

Glacial-relict symptoms in the Western Carpathian flora

Daniel Dítě · Michal Hájek · Ivana Svitková ·
Alica Košuthová · Rudolf Šoltés · Ján Kliment

Received: 28 April 2017 / Accepted: 28 February 2018 / Published online: 30 May 2018
© Institute of Botany, Academy of Sciences of the Czech Republic 2018

Abstract Glacial relicts have been regionally more common in glacial than in recent times. A rigorous assessment of which species are indeed glacial relicts is extremely difficult because direct evidence is untraceable or equivocal for many species. We aimed to identify species of the Western Carpathian flora (vascular plants, bryophytes and terrestrial lichens) that display apparent biogeographical and ecological symptoms, suggesting a wider regional or supra-regional distribution during glacial times, or at least before the middle-Holocene

climate optimum. We worked with the premise that exemplary relict species should tolerate continental and/or arctic climates, should have large distribution ranges with disjunctions, being regionally rare and ecologically conservative nowadays, should be associated with habitats that occurred during glacial times (tundra, steppe, peatland, open coniferous forest) and should display a restriction of ecological niches in the study region. The assessed species were primarily those with boreo-continental or arctic-alpine distribution. We demonstrated a conspicuous gradient of glacial-relict symptoms, with *Carex vaginata*, *Betula nana*, *Trichophorum pumilum*, *Nephroma arcticum*, *Saxifraga hirculus* and *Cladonia stellaris* topping the ranking. Based on the arbitrary ranking, 289 taxa can be considered high-probability relicts. For only a minority of them, there are any phylogeographical and/or palaeoecological data available from the study area. Biogeographical and ecological symptoms of 144 taxa suggest that they retreated rapidly after the Last Glacial Maximum whereas other species probably retreated later. The first principal component of biogeographical symptoms sorted species from circumpolar arctic-alpine species of acidic peatlands and wet tundra to strongly continental species of steppe, steppe-tundra and mineral-rich fens. This differentiation may mirror the altitudinal zonation of glacial vegetation in the Western Carpathians.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s12224-018-9321-8>) contains supplementary material, which is available to authorized users.

D. Dítě (✉) · I. Svitková · A. Košuthová
Institute of Botany, Plant Science and Biodiversity Center, Slovak
Academy of Sciences, Dúbravská cesta 9, SK-84523 Bratislava,
Slovak Republic
e-mail: daniel.dite@savba.sk

M. Hájek · A. Košuthová
Department of Botany and Zoology, Masaryk University,
Kotlářská 2, CZ-61137 Brno, Czech Republic

A. Košuthová
Department of Botany, Swedish Museum of Natural History,
P.O. Box 50007, SE-104 05 Stockholm, Sweden

R. Šoltés
Institute of High Mountains Biology, University of Žilina,
Tatranská Javorina 7, SK-059 56 Tatranská Javorina, Slovakia

J. Kliment
Botanical Garden of Comenius University, Blatnica 315, SK-038
15 Blatnica, Slovakia

Keywords Bryophytes · Biogeography · Central Europe · Habitat preferences · Glacial relict · Macroscopic terrestrial lichens · Vascular plants

Introduction

The concept of glacial relicts in regional floras of temperate Europe presently experiences a renaissance. Since the beginning of biogeography in Central Europe, relicts of the cold past have been considered an important group of species that are attractive for biogeographers, nature conservationists, or simply for nature lovers. They are also called glacial or postglacial relicts (Holmquist 1962; Pearson 1965; Rybníček 1966); the terminology has been used quite inconsistently worldwide. Together with endemics of European high mountains, glacial relicts represent the most ancient, but still quite numerous, component of regional species pools, playing an important role in the assembly of many recent communities in Central Europe. The concept of glacial relicts was later abandoned by mainstream science because of the difficulties with obtaining unequivocal evidence. Its renaissance is presently being triggered by the development of phylogeographical methods (e.g. Reisch et al. 2003; Vogler and Reisch 2013; Kajtoch et al. 2016) and increasing number of radiocarbon-dated paleoecological records (Hájek et al. 2011; Hájková et al. 2015; Gálová et al. 2016).

In Central and Eastern Europe, the term glacial relict refers to species which were quite common in the course of glacial times whereas during interglacials they retreated into refugia, i.e. into geographical regions or local microhabitats where habitat or climatic stability enabled them to survive (Pearson 1965; Stewart et al. 2010). There is increasing evidence that the distribution of postglacial (i.e. interglacial) refugia shapes species' geographical or richness patterns that are difficult to explain by present-day environmental conditions (Svenning and Skov 2010; Zobel et al. 2011; Horsák et al. 2012; Hájek et al. 2016; Jamrichová et al. 2017).

Traditionally, arctic-alpine species and boreal peatland species have been considered glacial relicts in the Central European flora (Soó 1938–39; Rybníček 1966; Liška and Pišút 1995; Lisická and Lackovičová 1998; Frahm 2012; Liška 2012). The palaeobotanical evidence allowing to track down distribution patterns in the cold past is available mostly for peatlands species. Fossil records suggest that some species indeed have been more common in late glacial times than recently and that some of these species recently dwell in long-lasting local refugia (Hájek et al. 2011; Hájková et al. 2015). There is, however, increasing evidence that not only cold and wet tundra, arctic-alpine scrubs, fens and

peatland forests, but also steppe (dry and meadow steppe, steppe-tundra), mesic forest-steppe (light-coniferous or even mixed temperate forests, meadow-steppe and tall-herb vegetation) and dark taiga have been important component of Central European glacial landscapes (Horsák et al. 2010, 2015; Juříčková et al. 2014; Magyari et al. 2014; Janská et al. 2017). During the climatically harshest periods, such as the Last Glacial Maximum (LGM), steppe-tundra was the dominant biome (Horsák et al. 2015; Hais et al. 2015). According to climate-based distribution models (Janská et al. 2017), the climate suitable for steppes occurred especially at lower elevations of the Western Carpathians, while tundra shrubs and dark taiga might occur at higher elevations and north of the mountain range. Fens, peatland forests and forest-steppe habitats could find climatically suitable places across the Western Carpathians, especially at middle elevations (Janská et al. 2017). During moister and warmer periods, peatlands and mosaic of coniferous forests, tall-herb vegetation and herb-rich steppe might have become more common. The latter group of habitats might increase in abundance during interstadials, experiencing heyday during late glacial and Early Holocene times. The species that were characteristic of glacial landscapes, although their distribution ranges had been changing, had disappeared rapidly with increasing productivity and spread of deciduous forests, either just at the beginning of the Holocene (in temperate-forest landscapes; Hájek et al. 2016), or at the transition between Early and Middle Holocene (in cold continental regions; Hájková et al. 2015; Jamrichová et al. 2017), or had not locally disappeared at all and became glacial relicts.

Considering this present-day knowledge on Quaternary development of the Central European landscape, we define glacial relict as at least partially light-demanding species that were regionally more common in any period before the spread of shaded deciduous or spruce forests in the Early and Middle Holocene. Distinguishing between relicts from glacial maxima and from interstadials would be much more complicated, but it may be partially done based on present-day habitat preferences. Continental species of zonal steppe and circumpolar stress-tolerant arctic-alpine species would be relicts of glacial maxima (Horsák et al. 2015), while boreal species of peatlands and sub-continental species of forest-steppe, tall-herb stands or open taiga would be relicts of interstadials and the Early Holocene.

Contrary to glacial relicts with clearly fluctuating abundances and/or changing distribution ranges during the last glacial cycle, endemics of European high mountains may represent local evolutionary elements, showing more or less stable scattered distribution over the Quaternary (Ronikier 2011), although they may be as cold-loving as boreocontinental and arctic-alpine glacial relicts. Hence, endemics of European high mountains were not considered in the analyses. The few exceptions are species with available direct palaeoecological evidence of their widespread distribution at low elevations and even in lowlands, and/or with frequent current occurrence in relict habitats at low elevations and at the same time with a distribution range extending Central and Southern European mountains (*Larix europaea*, *Pinus cembra*, *Swertia perennis*, *Cochlearia pyrenaica*, *Pleurospermum austriacum*).

In this study we focus on the Western Carpathians (see Kliment et al. 2016 for boundaries), an important biogeographical crossroad within Europe playing a major role in the Quaternary survival of contrasting biogeographical elements (Bálint et al. 2011; Mráz and Ronikier 2016) and representing an important interface between forest and grassland biomes during the Holocene (Fyfe et al. 2015; Jamrichová et al. 2017). We aim to review which species have been considered glacial relicts in local literature, regardless of whether this opinion has been supported by genetic or fossil data. For each of these species we evaluate its biogeographical and ecological symptoms which indicate whether it is a putative glacial relict. We further try to identify other species showing these ‘glacial relict symptoms’ and finally review the availability of genetic (phylogeographical) or fossil evidence concerning these species. The final list of glacial relicts of the Western Carpathian flora will be the first of its kind and individual species will be scored according to the strength of the relictual symptoms indicating the probability that each species is indeed a glacial relict. This list can serve as a basis for forthcoming genetic and palaeoecological studies and as a standard for biogeographical meta-analyses. We are aware that a more rigorous selection of glacial relicts is currently not possible due to missing genetic and palaeoecological evidence for many Central European species. In addition, such evidence may not be definite: Pollen data usually do not provide identifications at the species level, only a small part of the flora is being preserved as macrofossils, and palaeoecological cores usually capture only few square centimetres in a small number of sites rather than provide a complete

picture of a glacial landscape. Genetic structure may not be only a product of relictualism since glacial times but may mirror older migrations, very recent isolation or simply the biological traits of individual species (Stachurska-Swakoń et al. 2012; Wróblewska 2013a) that may be independent of Quaternary history. We regard palaeoecological, genetic and biogeographical proxies as complementary, with the latter being available for any species. At the present stage of knowledge it is impossible to create a list of glacial-relict species without invoking recent biogeographical and ecological symptoms. A putative Western Carpathian glacial relict should be a species which has its optimum in any habitat that is more common today than before the spread of dense forests (tundra, steppe, mesic forest-steppe, peatland), has quite a large distribution range suggesting its distributional dynamics during the glacial cycles, is biogeographically connected with circumpolar tundra or continental steppe vegetation, and is distributionally conservative (i.e. dispersal-limited; Hájek et al. 2011) and therefore recently quite rare and/or with narrowed ecological niche (Appendix). Considering the complexity of relictualism and insufficient direct evidence, expert-based arbitrary evaluation of the relictual symptoms is necessary. One possible solution is to abandon the effort to compile such a list, but here we decided to proceed using expert-based formal evaluation, underlain by recent knowledge of species and habitat history in the Western Carpathians. In this paper we therefore aim to identify and list species for which biogeographical and ecological symptoms suggest their glacial relict character in the Western Carpathian flora, to identify the major gradients of these symptoms, and to confront them with available palaeoecological and phylogeographical evidence.

Material and methods

List of relict species

Vascular plants, bryophytes and macroscopic terrestrial lichens, the major macroscopic components of tundra, steppe, taiga and peatland vegetation, were considered in this study. The primary list of species was created according to literature sources (Futák 1966 and subsequent volumes of the Flora of Slovakia; Dostál 1992; Lisická and Lackovičová 1998; Čerovský et al. 1999; Molnár 2003; Kaźmierczakowa et al. 2014; Šoltés 2004, 2014; for a comprehensive bibliography, see the Appendix) and our

expert knowledge. To rank traits of distribution and disjunctivity, we used distribution maps and/or databases (Willing 1978; Hultén and Fries 1986; Meusel and Jäger 1992; Kämefelt et al. 1994; Vitikainen 1994; Litterski and Ahti 2004; Bartha et al. 2015). Each species was scored according to its biogeographical and ecological traits that can be considered symptoms of glacial relictualism (see their list and justification in the Appendix). Scores for twelve individual symptoms were counted up to their total sum (*final score*); for symptoms 6–11 (see the Appendix), scores for the entire distribution range were used. This sum was used as a proxy for a probability that a given species is indeed a glacial relict. The species reaching the value of *final score* arbitrarily set to ≥ 10 were considered high-probability relicts and hence included into further analyses and on the list of the most probable relicts (Table 1). European high-mountain species were considered only if they show isolated populations outside temperate Europe or isolated low-elevation populations on relict habitats (fens, screes, rocks, steppe grasslands).

