.s.l. in grassland and dwarf-shrub vegetation such as the alliances 'Juniperion sibiricae' Br.-Bl. 1939 and 'Loiseleurio procumbentis-Vaccinion' on acid bedrock (granodiorites). Szeląg et al. (2007) reported the species from a plant community with *Festuca halleri* subsp. *scardica* and *Vaccinium gaultherioides*. No phytocoenological data on *P. serbica* exist from the Prokletje Mts.

Pilosella ullepitschii (Błocki) Szeląg

Pilosella ullepitschii is a Carpathian endemic with core distribution in the western Carpathians, where it occurs in more than 40 localities in two mountain ranges, the Vysoké and Západné Tatry Mts (Šingliarová and Mráz 2009). It is extremely rare in the eastern (Nemira Mts) and southern Carpathians (Bucegi Mts) having only four known occurrences; three small populations in the Nemira Mts and one large population in the Bucegi Mts. Mean disjunctions of these isolated localities from the core area are 680 km (Nemira) and 650 km (Bucegi Mts).

Conservation status

Pilosella alpicola is listed as 'Vulnerable' (VU) in Switzerland (Moser et al. 2002) and *P. ullepitschii* is treated as 'Near Threatened' (NT) in Slovakia (Feráková et al. 2001) and as R (rare – potentially endangered; species localized within restricted geographical areas or habitats) in Poland (Zarzycki and Szeląg 2006). Other countries do not list the taxa of the *Pilosella alpicola* group in their national Red data books or lists (Velchev 1984, Oltean et al. 1994, Phitos 1995, Conti et al. 1997, Stevanović 1999, Dihoru and Negrean 2009, Petrova and Vladimirov 2009). Based on our study, we propose to add particular species to the national Red Lists according to the IUCN Red List categories and criteria (2001) and guidelines for using the IUCN red list categories and criteria (2010). Their conservation status should be assessed as follows:

Pilosella alpicola as 'Endangered' (EN B2ab(i,ii,iii)) in Italy due to extremely few populations (3) of small size, strong habitat limitations as well as severe anthropogenic pressure (grazing, tourism, building of winter sport resorts);

Pilosella rhodopea as 'Near Threatened' (NT) in Albania, Greece, FYR Macedonia and Romania due to very limited and fragmented distribution at the range margins, and in Romania also due to reduced genetic variability;

Pilosella serbica as 'Near Threatened' (NT) in Serbia and Montenegro due to limited and fragmented distribution and partially small population size;

Pilosella ullepitschii as 'Endangered' (EN B2ab(i,ii,iii)) in Romania due to limited distribution (4 known locations), small population size, reduced genetic variability, ongoing secondary succession (spruce forest) which might cause reduction or extinction of populations in the Nemira Mts and increasing anthropogenic pressure (tourism, grazing) in the fourth location in the Bucegi Mts.

Concluding remarks

Our molecular data suggest a recent and monophyletic origin (with the exception of *P. alpicola* s.s.) of the closely related *P. alpicola* taxa (Šingliarová et al. 2011a, 2011b). We hypothesize that the modern range of the *P. alpicola* group is probably what remains from a wider and continuous primary range of their common progenitor (either one of the extant taxa or some already extinct taxon) during more favourable cold periods (Šingliarová et al. 2011a). During the warmer interglacials, the range of putative progenitors of the group has been split into subareas in the alpine belt or relic treeless localities in the Carpathians and the Balkans (Alps?). Here, after gene-flow break, *P. ullepitschii*, *P. serbica* and *P. rhodopea* probably evolved in vicariance by adaptation to local conditions. We hypothese that the Balkan *P. rhodopea* (or unknown extinct 'interstep' ancestor) underwent a northwesterly range expansion during cold periods, where its distribution range met those of *P. glacialis*, or some closely related taxon, and they hybridized giving rise to the allopolyploid *P. alpicola*. The first putative parent probably subsequently went extinct and left only its progeny: the hybridogeneous *P. alpicola*.

It seems that the recent distribution of the *P. alpicola* group is shaped by waves of expansions, shifts and fragmentations of the original range as well as extinctions of numerous intervening populations. Small isolated populations were and still are (Cozia Mts, Nemira Mts) especially vulnerable because of loss of genetic diversity (Šingliarová et al. 2008, 2011b) and thus putatively reduced plasticity and fitness (Barrett and Konh 1991, Ellstrand and Elam 1993).

Acknowledgements – We thank Róbert Lakoštík for valuable help in the field and Iva Hodálová (Bratislava) for helpful suggestions. We are indebted to the curators of herbaria listed in 'Material and methods' for allowing us to study herbarium specimens and helping us with reading of scheds. We are indebted to Mihai Puşcaş (Cluj) for providing some literature and Günter Gottschlich for sharing his own data and revisions. We are also grateful to Karol Marhold (Bratislava) for providing herbarium revisions from B. This study was financially supported by the Research and Development Support Agency (grant no. APVV-0320-10), Scientific Grant Agency of the Slovak Republic (grants no. VEGA 02/0075/11, 01/0028/08 and 2/0121/09) and Millenium Seed Bank of the Royal Botanical Garden, Kew.

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