Relicts from the Last Glacial Maximum, interstadials and the Early Holocene

We further attempted to separate relicts from glacial maxima by summing selected biogeographical symptoms (3 – discontinuity of the distribution range; 4 – conservatism) with the affinity to the habitats that might be abundant during the LGM (steppe, fens and tundra; categories 6, 7 and 11 in Appendix); the habitat affinity was downweighted by dividing the scores by two. The threshold of this *full-glacial score* for inclusion among relicts from the LGM was arbitrarily set to 5.5 because this value best fitted the traditional paradigm and was hence the most conservative.

Palaeoecological and phylogeographical evidence for relict status

We further reviewed (i) whether each species was recorded as a macrofossil in the Western Carpathians or adjacent lowlands from any period of Pleistocene or Early Holocene. These data were taken from the Czech and Slovak Macrofossil Database (www.sci.muni.cz/botany/mirecol/paleo); (ii) whether each species was recorded in fossil pollen spectra from the same periods (see Jamrichová et al. 2017 for a reference list) and (iii) whether there is any study showing any phylogeographical pattern for the

species, with at least one population from the Western Carpathians included in the analyses.

Data analysis

As the last step, we subjected the resulting species-by-symptom matrix to principal component analysis (PCA) where individual species acted as ‘samples’ whereas individual symptoms acted as ‘species’. Only biogeographical symptoms were analysed. Habitat affinity (scores for the entire distribution range), niche contraction and taxonomic groups were *a posteriori* projected into the ordination space using the classification of the species. To visualize the pattern for species with the highest final score, we subjected a full species-by-symptom matrix (12 biogeographical and ecological symptoms) to redundancy analysis (RDA) with the final score set as a single explanatory variable. Ordination analyses were performed in R (R Core Team 2016) using library ‘vegan’ (Oksanen et al. 2016).

The nomenclature follows Tutin et al. (1964–1993) for vascular plants, Hill et al. (2006) for mosses, Górski and Váňa (2014) for hepatics, and Guttová et al. (2013) for lichens. Considering the new results published in this issue of *Folia Geobotanica*, *Pedicularis hacquetii* was merged with *P. exaltata* (Těšitel et al. 2018, this issue).

Results

The list of relict species

The final number of 289 species (206 vascular plant, 46 bryophyte and 37 terrestrial lichen species) reached a *final score* of at least 10 (Table 1). Only 41 of them (Table S2 in the Electronic supplementary material) have been ever at least regionally analysed phylogeographically in the Western Carpathians (14%), and for only 51 of them any micro- or macrofossils from the last glacial or Early Holocene times were found in the Western Carpathians or beyond (17.6%). Less than half of these species (126; 43.5%) have an affinity to arctic-alpine tundra habitats in the Western Carpathians (values of habitat affinity 2–3), 69 species have an affinity to fens, 32 species to bogs, 37 species to mesic forest-steppe (light-coniferous temperate forests, meadow-steppe grasslands and tall-herb stands) and 45 species have an affinity to dry steppe; but note that some species have an affinity (score = 2) to two habitats.

Table 1 List of putative glacial or Early Holocene relicts of the Western Carpathians

<i>Betula nana</i> (V; m, p, g; 22) W	<i>Cryptogramma crispa</i> (V; 15) A
<i>Carex vaginata</i> (V; 22) G	<i>Ranunculus pygmaeus</i> (V; g; 15) A
<i>Cladonia stellaris</i> (L; 22) A	<i>Veratrum nigrum</i> (V; 15) F,G
<i>Trichophorum pumilum</i> (V; m; 21) W	<i>Triglochin maritima</i> (V; g, m; 15) W
<i>Nephroma arcticum</i> (L; 21) A	<i>Astragalus australis</i> (V; m; 15) A
<i>Flavocetraria nivalis</i> (L; g; 21) A	<i>Eriophorum gracile</i> (V; 15) W
<i>Saxifraga hirculus</i> (V; p; 20) W	<i>Ranunculus reptans</i> (V; 15) W
<i>Peltigera scabrosa</i> (L; 19) A	<i>Saussurea alpina</i> (V; 15) A
<i>Flavocetraria cucullata</i> (L; g; 19) A	<i>Thalictrum simplex</i> (V; 15) G
<i>Ledum palustre</i> (V; 19) W	<i>Cetraria ericetorum</i> (L; 15) A
<i>Salix lapponum</i> (V; g; 18) A	<i>Stereocaulon alpinum</i> (L; 15) A
<i>Gentianella tenella</i> (V; g; 18) A	<i>Carex chordorrhiza</i> (V; m; 15) W
<i>Carex magellanica</i> (V; 18) W	<i>Salix myrtilloides</i> (V; m; 15) W
<i>Linnaea borealis</i> (V; g; 18) F	<i>Carex pauciflora</i> (V; 15) W
<i>Cladonia macrophyllodes</i> (L; 18) A	<i>Drepanocladus longifolius</i> (B; 15) W
<i>Andromeda polifolia</i> (V; m; 18) W	<i>Tephroses longifolia</i> s.l. (V; 15) F,G
<i>Carex buxbaumii</i> (V; 18) W	<i>Trichophorum alpinum</i> (V; 15) W
<i>Dendranthema zavadskii</i> (V; 17) G	<i>Cladonia acuminata</i> (L; 15) A,F
<i>Kobresia simpliciuscula</i> (V; 17) A	<i>Hierochloa odorata</i> (V; 15) F,G
<i>Veronica paniculata</i> (V; 17) F	<i>Rhytidium rugosum</i> (B; g; 15) G
<i>Gymnomitrium corallioides</i> (B; 17) A	<i>Primula farinosa</i> (V; g, p; 14) W
<i>Ligularia sibirica</i> (V; g; 17) W	<i>Encalypta rhabdocarpa</i> (B; m; 14) A
<i>Peltigera aphthosa</i> (L; 17) F	<i>Andreaea obovata</i> (B; 14) A
<i>Rubus chamaemorus</i> (V; g; 17) W	<i>Draba fladnizensis</i> (V; 14) A
<i>Salix starkeana</i> (V; 17) G,W	<i>Hygrohypnum polare</i> (B; 14) A
<i>Trifolium lupinaster</i> (V; 16) A	<i>Juncus castaneus</i> (V; 14) W
<i>Hilpertia velenovskyi</i> (B; g; 16) G	<i>Loiseleuria procumbens</i> (V; 14) A
<i>Meesia longiseta</i> (B; 16) W	<i>Saxifraga hieraciifolia</i> (V; 14) A
<i>Arctostaphylos alpinus</i> (V; 16) A	<i>Sciuro-hypnum glaciale</i> (B; 14) A
<i>Carex atrofusca</i> (V; g; 16) A	<i>Scorpidium revolvens</i> s. str. (B; 14) W
<i>Tofieldia pusilla</i> (V; 16) A	<i>Tetralophozia setiformis</i> (B; 14) A
<i>Ligularia glauca</i> (V; 16) F	<i>Woodsia alpina</i> (V; 14) A
<i>Alectoria nigricans</i> (L; 16) A	<i>Physconia muscigena</i> (L; g; 14) A
<i>Cetraria aculeata</i> (L; g; 16) A,G	<i>Carex bigelowii</i> (V; g; 14) A
<i>Cladonia magyarica</i> (L; 16) G	<i>Aster alpinus</i> (V; 14) A
<i>Thamnolia vermicularis</i> (L; g; 16) A	<i>Carex capillaris</i> (V; 14) A,W
<i>Sparganium angustifolium</i> (V; m; 16) W	<i>Juniperus sabina</i> (V; 14) G
<i>Polygonum viviparum</i> (V; m; 16) A	<i>Pseudocalliergon trifarium</i> (B; m; 14) W
<i>Trichophorum cespitosum</i> (V; 16) W	<i>Dicranum groenlandicum</i> (B; 14) A
<i>Carex lachenalii</i> (V; 16) W	<i>Meesia uliginosa</i> (B; 14) A
<i>Astragalus alpinus</i> (V; 16) A	<i>Astragalus frigidus</i> (V; 14) A
<i>Cetrariella delisei</i> (L; 16) A	<i>Glaux maritima</i> (V; 14) W
<i>Cladonia amaurocraea</i> (L; 16) A	<i>Ligusticum mutellinoides</i> (V; 14) A
<i>Cladonia ecmocyna</i> (L; 16) A	<i>Tritomaria scitula</i> (B; 14) A
<i>Cladonia macroceras</i> (L; 16) A	<i>Cerastium cerastoides</i> (V; 14) A
<i>Vaccinium uliginosum</i> (V; g, m; 16) W	<i>Dianthus superbus</i> (V; 14) A,G

Table 1 (continued)

<i>Scorpidium scorpioides</i> (B; m; 16) W	<i>Dracocephalum ruyschiana</i> (V; 14) G
<i>Selaginella selaginoides</i> (V; p, m; 16) A	<i>Woodsia ilvensis</i> (V; 14) F
<i>Thesium ebracteatum</i> (V; 16) G	<i>Anemone narcissiflora</i> (V; 14) A
<i>Nephroma expallidum</i> (L; 16) A	<i>Veratrum album subsp. lobelianum</i> (V; 14) A,F
<i>Cladonia uncialis</i> (L; 16) A,G	<i>Alectoria ochroleuca</i> (L; 14) A
<i>Peltigera venosa</i> (L; 16) A	<i>Scheuchzeria palustris</i> (V; 14) W
<i>Potamogeton obtusifolius</i> (V; m; 16) W	<i>Betula pubescens</i> agg. (V; m; 14) W
<i>Cladonia botrytes</i> (L; g; 16) F	<i>Cochlearia pyrenaica</i> (V; g; 13) W
<i>Stipa eriocalis</i> (V; g; 15) G	<i>Schistidium boreale</i> (B; 13) A
<i>Helictotrichon desertorum</i> (V; 15) G	<i>Andreaea blyttii</i> (B; 13) A
<i>Gyalidea asteriscus</i> (L; 15) G	<i>Andreaea rothii</i> (B; 13) A
<i>Pulsatilla vernalis</i> (V; g; 15) A	<i>Anthelia juratzkana</i> (B; 13) A
<i>Drepanocladus sendtneri</i> (B; m; 5) W	<i>Carex rupestris</i> (V; 13) A
<i>Bucegia romanica</i> (B; g; 15) A	<i>Cerastium alpinum</i> (V; 13) A
<i>Carex pediformis subsp. rhizoides</i> (V; 15) F,G	<i>Cortusa matthioli</i> (V; 13) A
<i>Kobresia myosuroides</i> (V; 15) A	<i>Oreoweisia torquescens</i> (B; 13) A
<i>Oreas maritima</i> (B; 15) A	<i>Solorina octospora</i> (L; 13) A
<i>Pedicularis oederi</i> (V; 15) A	<i>Juncus triglumis</i> (V; 13) A
<i>Saxifraga cernua</i> (V; 15) A	<i>Pinguicula alpina</i> (V; 13) A
<i>Sibbaldia procumbens</i> (V; 15) A	<i>Viola epipsila</i> (V; 13) W
<i>Catoscopium nigratum</i> (B; m; 15) A,W	<i>Saxifraga paniculata</i> (V; g, m; 13) A,G
<i>Oxytropis campestris</i> (V; g; 15) A	<i>Saxifraga oppositifolia</i> (V; g, m; 13) A
<i>Rhodiola rosea</i> (V; g; 15) A	<i>Warnstorfia sarmentosa</i> (B; m; 13) W
<i>Pulsatilla patens</i> (V; g; 15) G	<i>Salix herbacea</i> (V; g; 13) A
<i>Allium schoenoprasum subsp. alpinum</i> (V; 15) A	<i>Carex fuliginosa</i> (V; 13) A
<i>Allium strictum</i> (V; 15) G	<i>Angelica archangelica</i> (V; 13) A
<i>Conostomum tetragonum</i> (B; 13) A	<i>Astragalus norvegicus</i> (V; 13) A
<i>Ephedra distachya</i> (V; 13) G	<i>Aulacomnium turgidum</i> (B; 13) A
<i>Oxyria digyna</i> (V; 13) A	<i>Epilobium anagallidifolium</i> (V; 12) W
<i>Pedicularis sceptrum-carolinum</i> (V; g; 13) W	<i>Fontinalis hypnoides</i> (B; 12) W
<i>Pedicularis verticillata</i> (V; 13) A	<i>Luzula spicata</i> (V; 12) A
<i>Syntrinchia norvegica</i> (B; 13) A	<i>Viola biflora</i> (V; 12) A
<i>Toninia rosulata</i> (L; 13) G	<i>Juncus gerardii</i> (V; m; 12) W
<i>Arctostaphylos uva-ursi</i> (V; 13) A	<i>Hackelia deflexa</i> (V; 12) F
<i>Sedum annuum</i> (V; 13) F	<i>Carex lasiocarpa</i> (V; m; 12) W
<i>Tetraplodon angustatus</i> (B; 13) A,F	<i>Allium victorialis</i> (V; 12) F,A
<i>Vaccinium microcarpum</i> (V; 13) W	<i>Pseudobryum cinclidioides</i> (B; 12) W
<i>Cinclidium stygium</i> (B; m; 13) W	<i>Polemonium caeruleum</i> (V; p; 12) W
<i>Drepanocladus polygamus</i> (B; m; 13) W	<i>Solorina bispora</i> (L; 11) A
<i>Adenophora lilifolia</i> (V; g; 13) F,G	<i>Serratula lycopifolia</i> (V; g; 11) G
<i>Empetrum nigrum</i> (V; 13) W	<i>Bartsia alpina</i> (V; 11) A
<i>Pseudocalliergon lycopodioides</i> (B; 13) W	<i>Iris aphylla</i> (V; g; 11) G
<i>Sagina saginoides</i> (V; 13) A	<i>Thalictrum foetidum</i> (V; 11) G
<i>Solorina spongiosa</i> (L; 13) A,W	<i>Amygdalus nana</i> (V; 11) G
<i>Carex limosa</i> (V; m; 13) W	<i>Bryum schleicherii</i> (B; 11) W
<i>Rhynchospora alba</i> (V; m; 13) W	<i>Carex dioica</i> (V; 11) W
<i>Diphasiastrum alpinum</i> (V; 13) A	<i>Carex supina</i> (V; 11) G
<i>Drosera anglica</i> (V; 13) W	<i>Cicuta virosa</i> (V; 11) W
<i>Lathyrus pisiformis</i> (V; 13) F	<i>Omalotheca supina</i> (V; 11) A
<i>Sagina nodosa</i> (V; 13) W	<i>Salix hastata</i> (V; 11) A
<i>Sphagnum majus</i> (B; 13) W	<i>Cladonia foliacea</i> (L; 11) G
<i>Sphagnum platyphyllum</i> (B; 13) W	<i>Solorina saccata</i> (L; 11) A
<i>Cladonia macrophylla</i> (L; 13) A	<i>Linum flavum</i> (V; g; 11) G
<i>Cladonia turgida</i> (L; 13) A,F	<i>Anemone sylvestris</i> (V; 11) F,G
<i>Eriophorum vaginatum</i> (V; m; 13) W	<i>Cystopteris montana</i> (V; 11) F
<i>Potamogeton alpinus</i> (V; m; 13) W	<i>Empetrum hermaphroditum</i> (V; 11) A
<i>Listera cordata</i> (V; 13) F	<i>Vaccinium oxycoccos</i> (V; 11) W
<i>Viola rupestris</i> (V; 13) F,G	<i>Stipa capillata</i> (V; g; 11) G
<i>Astragalus penduliflorus</i> (V; 12) A	<i>Bassia prostrata</i> (V; 11) G

Table 1 (continued)

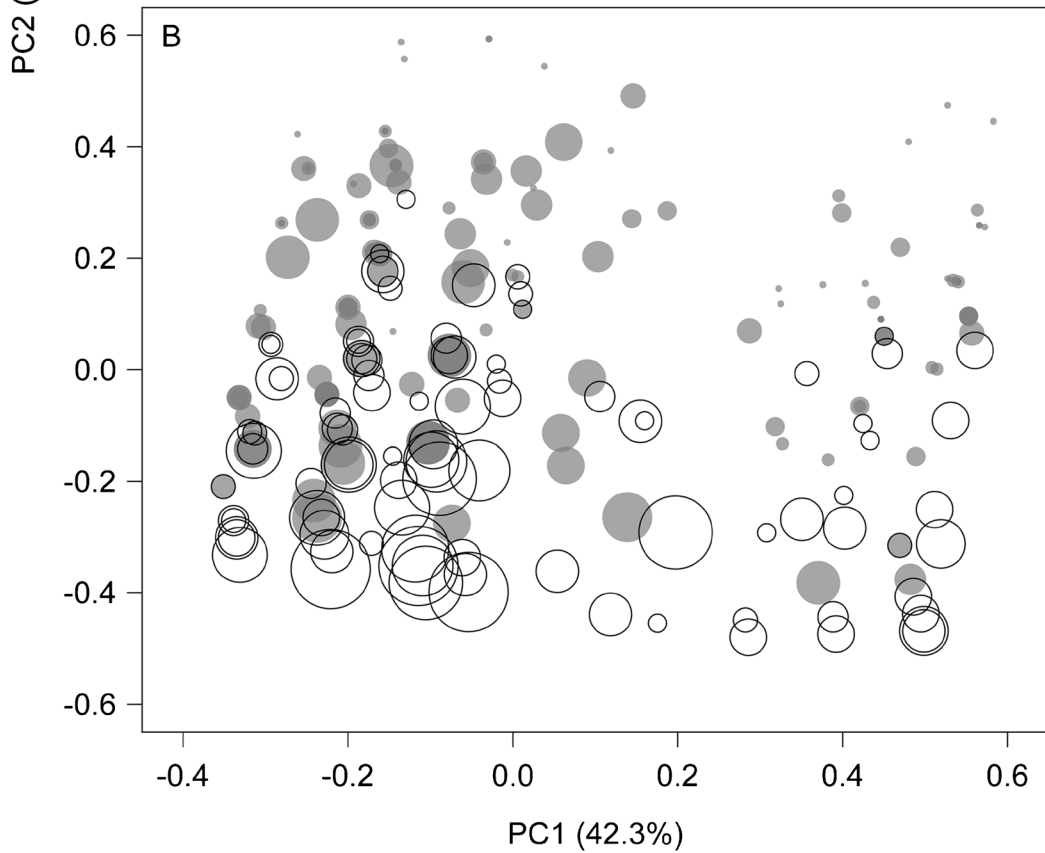
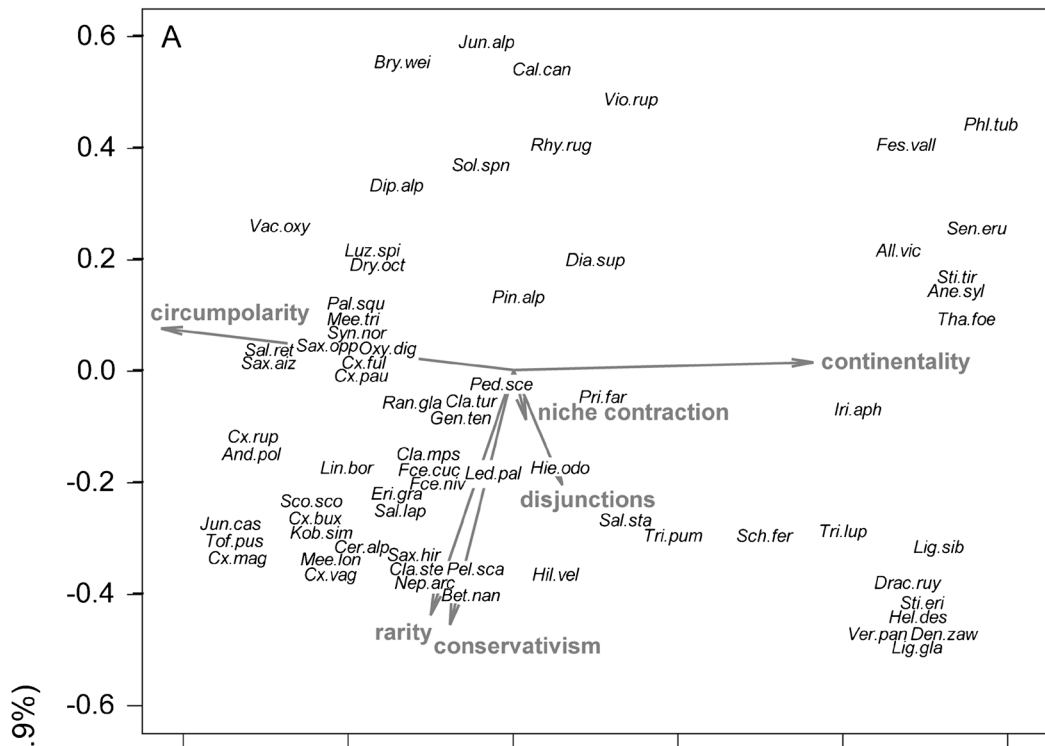
<i>Draba dubia</i> (V; 12); A	<i>Carex diandra</i> (V; 11) W
<i>Schoenus ferrugineus</i> (V; 12) W	<i>Stipa tirsia</i> (V; 11) G
<i>Salix phylicifolia</i> (V; m; 12) A	<i>Adonis vernalis</i> (V; 10) G
<i>Ranunculus glacialis</i> (V; g; 12) A	<i>Toninia sedifolia</i> (L; 10) G
<i>Hedysarum hedysaroides</i> (V; 12) A	<i>Campanula sibirica</i> (V; g; 10) G
<i>Chamorchis alpina</i> (V; 12) A	<i>Stipa pennata</i> (V; g; 10) G
<i>Swertia perennis</i> (V; 12) A	<i>Juncus trifidus</i> (V; 10) A
<i>Arabis alpina</i> (V; g; m; 12) A	<i>Astragalus austriacus</i> (V; 10) G
<i>Salix reticulata</i> (V; m; 12) A	<i>Potentilla crantzii</i> (V; 10) A
<i>Saxifraga aizoides</i> (V; m; 12) A	<i>Stellaria longifolia</i> (V; 10) W
<i>Dryas octopetala</i> (V; g, p, m; 12) A	<i>Utricularia minor</i> (V; 10) W
<i>Pinus cembra</i> (V; g, p, m; 12) F	<i>Salix rosmarinifolia</i> (V; m; 10) W
<i>Veronica alpina</i> (V; g; 12) A	<i>Pleurospermum austriacum</i> (V; p; 10) F
<i>Astragalus excapus</i> (V; g; 12) G	<i>Larix decidua</i> (V; g; p, m; 10) F
<i>Carex atrata</i> (V; 12) A	<i>Cimicifuga europaea</i> (V; 10) F
<i>Erigeron uniflorus</i> (V; 12) A	<i>Carex humilis</i> (V; 10) G
<i>Jungermannia exsertifolia</i> (B; 12) A	<i>Fulgensia fulgens</i> (L; 10) A
<i>Jungermannia polaris</i> (B; 12) A	<i>Carex aproinquata</i> (V; m; 10) W
<i>Juniperus communis subsp. alpina</i> (V; 12) A	<i>Calliargon giganteum</i> (B; m; 10) G
<i>Lloydia serotina</i> (V; 12) A	<i>Agropyron cristatum</i> (V; 10) G
<i>Saxifraga adscendens</i> (V; 12) A	<i>Astragalus danicus</i> (V; 10) G
<i>Scorzonera parviflora</i> (V; 12) W	<i>Oxytropis pilosa</i> (V; 10) G
<i>Silene acaulis</i> (V; 12) A	<i>Calla palustris</i> (V; m; 10) W
<i>Veronica fruticans</i> (V; 12) A	<i>Conioselinum tataricum</i> (V; 10) F
<i>Solorina crocea</i> (L; 12) A	<i>Drosera rotundifolia</i> (V; 10) W
<i>Scorzonera purpurea</i> (V; g; 12) G	<i>Peucedanum oreoselinum</i> (V; 10) F,G
<i>Cotoneaster melanocarpos</i> (V; 12) F	<i>Scorzonera humilis</i> (V; 10) F,W
<i>Echium russicum</i> (V; 12) G	<i>Hippuris vulgaris</i> (V; m; 10) W
<i>Iris pumila</i> (V; 12) G	<i>Tomentypnum nitens</i> (B; m; 10) W
<i>Gentiana nivalis</i> (V; g; 12) A	<i>Bryum weigelii</i> (B; 10) W
<i>Pedicularis hacquetii/exaltata</i> (V; g; 12) G,A	<i>Calamagrostis canescens</i> (V; 10) F,W
<i>Peucedanum carvifolia</i> (V; 12) F,G	<i>Crambe tatarica</i> (V; 10) G
<i>Psora decipiens</i> (L; 12) G	<i>Festuca vallesiaca</i> (V; 10) G
<i>Helodium blandowii</i> (B; m; 12) W	<i>Juncus alpinus</i> (V; 10) W
<i>Lysimachia thyrsoiflora</i> (V; m; 12) W	<i>Botrychium multifidum</i> (V; 10) F
<i>Meesia triquetra</i> (B; m; 12) W	<i>Dryopteris expansa</i> (V; 10); F
<i>Paludella squarrosa</i> (B; m; 12) W	<i>Phlomis tuberosa</i> (V; 10) G
<i>Hamatocaulis vernicosus</i> (B; m; 12) W	<i>Potentilla palustris</i> (V; 10) W
<i>Artemisia santonicum</i> (V; 12) G	<i>Senecio erucifolius</i> (V; 10) G
<i>Crepis sibirica</i> (V; 12) F,G	<i>Equisetum pratense</i> (V; 10) F

The list presents species which reached the highest score in our evaluation of biogeographical and ecological symptoms ([Appendix](#)). The distinguishing between glacial relicts (in bold) and Early Holocene relicts (in italic) is based on the *full-glacial score* as calculated and presented in [Table S1](#). The species are sorted by their *final score* and then by the *full-glacial score* ([Table S1](#)). The codes in the parenthesis indicate the taxonomic group (V – vascular plant; B – bryophyte; L – macroscopic terrestrial lichen), existence of any phylogeographical study from Central Europe (g), existence of fossil pollen (p) or macrofossil (m) data from the study area or its close surroundings. The code after the parenthesis indicates the current habitat of the species in the Western Carpathians: A – alpine and subalpine treeless habitats; G – grasslands (including steppe, treeless mesic forest-steppe and rocky grasslands; excluding the A category); W – wetlands (bog, fens, lakes); F – forests including dark taiga, light coniferous forests, open oak forests and forest steppe

Relicts from the Last Glacial Maximum, from interstadials and the Early Holocene

The biogeographical and ecological symptoms for 143 species suggest that they retreated rapidly after the LGM (*full-glacial score* ≥ 5.5) whereas 146 species could be still quite frequent as long as during the Early Holocene.

The highest full-glacial score (8.5) is indicated for *Trichophorum pumilum*. The PCA of biogeographical symptoms sorted species from circumpolar species of fens, acidic wetlands and tundra to continental species of steppe and forest-steppe that often exhibit contracted niches in the Western Carpathians ([Fig. 1](#); [Fig. S1](#)). Most bryophytes were distributed at the ‘circumpolar’



◀ **Fig. 1 a** – PCA plot of biogeographical symptoms of individual species from the final list of relicts (Table 1) showing trait-species relationships. For brevity, only species with a high final score (≥ 18) and a subset of the other species (20%) are displayed. **b** – PCA scatterplot (B) showing the position of each species where circle size is proportional to the final score and circle colour depicts putative relicts of the Last Glacial Maximum (white circles) and Early Holocene (grey circles). Variances explained by the first two principal components are given in parentheses. Ordination plots are scaled symmetrically. See Table S1 in the Electronic supplementary material for explanations of abbreviations

end of the first axis, while vascular plants covered entire gradient, lichens being intermediate (Fig. S1).

The second PCA axis followed conservatism, rarity and disjunctivity in distribution ranges, independently of habitat preferences, and correlated partially with high final scores of species. Species showing rather wide moisture tolerances that are characteristic of Siberian and Central Asian steppe and forest steppe, disjunctively occurring in Europe as putative full-glacial or later relicts (Holub 1999; Horsák et al. 2015; Roleček et al. 2015), reached extreme scores along both the first and the second axis (*Veronica paniculata*, *Ligularia glauca*, *L. sibirica*, *Dendrothema zawadskii*, *Helictotrichum desertorum*, *Stipa eriocaulis*, *Dracocephalum ruyshiana*).

The species with the highest final score (> 20) are *Carex vaginata*, *Trichophorum pumilum*, *Betula nana* (now extinct in the study area), *Cladonia stellaris*, *Nephroma arcticum*, *Flavocetraria nivalis* and *Saxifraga hirculus*. These species display quite a wide habitat niche in their entire distribution range (3–5 habitats as defined in this study), contraction of ecological niche in the Western Carpathians, as well as high levels of rarity and conservatism in this mountain range (Fig. 2). These species show an affinity to more habitats including tundra, taiga, fens and bogs, with *Trichophorum pumilum* and *Saxifraga hirculus* being characteristic of continental steppe-tundra landscapes (Horsák et al. 2015) and high-ranked lichens being even characteristic of palusa mires (Lavrinenko and Lavrinenko 2015). Both the RDA (Fig. 2) and PCA (Fig. 1) demonstrate that high-ranked species show high level of conservatism, rarity and niche contraction in general, and that their biogeographical and habitat affinities are not distinctive.

Concerning purely steppe or forest-steppe species, the highest-ranked species are *Dendrothema zawadskii* (reported as glacial relict by Holub 1999), *Veronica*

paniculata, *Ligularia glauca*, *Salix starkeana*, *Trifolium lupinaster* (which is, however, restricted to alpine tundra in the study region) and the moss *Hilpertia velenovskyi*, which is specialized to loess substrates. The highest-ranked steppe lichen is the loess species *Gyalidea asteriscus*. The highest-ranked wetland bryophytes are *Meesia longiseta* (now extinct in the study area) and *Scorpidium scorpioides* (recently occurring only in the Kubínska hoľa Mts in Slovakia and few sites in the Nowy Targ basin; Dítě and Šoltés 2010; Ochyra et al. 1988), the highest-ranked species of acidic peatlands is *Carex magellanica* (recently occurring in one locality in Slovakia; Dítě and Pukajová 2003) and the highest-ranked fen vascular-plant specialists (habitat affinity scored to 3) are *Eriophorum gracile* and *Primula farinosa*. The highest-ranked vascular plant species tightly specialized to tundra was *Kobresia myosuroides*.

Palaeoecological and phylogeographical evidence for relict status

The results of individual phylogeographical studies, based on the AFLP method (most cases), microsatellites, allozymes and rarely other methods (ITS, RADseq), covering altogether 41 species, have been categorized with respect to geographical structuring of lineages in Central Europe and population characteristics in the Western Carpathians (Table S2). The vast majority of analysed species showed low (single lineage or more geographically unstructured lineages) or moderate (narrow-range but not specifically Carpathian) level of geographical structure (categories 1 and 2 in Table S2) in Europe or at least in Central Europe (including the entire Carpathians, the Alps and the Sudetes). This result may suggest that the species' distribution was more widespread in the past, allowing genetic exchange. If the genetic structure was generally shallow, then Western Carpathian populations usually showed either unique alleles, or high within-population variation, or small-scale genetic variation (meeting of different haplotypes), suggesting that their recent occurrence in the study area is not a product of a very recent dispersal event or anthropogenic introduction. These features characterize especially arctic-alpine and high-mountain species (e.g. Schönswetter et al. 2004b; Albach et al. 2006; Eidesen et al. 2007; Reisch 2008; Alsos et al. 2009; Höhn et al. 2009; Lendvay et al. 2014; György et al. 2016) which occurred at lower elevations than today during the last glacial times, which was in

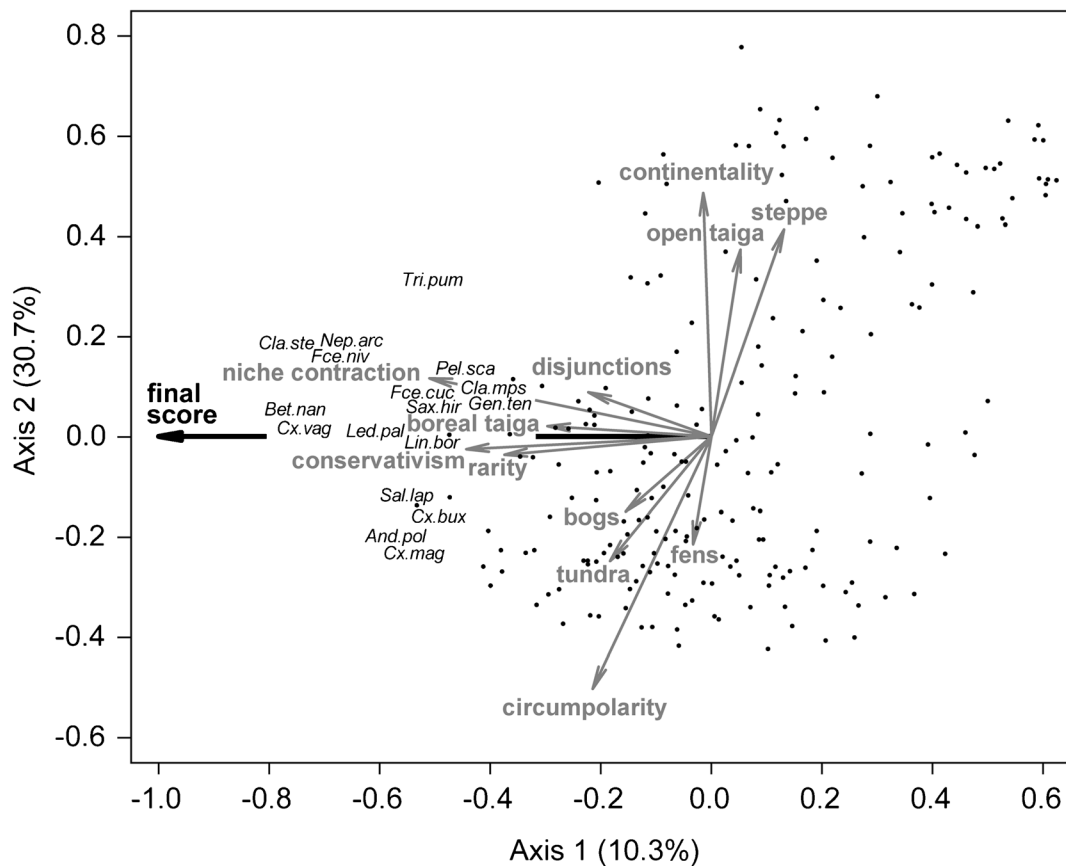


Fig. 2 RDA plot showing relationships between final score (i.e. the strength of glacial-relict symptoms) for individual species listed in Table 1 and species traits. The final score for individual species was the single constraining variable. Position of species with high final

score (≥ 18) is depicted, the remaining species are displayed as dots. Variances explained by the axes are given in parentheses. The ordination plot is scaled symmetrically. See Table S1 in the Electronic supplementary material for explanations of abbreviations

some cases confirmed palaeoecologically (*Pinus cembra*), or by existence of refugial low-elevation populations on relict habitats (*Vaccinium uliginosum*, *Pedicularis hacquetii/exaltata*, *Rhodiola rosea*, *Saxifraga paniculata*). This group, however, includes also some steppe, forest-steppe and fen species. Narrow-range but not specifically Carpathian lineages, frequently meeting in the Western Carpathians, were found especially for steppe and forest-steppe species (Meindl 2011; Sabovljević and Frahm 2011; Becker 2012; Wagner et al. 2012; Durka et al. 2013; Cieślak 2014; Kajtoch et al. 2016; Szczecińska et al. 2016; Plenk et al. 2017; Hedenäs 2015, 2017), for *Larix europaea* (Wagner et al. 2015a) and for those arctic-alpine and boreocontinental species which are recently very rare and possibly quite rare also in the past (e.g. *Gentiana nivalis*, *Ranunculus pygmaeus*, *Cochlearia pyrenaica*, *Dryas octopetala*; for details see Koch et al. 2003; Schönswetter et al. 2006b;

Skrede et al. 2006; Cieślak et al. 2007; Winkler et al. 2012; Alvarez et al. 2012). In some cases, more widespread lineages occur sympatrically with specific Carpathian ones (*Gentianella tenella*, *Arabis alpina*, *Ranunculus glacialis*, *Linnaea borealis*, *Pulsatilla vernalis*, *Thamnomia vermicularis*; for details see Schönswetter et al. 2003, 2004a; Koch et al. 2006; Ehrich et al. 2007; Ronikier et al. 2008, Ronikier 2011; Wróblewska 2013a; Onuț-Brännström et al. 2017). For the latter species, Onuț-Brännström et al. (2017), however, demonstrated that the evolutionary split between the widespread and Alpine-Carpathian lineages is probably older than the LGM and different lineages could have different glacial history. Coexistence of different lineages in the Western Carpathians was demonstrated also for the steppe species *Iris aphylla*, which shows quite uniform genetic structure, suggesting wider distribution during the Late Glacial

and Early Holocene (Wróblewska 2008, Wróblewska et al. 2010), but also has one genetically specific diploid population occurring in the Slovak Karst. The genetic structure of the steppe moss species *Rhytidium rugosum* suggests that the distribution of this species in Europe was fragmented during the LGM, but the species occurred in the Western Carpathian region and expanded after the LGM (Hedenäs 2017). The genetic structure of the two latter steppe species fits our scoring results that categorized them as the Late Glacial / Early Holocene relicts. For another putative Early-Holocene steppe relict *Stipa capillata*, Hensen et al. (2010) found that Western-Carpathian populations formed a heterogeneous but well supported group with private alleles, clearly separated from the German and Swiss populations. The species hence might be quite abundant during the LGM in the Western Carpathians but were not the main genetic source for the post-glacial colonization of Western Europe.

For some species with low or moderate level of geographical structure, genetic data suggest post-glacial migration from Western Carpathians (or Alps or generally Central Europe) to Scandinavia (*Saxifraga paniculata*, *Arabis alpina*, *Gentianella tenella*, *Veronica alpina*, *Carex bigelowii*, *Gentiana nivalis*; Albach et al. 2006; Schönschwetter et al. 2004a, 2008; Ronikier 2011; Alvarez et al. 2012). *Carex atrofusca* and *Saxifraga oppositifolia* once arrived in the Western Carpathians from Asia but communicated with populations from the Alps during the glacial cycles (Skrede et al. 2006; Schönschwetter et al. 2006a; Winkler et al. 2012).

The specific cases are *Rubus chamaemorus*, *Triglochin maritima*, the lichens *Cetraria aculeata*, *Flavocetraria cucullata* and *F. nivalis*, and the bryophyte *Bucegia romanica*. These species have been analysed phylogeographically in Europe, but Western Carpathian populations have not been included. The pattern for *R. chamaemorus* suggests a refugium outside Europe during the LGM (Ehrich et al. 2008), supporting the classification of the species as a relict from Late Glacial / Early Holocene according to our scoring (Table 1). For *Triglochin maritima* the phylogeographical pattern suggests full-glacial refugia in inland Europe (Lambracht et al. 2007), again supporting our classification based on scoring. For the two *Flavocetraria* species, the results showed the persistence during the glacial times even in far north in the arctic zone (Geml et al. 2010). The observation of

C. aculeata shows distinct populations from temperate Europe from those in North and South Poles (Printzen et al. 2013). The genetic structure of *Bucegia romanica* was quite uniform in Europe, but Eastern Carpathian populations clustered together (Konstantinova et al. 2014), resembling the pattern for other potential arctic-alpine glacial relicts (Table S2).

Additionally to these phylogeographical symptoms, the genetic structure of some species suggests that post-glacial extinction and/or dispersal limitation shaped their genetic diversity; the genetic distance between isolated populations was high and/or high amount of private alleles was found for some Western Carpathian populations (Table S2). This result concerns mostly steppe species (Cieślak 2013; Kajtoch et al. 2016; Prausová et al. 2016), but also fen species *Ligularia sibirica* (Šmídová et al. 2011). A similar result was obtained for populations of *Pedicularis sceptrum-carolinum* (Wróblewska 2013b) and *Betula nana* (Jadwiszczak et al. 2012) in non-Carpathian regions of Poland.

Macrofossil evidence for the glacial or Early Holocene occurrence in the Western Carpathians or adjacent lowland is available for 26 species (Table 1). For further 13 species, macrofossil data from the surrounding regions (Pannonian lowland, Bohemian Massif, Eastern Carpathians) suggest wider distribution in Central Europe before the climate optimum. Macrofossil evidence is available especially for peatland and aquatic species (Hájková et al. 2012; Dítě et al. 2013; Gálová et al. 2016), but Szafer (1950) reports also macrofossils of species of rocks and tundra from the late glacial in the Pieniny Mts (*Dryas octopetala*, *Astragalus australis*, *Encalypta rhabdocarpa*). Five species were reported by both microfossils (pollen, spores) and macrofossils (*Betula nana*, *Pinus cembra*, *Larix decidua*, *Selaginella selaginoides* and *Dryas octopetala*), and three species have been reported only by pollen data (*Primula farinosa*, *Pleurospermum austriacum*, *Polemonium caeruleum*; e.g. Jankovská and Pokorný 2008; Hájková et al. 2013; Gálová et al. 2016).

Finding fossil evidence for a contraction of species ranges during the climate optimum is even more difficult. This pattern is evident for the eight above-mentioned species that can be distinguished in the pollen records. Before the climate optimum they are frequently reported from warm, low-elevation regions recently encroached by warm-temperate deciduous trees

or intensively managed for agriculture (Rybníčková and Rybníček 2014; Jankovská and Pokorný 2008; Hájková et al. 2013; Jamrichová et al. 2014; Hájek et al. 2016). Also macrofossils sometimes report the lowland or low-elevation occurrence of species that recently occur only in mountains or mountain basins, such as *Catoscopium nigratum*, *Pseudocalliergon trifarium* or *Potamogeton alpinus* in the Borská lowland, Podunajská lowland and Malé Karpaty Mts (Jamrichová et al. 2014; Hájková et al. 2015; Gálová et al. 2016). In these regions, even the boreal or continental species that recently do not occur in Central Europe or in the Western Carpathians were reported (e.g. *Blysmus rufus*, *Calliergon richardsonii*, *Potamogeton filiformis*, *Betula humilis*; Magyari et al. 1999; Hájková et al. 2015; Gálová et al. 2016 and A. Šolcová, unpublished data).

Discussion

Our study represents the first attempt to compile a comprehensive expert-based list of potential glacial relicts, which could be utilized in biogeographical analyses and conservation planning. The final list produced in this study is based on current premises of landscape development in East-Central Europe during glacial times (Jankovská and Pokorný 2008; Feurdean et al. 2014; Janská et al. 2017; Jamrichová et al. 2017) and was created using biogeographical characteristics of individual species of the Western Carpathian flora, especially those concerning distribution range and habitat affinity. We therefore tried to formally reproduce the way how botanists used to identify glacial or Early-Holocene relicts among species of the Central European flora.

Weaknesses and ambiguities of the approach

Considering that accurate and unbiased quantitative determinations of relict statuses of individual species are not possible, especially if direct evidences from palaeoecology and phylogeography are largely missing, one should interpret our list of relict species with caution. There are at least three aspects that should be especially taken in account.

First, the results should be seen as a general picture rather than as firm evidence for each individual species, because there is still quite high probability that a species was miscategorized by our approach.

Second, the final categorization of species is not binary. Rather, we are presenting gradients of glacial-relict symptoms, arbitrarily divided into three fuzzy species groups (full-glacial relicts, Late Glacial / Early Holocene relicts, other species). The division between relicts and other species was done arbitrarily using a value of the final score equal to 10, because this value allowed to include all species for which there is strong palaeoecological and phylogeographical evidence and/or a strong consensus in the literature (e.g. *Pleurospermum austriacum*, *Larix decidua*, *Gentiana nivalis*, *Crambe tataria*, *Agropyron cristatum* with final scores of 10, or *Pinus cembra*, *Meesia triquetra*, *Paludella squarrosa* or *Carex dioica* with final scores of 11–12). The low final score hence cannot be interpreted as weaker evidence of a relict status. An individual species may possess only one or few symptoms indicating its relict status. For example, the final score of some species that might had been more common in glacial loess steppe than in the current landscape was lowered by their ability to colonize human-made habitats, causing their low ecological conservatism and absence of large discontinuities in their distribution ranges.

Third, distinguishing between European mountain species, i.e. local elements with long-term stability in their distribution ranges during the Quaternary (as largely confirmed by phylogeography, Ronikier 2011) and narrow-range relicts from the last glacial period, is not always unequivocal either. We finally included only few European mountain species, whose populations show lowland distribution at obviously relict sites, such as *Swertia perennis* or *Pedicularis exaltata/hacquetii*. We nevertheless acknowledge that there is a great risk of miscategorization in the case of European mountain species. For example, *Calianthemum coriandrifolium*, which is considered a separate taxon with closely allied species in Central Asia (Pawlowska 1966), was not considered although it may benefit from a glacial climate and might had been distributed more widely in the Western Carpathians during the last glacial. We further did not consider species with Southern and Southeastern European (to Caucasian) or Pannonian distribution which might survive the last glacial in the Western Carpathians as interglacial relicts in fragmented populations and might be somewhat more abundant during Early Holocene. The reason was that these species might had been still common during warm periods of the Middle Holocene, especially in habitats managed by humans (*Daphne cneorum*, *Artemisia pancicii*,

Asyneuma canescens, *Dracocephalum austriacum*, *Danthonia alpina*), or their distribution in the Western Carpathians might have been quite restricted during the entire Holocene. We therefore followed the boreo-continental focus of our study and did not include species with narrow European distribution ranges in most cases.

The presented list of glacial and Early Holocene relicts in the context of the traditional paradigm

Using the formal approach we were able to identify the species which were not previously identified as glacial or Early Holocene relicts for the Western Carpathians by any of the authors but show analogous biogeographical and ecological symptoms (e.g. *Trifolium lupinaster*, *Dianthus superbus*, *Scorzonera parviflora*, *Utricularia minor*, *Peltigera scabrosa*, *Flavocetraria nivalis*, *F. cucullata*, *Gyalidea asteriscus*, *Hamatocaulis vernicosus*, *Bucegia romanica*). Some species such as *Veratrum nigrum*, *Veronica paniculata* and *Thalictrum simplex* have been acknowledged to be Early Holocene relicts (Roleček et al. 2014, 2015), but we found that their biogeographical and ecological symptoms do not differ from species traditionally considered full-glacial relicts. Most of the abovementioned species frequently occur also in southern Siberia, where the recent climate is analogous to the glacial climate in Europe (Chytrý et al. 2017). Finally, we show the probable relict status for some species that have been reported as glacial relicts in some European regions, but not from the Western Carpathians. The example is *Viola rupestris*, a species characteristic of dry and cold areas in the Siberian analogue of the European glacial (Chytrý et al. 2017). Its wider distribution during glacial times than today was genetically confirmed for the Massif Central in France (Nordal et al. 2005) and hypothesized for the Netherlands (Weeda 1992). Other examples are the cold-loving hepatic species *Gymnomitrium corallioides*, reported as a glacial relict from the Bohemian Massif (Kučera et al. 2012), the alpine clubmosses *Selaginella selaginoides* and *Diphasiastrum alpinum*, reported as important components of glacial communities of lowland parts of Ukraine (Karpjuk et al. 2015), with frequent fossil data found also in the Western Carpathians (Jamrichová et al. 2017), and the spring species *Swertia perennis*, considered a glacial relict in Romania (Stoicovici 1984). On the other hand, some other species considered glacial or Early-Holocene relicts by other

authors did not fulfil our formal criteria for inclusion on our list of Western Carpathian relicts (e.g. *Carex bohemica*, *Juncus squarrosus*, *Lycopodiella inundata* and *Sparganium minimum*, suggested by Soó 1938-39; *Hypnum pratense*, suggested by Rybníček 1966; *Festuca amethystina* and *Libanotis pyrenaica*, suggested by Roleček et al. 2015; and *Carex hostiana* and *Pedicularis palustris*, suggested by Hájek et al. 2011; but see the previous chapter of the Discussion).

It is necessary to note that some species showing clear symptoms of relictualism in Central Europe are not listed because they simply do not occur in the Western Carpathians. An illustrative example is the steppe species *Krashennikovia ceratoides* which is considered a relict of the full-glacial loess steppe (Horsák et al. 2015) but recently grows only outside the study area in the Pannonian lowland and margins of the Bohemian Massif. Another example is *Betula humilis*, whose herbarium specimens were collected in the lowlands surrounding the Western Carpathians but never directly in the Western Carpathians.

Palaeoecological and phylogeographical evidence for relict status

The results of palaeoecological studies were not crucial for the inclusion of species on the final list, because they are not available for all species. On the other hand, they provide strong support for inclusion on the list in several cases, such as *Pinus cembra*, *Larix decidua*, *Betula nana* or *Pleurospermum austriacum*, for which fossil data well demonstrate wider distribution during glacial times than recently. For *P. cembra*, this conclusion is well supported by genetic data (Lendvay et al. 2014) as well. For 51 listed species occurrence in glacial or Early Holocene times has been evidenced. There is a much more numerous group of species with evidenced occurrence in the glacial landscape of the Western Carpathians, which, however, did not fulfil our criteria for inclusion on the list because of their recent commonness and quite progressive biogeographical behaviour. Szafer (1950) or Hájková et al. (2012), for example, report species such as *Eupatorium cannabinum*, *Carex otrubae*, *Ditrichum flexicaule* s.str., *Cirriphyllum cirrosum* or *Barbula fallax* to grow in the late-glacial landscape of the Western Carpathians, but their recent wide distribution disproves their relict status. Szafer (1950) further reports the late-glacial occurrence of several European mountain species in the

Western Carpathians (*Cirsium erisithales*, *Linum extraaxilare*, *Salix retusa*, *Thymus carpathicus*, *Viola lutea*), and the glacial occurrence of some other European high-mountain species has been documented by genetic methods (Ronikier 2011). None of these species appeared on our list, because European mountain species have not been considered, as the occurrence of these species during glacial or Early Holocene times cannot itself indicate that the species is a glacial relict with a recently contracted distribution range.

Neither the results of phylogeographical studies could be decisive for creating the list. Although modern molecular and phylogeographical studies unravel a great variety of different biogeographical patterns for individual, especially arctic-alpine species, with the post-glacial long-distance dispersal involved (Wirtz et al. 2008; Schmitt et al. 2009), such data are available only for a minority of species. In addition, most of studies cover the area of the Western Carpathians only marginally. In addition, the results of phylogeographical analyses may be interpreted equivocally in some cases. A shallow phylogeographical structure at the Central European scale was found for many phylogeographically analysed species. It may indicate that populations of these species have been interconnected during glacial times, supporting their classification as glacial relicts. On the other hand, such results do not exclude the rather recent colonization of the Western Carpathians or simply indicate a great level of recent genetic exchange because of excellent pollen, seed or spore dispersal. However, it is difficult to distinguish between these explanations. In most cases, the existence of private alleles (if ever analysed) or diversified Carpathian haplotypes supports the inclusion on to our list.

Some species listed in the final table – *Cochlearia pyrenaica*, *Primula farinosa*, *Ranunculus glacialis*, *Dryas octopetala* (Koch 2002; Schönswetter et al. 2003; Theodoridis et al. 2017), *Salix lapponum* s.l. (Hroneš 2011) and single lineages of *Dryas octopetala* (Skrede et al. 2006) and *Thamnolia vermicularis* (Onuț-Brännström et al. 2017) – displayed in Central Europe a phylogeographical structure which was similar to European high-mountain species (compare Ronikier 2011) which were not considered in our study. Clearly delimited Carpathian haplotypes with a high number of private alleles have been found, suggesting that these species occurred in the Western Carpathians during the LGM but did not communicate genetically with other European populations. It implies that the distribution

ranges in the individual mountain ranges (the Alps, the Carpathians, the Sudetes and the Balkan mountains) were not interconnected. Nevertheless, the species might have been more widespread within the Carpathian mountain range. For *Primula farinosa* the historical wider distribution within the Carpathians is supported by genetic similarity between distant Western Carpathian and Eastern Carpathian populations (Theodoridis et al. 2017) and by pollen records from the Pannonian lowland (Hájková et al. 2013).

Quite a strong support for a wide distribution during the glacial maxima is available for *Gentiana nivalis*, showing one widespread genotype across Europe, including the Western Carpathians, along with specific genotypes in the Alps (Alvarez et al. 2012). Hypothetically, a wide glacial distribution is genetically supported also for the lichen species *Flavocetraria cucullata*, *F. nivalis* and *Cetraria aculeata*, but populations from the Western Carpathians were not included (Geml et al. 2010; Fernández-Mendoza and Printzen 2013). For *Flavocetraria* species, the high genetic diversity observed in the Arctic indicates long-term survival at high latitudes, whereas the estimated migration rates and weak geographical population structure suggest a continuing long-distance gene flow between continents that has prevented pronounced genetic differentiation. For *Cetraria aculeata*, Fernández-Mendoza and Printzen (2013) has suggested that the species has evolved in Southern Europe, diversified in the Northern Hemisphere and colonized the Southern Hemisphere during the Pleistocene. Southern European and circumpolar populations differ not only genetically, but also physiologically. Apart from the abovementioned species *Thamnolia vermicularis* (Onuț-Brännström et al. 2017), the only lichen species on our list that have been analysed phylogeographically with an inclusion of data from the study area are *Cladonia botrytes* (Košuthová et al. 2013) and *Physconia muscigena* (Starosta 2016). Individuals of *C. botrytes* from the arctic zone and the Western Carpathians appeared to be genetically similar. *Physconia muscigena* appeared to be genetically variable, albeit independently of geography, with Western Carpathian populations being similar even to Canadian ones according to ITS sequences. These results may suggest that the recently observed disjunctions appeared quite recently (e.g. during the Holocene warming), supporting the hypothesis of their relict origin, but frequent long-distance dispersal events may explain these patterns as well.

Relict status of different taxonomic groups (vascular plants, lichens, bryophytes)

In general, vascular plants reached higher scores in the evaluation of relict status, followed by lichens and, finally, by bryophytes. Vascular plants usually display greater dispersal constraints than bryophytes or lichens (Hájek et al. 2011) and they dispose of long-lived clonal organs. This determines the long-term survival in suboptimal conditions (refugia) and therefore increases the probability of a species becoming a glacial relict. The highest-ranked species are usually rare, surviving at a single or few sites only. The examples are *Carex vaginata* at a single site on the Kubínska hoľa ridge (Bernátová 2011), *Trichophorum pumilum* occurring in last ten travertine sites (Dítě et al. 2013), the extinct species *Betula nana* (Eliáš jr et al. 2015) or *Saxifraga hirculus*, short-lived species with few individuals surviving in a spring fen at the foothills of the Polish part of the Tatra Mts (Ratyńska and Czortek 2014). If the entire distribution range is considered, these highly scored vascular plants usually have large habitat niches spanning from wetland or steppe to mesic habitats, although they are recently rare and specialized in the Western Carpathians. The possible explanation is that a broader realized niche enabled them to spread during glacial times and to become quite widespread and, simultaneously, enabled them to find a habitat where they could survive the climatically or competitively harsh conditions of the Holocene.

Although terrestrial lichens have propagules with better dispersal ability (Wagner et al. 2006; Werth et al. 2007; Jüriado et al. 2011) allowing the long-distance dispersal (Buschbom 2007; Wirtz et al. 2008), they can show clear symptoms of glacial relictualism (see also Liška and Pišút 1995; Lisická and Lackovičová 1998; Lisická 2005; Liška 2012). The reason is probably the physiological adaptation of some lichen species to coldness and/or drought, and weak competitive ability caused by slow growth rates. Some lichen species are hence extremely cold-tolerant or even cold-loving, such as high-scored species *Cladonia stellaris* (Litterski and Ahti 2004; Košuthová et al. 2015; Printzen 2008) and *Nephroma arcticum* (Lisická 2005), and sensitive to increased temperature (Ahti 1961; Cornelissen et al. 2001; Aptroot et al. 2015). Contrary to bryophytes, their ecological requirements and dispersal are further affected by their symbiotic nature, with mycobionts playing a more important role in dispersal limitation (Bendiksby et al. 2014). The ascospores of *Nephroma arcticum*, for

example, are too large to allow effective wind dispersal, which is common in most other lichen species (Bendiksby et al. 2014). Another glacial-relict lichen species, the cold-tolerant *Cladonia stellaris* (Košuthová et al. 2015; Aptroot et al. 2015), relies on vegetative rather than generative reproduction (Košuthová and Šibík 2013). These life history traits support the existence of a disjunctive distribution pattern of these species resulting from a broader past distribution. A broader distribution of relict lichens in the past may be anticipated also from the fact that the dry arctic tundra, which was probably quite abundant during cold and dry glacial maxima, is frequently strongly dominated by lichens (Dierssen 1996). In the analogical landscapes of southern Siberia, glacial climate supports regionally high species richness of bryophytes and lichens (Chytrý et al. 2017), with *Peltigera aphthosa* and *Flavocetraria nivalis*, high-ranked species in our list, acting as important indicators of a cold and dry climate.

Among the three groups of organisms included into our study, bryophytes seem to be the least constrained by dispersal and the least specialized for growing cold and dry habitats. In southern Siberia, cold and dry areas have been characterized mostly by generalist or widespread bryophyte species such as *Abietinella abietina*, *Tortula ruralis*, *Sanionia uncinata* or *Brachythecium mildeanum* (Chytrý et al. 2017), with only two species out of 15 fitting our criteria for being considered glacial relicts in the Western Carpathians (*Rhytidium rugosum*, *Aulacomnium turgidum*). The highest-ranked bryophytes on our list are thus *Gymnomitrium corallioides*, a rare arctic hepatic which is even rarer in temperate Europe, growing in high mountains (Kučera et al. 2009) or in cold microclimates on low-elevation scree (Růžička et al. 2012), and *Hilpertia velenovskyi*, a rare species of loess steppes in Central Europe. Sabovljević et al. (2006) consider the latter species relict of full-glacial loess steppe, in line with analogous cases of vascular plants and snails (Horsák et al. 2015). The genetic structure of this species is quite uniform in Europe (Sabovljević et al. 2006), being different from the Chinese one, but showing one genetically distant population in Germany. These results may support a wider distribution during glacial times and recent fragmentation, combined with long-distance dispersal events, but more detailed research is needed. Recent records of this species from the strongly cold-continental climate of Yakutia (Sofronova et al. 2014) indicate it might tolerate the Central European glacial climate.

Relict status of steppe versus tundra species

In contrast to some historical studies aiming at identifying glacial relicts in the Central European flora, which were focused predominantly on tundra and peatlands (Rybníček 1966; Šoltés 2004), we included a couple of species showing habitat affinity to steppe, steppe-tundra and mesic forest-steppe vegetation (light-coniferous forests and associated grasslands). This decision is in line with the recent paradigm about steppe-tundra as a key biome of the full glacial landscape (Horsák et al. 2015; Chytrý et al. 2017). In the Western Carpathians, the steppes and steppe-tundra probably occupied low elevations; mesic forest-steppe and taiga occupied suitable habitats at middle elevations and alpine tundra occupied the highest elevations (Ložek 1973; Rybníčková and Rybníček 2006; Juříčková et al. 2014; Horáček et al. 2015; Janská et al. 2017), possibly with a similar position of the treeline as today (Rybníčková and Rybníček 2006; Janská et al. 2017). Nevertheless, steppes currently occupy only marginal territories of the Western Carpathians and this pattern restricted the number of steppe species in our list simply because some of the steppe relicts do not occur in our study area. Those species that still occur in steppes at low elevations of the Western Carpathians frequently show such a wide distribution and such a low level of conservatism that one cannot easily deduce the restriction of their distribution between the last glacial and recent times. Although genetic structure or habitat affinity of some steppe or forest-steppe species may suggest their relict status, they did not pass to the final list based on scoring of recent biogeographical and ecological symptoms, namely the vascular plants *Stipa pulcherrima*, *Cytisus ratisbonensis*, *Festuca amethystina*, *Linum hirsutum*, *Libanotis pyrenaica*, *Thalictrum minus*, *Peucedanum alsaticum*, *Pulsatilla pratensis* and *Melica transsylvanica* (Roleček et al. 2015; Kajtoch et al. 2016). Considering the arbitrary nature of our classification criteria, they might be called slight glacial or Early Holocene relicts.

Some of the steppe species included on the final list of glacial relicts are confined to warm regions of Central Europe even though they tolerate low temperatures in Central Asia. However, their affinity to warm regions has nothing to do with temperature demands; instead, they only require steppe conditions with summer drought and disturbances and avoid regions were encroached by forests during the Middle Holocene

(Hájek et al. 2016). The example could be the moss *Rhytidium rugosum*, which is seemingly warmth-demanding in Central Europe but characteristic of the cold and wet climate in Central Asian mountains, which is considered an analogy of the European full glacial climate (Chytrý et al. 2017). In addition, both macrofossil and genetic data show that *R. rugosum* was widely distributed in the European lowlands north of the Alps during the glacial period (Hedenäs 2017) and may even show northern glacial refugia close to the ice sheet (Hedenäs 2015).

Relicts from the LGM and Early Holocene

The relicts listed in our review are divided into full-glacial relicts (from the LGM) and relicts from the Late Glacial or Early Holocene. This division is only indicative and complies with the traditional view that species of meadow steppes, mesic forest-steppes (including light-coniferous temperate forests), dark taiga forests or ombrotrophic bogs, moreover those with quite compact distribution ranges, cannot be regarded as true glacial relicts, because they were still possibly widespread during the late glacial and Early Holocene. In our study, the biogeographical symptoms that suggest regional extinctions rather than early-Holocene migrations are: rarity, ecological conservatism, disjunctivity in distribution range and niche contraction. A more rigorous differentiation of relicts from the LGM against relicts from younger periods is hindered by a lack of data. In addition, border between these two categories is not sharp, because the relicts from the Late Glacial/Early Holocene might or might not occur in the study area during the LGM. Some species of meadow steppe, light-coniferous temperate forests, dark taiga forests or bogs, probably survived the dry period of the LGM in hydrologically specific habitats such as wet river floodplains, concave structures on slopes or wet tundra, yet could be restricted in their distribution during the LGM.

Despite these limitations, there is an obvious concordance between our results and independent evidence. For *Rubus chamaemorus*, a large-scale genetic study suggests that it came to Central Europe after the LGM (Ehrich et al. 2008), matching perfectly our scoring of the species as a relict since Late Glacial or Early Holocene. *Larix decidua*, listed in the same category in our study, appeared to be the most distributed during the first two early Weichselian interstadials and then in the Early Holocene in the synthesis of Wagner et al. (2015b).

The highest full-glacial score was calculated for *Trichophorum pumilum*, a species of weak competitive ability with a notably disjunctive Eurasian and North American distribution range that tolerates strongly continental conditions. Its disjunct populations in Europe are quite isolated, being restricted to different relict habitats such as travertine fens and salt-rich springs in Slovakia, subalpine calcareous fens in the Alps and arctic tundra in Norway (Dítě et al. 2013). Macrofossil data suggest a wider distribution during the last glacial, at both continental and regional scale (Dítě et al. 2013), fitting with our scoring based on recent biogeographical and ecological symptoms.

Conclusions

Our study is the first attempt to integrate past and present views on the concept of glacial relicts in the Western Carpathian landscape and, using a formal approach, to provide the first comprehensive list of species that display greatest biogeographical and ecological symptoms suggesting their relict status. We demonstrated that under the current state of palaeoecological and phylogeographical knowledge, the expert-based evaluation of biogeographical and ecological characteristics of individual species is still an essential approach to compiling a comprehensive list of potential glacial relicts. Phylogeographical or palaeoecological data are available only for $\approx 14\text{--}18\%$ percent of species, respectively, and in many cases they are insufficient for definitive approval of the species' relict status. We are aware that our approach might bring some confounding results, be it false inclusion of the species that came lately to the study area by long-distance dispersal or omission of some species confined to specific habitats. Further palaeoecological and phylogeographical studies will surely improve this knowledge. Despite this, we consider the resulting list an important contribution to the long-lasting debate on the relict status of rare species of the Western Carpathian flora and an important benchmark for future studies that will lead to a more rigorous understanding of the history of the Western Carpathian flora.

Acknowledgements M.H. was supported by the Czech Science Foundation (project no. 17-05696S) and together with A.K. also by institutional support of Masaryk University. A.K. would like to thank to the MAD project between SAV-AV ČR 16-07. Authors are grateful to Marek Svitok, Filip Kolář and two anonymous reviewers for their valuable comments on the previous versions of manuscript and to Marek Svitok for help with data analysis.

Appendix: Symptoms used for primary scoring of species

1. Continentality

Justification

Glacial-relict species should tolerate continental climate that occurred during glacial times in East-Central Europe (Janská et al. 2017). The level of continentality in glacial times resembles the present-day continentality in southern Siberia (steppe species) or Central-Asian mountains (tundra species).

Scale

0 – No occurrence in strongly continental regions of Siberia or Central Asia.

1 – Slight signs of continentality tolerance; the species either (i) shows somewhat continental tendency in Europe but does not grow outside Europe, or (ii) occurs in strongly continental regions of Siberia or Central Asia but not in steppe or steppe-tundra habitats, and its general distribution range is not primarily continental (typically the fen species).

2 – The distribution range is primarily continental-Eurosiberian, but with many exceptions or this distribution range does not fit perfectly the steppe zone.

3 – The species has main distribution range in continental steppe zone of Siberia, with only few isolated populations in Europe.

2. Circumpolarity

Justification

Glacial-relict species should tolerate harsh climatic conditions that occur in the arctic and boreal zone. They should furthermore have quite large (circumpolar) distribution ranges that (i) suggest their good dispersal ability, a prerequisite of effective colonization of cold landscapes after a temperature drop or glacier retreat, and (ii) guarantee that the species are not local/regional endemics with an unclear history.

Scale

0 – No circumpolarity.

1 – The distribution range lies only in the arctic-alpine or arctic-boreal zone of Europe.

2 – The distribution range lies in the arctic-alpine or arctic-boreal zone of the two continents.

3 – The distribution range lies in the arctic-alpine or arctic-boreal zone of the three continents.

3. Discontinuity of the distribution range

Justification

Once widespread glacial-relict species should narrow their distribution ranges towards recent times and persist regionally only in suitable refugia.

Scale

0 – The species has a completely continuous distribution in Europe.

1 – The species has a large main distribution range in any macroclimatic zone and smaller distribution ranges with rather small disjunction(s). Isolated sites, if any, are located close to the main distribution range.

2 – The species has a clear disjunction(s) with a main distribution range in the arctic or the continental steppe zone (e.g. a disjunction between southern Siberia and Europe or a disjunction between high-arctic zone and the highest Central-European mountains).

3 – The species has a highly discontinuous (disjunctive) distribution range with several small distribution ranges in climatically analogous regions (e.g. arctic-alpine species that are quite rare also in the arctic zone, Eurosiberian species that have a discontinuous distribution in both Europe and Siberia and species of relict habitats with only isolated populations).

4. Conservatism of the regional distribution

Justification

West-Carpathian glacial-relict species should be quite conservative in terms of both their regional distribution range and habitat affinity, suggesting low dispersal ability and a close affinity to long-lasting refugia (compare Hájek et al. 2011), not spreading rapidly in secondary habitats.

Scale

0 – The species is quite widely distributed in the present-day landscape of the Western Carpathians, spreading in secondary habitats, including heavily disturbed anthropogenic habitats far from environmentally specific refugia.

1 – The species grows in target relict habitats that during the late Holocene had spread widely into man-made secondary habitats (e.g. deforested summit pastures, human-made fen grasslands).

2 – The species has a strong affinity to long-lasting refugia (statistically significant, if tested in Hájek et al. 2011), but is able to colonize secondary habitats.

3 – The species has an obligate affinity to long-lasting refugia of target habitats (typically peatlands, screes, rocks or travertines), occupying only a small number of sites of the given habitat in the Western Carpathians (hypothetically those with the largest stability), not occurring in many ecologically suitable places and never occurring in secondary habitats.

5. Rarity

Justification

Glacial-relict species are typically regionally rare. This symptom correlates with the previous one, but distinguishes between rare and frequent refugial habitats, rare habitats being even more relictual than frequent ones (i.e. with a smaller decline towards recent times).

Scale

0 – The species occurs in most local communities in its optimal habitat.

1 – The species does not occur in most of local communities in its optimal habitat but occupies more than 20 sites in the Western Carpathians.

2 – The species occupies 6–20 sites in the Western Carpathians in less than 5 orographical units.

3 – The species occupies only 1–5 sites in the Western Carpathians or only one orographical unit.

6. Affinity to dry or saline steppe vegetation

Justification

During glacial times, especially during the glacial maxima, this habitats had a much wider distribution in East-Central Europe than today (Janská et al. 2017).

Scale

For scale see category 11.

7. Affinity to tundra vegetation

Justification

This habitats had a much wider distribution in East-Central Europe than today during glacial times, including the LGM, when especially scrubby and tall-herb tundra might occur (Janská et al. 2017).

Scale

For scale see category 11.

8. Affinity to taiga vegetation

Justification

This habitats had a much wider distribution in East-Central Europe than today. During the LGM it was probably restricted to a small territory north of the Western Carpathians and few small patches in the mountains (Janská et al. 2017), but it became quite common in interstadials, the Late Glacial and the Early Holocene.

Scale

For scale see category 11.

9. Affinity to acidic peatlands (bogs) and non-calcareous arctic-alpine lakes

Justification

These habitats, especially peatlands, had a much wider distribution in East-Central Europe than today, being quite common especially in wetter periods, such as interstadials and the Early Holocene, and heavily restricted during the LGM. Their character species are, however, able to grow also in wet tundra and peatland forests where they could survive the LGM.

Scale

For scale see category 11.

10. Affinity to fens and springs

Justification

Contrary to bogs, fens might had occurred much more frequently under the climate of glacial maxima, which was characterized by low precipitation. Fen species also frequently dwell in Siberian peatland forests, a habitat that could be supported by the glacial climate as well (Janská et al. 2017).

Scale

For scale see category 11.

11. Affinity to mesic forest-steppe habitats (light-coniferous temperate forests, meadow-steppe and tall-herb habitats)

Justification

These habitats (dominated by pine, larch, birch or herbs) had a much wider distribution in East-Central Europe

than today, being quite common also in interstadials and the Early Holocene, and might had occurred in the wettest places also during glacial maxima.

Scale

Each species is scaled according to its habitat affinity known in both the entire distribution range and the Western Carpathians. Two values are hence always provided, but in some analyses only one of them, or the difference between the two, is used. The following scale is used:

0 – The species never grows in this habitat.

1 – The species has its optimum in other habitats but grows rarely also in this habitat, especially at long-lasting refugia (e.g. old fens, alpine screes).

2 – The species' ecological niche spans more habitats than only this one but grows frequently in this habitat.

3 – The species is diagnostic of this habitat. If this score is used, zero scores are set to other habitats.

Symptom derived from the previous ones:

12. Contraction of an ecological realized niche.

Glacial-relict species typically have a wider habitat niche in their climatic zone than in their refugial area, which determined their regional survival by making it easier to find a postglacial refugium; the ecological niche becomes contracted to this refugial habitat. Nevertheless, to apply this trait in our scoring correctly, we should restrict the niche evaluation only to species tightly associated with target habitats (i.e. habitats which were more common in glacial times than today, i.e. categories 6–11).

Value

We calculated two values indicating niche contraction and used the higher value for each species: (1) the difference between the sum of scores for categories 6–11 given for the entire distribution range and the sum of scores for categories 6–11 given for the Western Carpathians (negative values were changed to zero values whereas positive values indicated restriction of a realized niche); and (2) the difference between the number of habitats with a non-zero value of the habitat in the entire distribution range and in the Western Carpathians (if the resulting, i.e. greater, value exceeded 3, it was lowered to 3 in order to keep the same range, i.e. 0–3, for this and all other variables, i.e. 1–11).

References

- Ahti T (1961) Taxonomic studies on reindeer lichens (*Cladonia*, subgenus *Cladina*). *Arch Soc Zool-Bot Fenn Vanamo* 32:1–160
- Albach D, Schönswetter P, Tribsch A (2006) Comparative phylogeography of the *Veronica alpina* complex in Europe and North America. *Molec Ecol* 15:3269–3286
- Alsos IG, Alm T, Normand S, Brochmann C (2009) Past and future range shifts and loss of diversity in dwarf willow (*Salix herbacea* L.) inferred from genetics, fossils and modelling. *Global Ecol Biogeogr* 18:223–239
- Alvarez N, Manel S, Schmitt T, IntraBioDiv Consortium (2012) Contrasting diffusion of Quaternary gene pools across Europe: The case of the arctic–alpine *Gentiana nivalis* L. (Gentianaceae). *Flora* 207:408–413
- Aptroot A, Stapper NJ, Košuthová A, Cáceres ME (2015) Lichens. In Watts R (ed) *Climate Change*, 2nd Edition, Elsevier, pp 295–307
- Bálint M, Ujvárosi L, Theissinger K, Lehrian S, Mészáros N, Pauls SU (2011) The Carpathians as a major diversity hotspot in Europe. In Zachos FE, Habel JC (eds) *Biodiversity hotspots*. Springer Verlag, Berlin, pp 189–205
- Bartha D, Király G, Schmidt D, Tiborcz V, Barina Z, Csiky J, Jakab G, Lesku B, Schmotzer A, Vidéki R, Vojtkó A, Zólyomi Sz (2015) *Distribution atlas of vascular plants of Hungary*. University of West Hungary Press, Sopron, 329 pp
- Becker T (2012) Die Steppenreliktart *Astragalus exscapus* – eine Schlüsselart der Steppenreste Mitteleuropas? In Baumbach H, Pfütenreuter S (eds) *Steppenlebensräume Europas—Gefährdung, Erhaltungsmaßnahmen und Schutz*. Thüringer Ministerium für Landwirtschaft, Forsten, Umwelt und Naturschutz, Erfurt, pp 69–90
- Bendiksby M, Mazzoni S, Jørgensen MH, Halvorsen R, Holien H (2014) Combining genetic analyses of archived specimens with distribution modelling to explain the anomalous distribution of the rare lichen *Staurolemma omphalarioides*: long-distance dispersal or vicariance? *J Biogeogr* 41:2020–2031
- Bernátová D (2011) *Carex vaginata* – new species in the Western Carpathians. *Biologia* 66:429–432
- Buschbom J (2007) Migration between continents: geographical structure and long-distance gene in *Porpidia flavicunda* (lichen-forming *Ascomycota*). *Molec Ecol* 16:1835–1846
- Cieślak E (2013) Variation and genetic structure of *Serratula lycopifolia* populations (Vill.) Kern. (Asteraceae) in Poland and adjacent regions. *Acta Soc Bot Poloniae* 82:67–75
- Cieślak E (2014) Phylogeography of Pontic-Pannonian species in Central Europe. *Polish Bot Stud* 30:1–53
- Cieślak E, Ronikier M, Koch MA (2007) Western Ukrainian Cochlearia (Brassicaceae) – the identity of an isolated edge population. *Taxon* 56:112–118
- Cornelissen JHC, Callaghan TV, Alatalo JM, Michelsen A, Graglia E, Hartley AE, Hik DS, Hobbie SE, Press MC, Robinson CH, Henry GHR, Shaver GR, Phoenix GK, Gwynn Jones D, Jonasson S, Chapin FS, Molau U, Neill C, Lee JA, Melillo JM, Sveinbjörnsson B, Aerts R (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *J Ecol* 89: 984–994
- Čeřovský J, Feráková V, Holub J, Procházka F (eds) (1999) *Červená kniha ohrozených a vzácných druhov rastlín a živočíchov SR a ČR 5, Vyššie rastliny [Red data book of rare and endangered vascular plant and animal species of Slovakia and Czech Republic 5, Vascular plants]*. Príroda, Bratislava [in Czech and Slovak]
- Dierssen K (1996) *Vegetation Nordeuropas*. Ulmer, Stuttgart
- Dítě D, Pukajová, D (2003) *Carex magellanica* subsp. *irrigua* – a new taxon in the Western Carpathians. *Biologia* 58:791–796
- Dítě D, Šoltés R (2010) Rozšírenie druhu *Scorpidium scorpioides* na Slovensku: Minulosť a súčasnosť [Distribution of *Scorpidium scorpioides* in Slovakia: past and present]. *Bryonora* 46:66–69 [in Slovak]
- Dítě D, Hájek M, Hájková P, Eliáš jun. P (2013) The occurrence of the relict plant, *Trichophorum pumilum*, in the Western Carpathians in the context of its distribution and ecology in Eurasia. *Preslia* 85:333–348
- Dostál J (1992) *Velký klúč na určovanie vyšších rastlín II [Big determination key to vascular plants II]*. SPN, Bratislava [in Slovak]
- Durka W, Nossol C, Ruprecht E, Wagner V, Welk E, Hensen I (2013) Extreme genetic depauperation and differentiation of both populations and species in Eurasian feather grasses (*Stipa*). *Pl Syst Evol* 299:259–269
- Ehrich D, Gaudeul M, Assefa A, Koch MA, Mummenhoff K, Nemomissa S, IntraBioDiv Consortium, Brochmann C (2007) Genetic consequences of Pleistocene range shifts: Contrast between the Arctic, the Alps and the East African mountains. *Molec Ecol* 16:2542–2559
- Ehrich D, Alsos IG, Brochmann C (2008) Where did the northern peatland species survive the dry glacials: cloudberry (*Rubus chamaemorus*) as an example. *J Biogeogr* 35:801–814
- Eidsen PB, Alsos IG, Popp M, Stensrud Ø, Suda J, Brochmann C (2007) Nuclear vs. plastid data: Complex Pleistocene history of a circumpolar key species. *Molec Ecol* 16:3902–3925
- Eliáš jr P, Dítě D, Kliment J, Hrivnák R, Feráková V (2015) Red list of ferns and flowering plants of Slovakia, 5th edition (October 2014). *Biologia* 70:218–228
- Fernández-Mendoza F, Printzen C (2013) Pleistocene expansion of the bipolar lichen *Cetraria aculeata* into the Southern hemisphere. *Molec Ecol* 22:1961–1983
- Feurdean A, Perşoiu A, Tanţău I, Stevens T, Magyari E, Enikő K, Sümegi P, Tóth M (2014) Climate variability and associated vegetation response throughout Central and Eastern Europe (CEE) between 60 and 8 ka. *Quatern Sci Rev* 106:206–224
- Frahm JP (2012) The phytoecography of European bryophytes. *Bot Serbica* 36:23–36
- Futák J (ed) (1966) *Flóra Slovenska I [Flora of Slovakia I]*. Veda, Bratislava [in Slovak]
- Fyfe RM, Woodbridge J, Roberts N (2015) From forest to farmland: Pollen-inferred land cover change across Europe using the pseudobiomization approach. *Global Change Biol* 21: 1197–1212
- Gálová A, Hájková P, Čierniková M, Petr L, Hájek M, Novák J, Rohovec J, Jamrichová E (2016) Origin of a boreal birch bog woodland and landscape development on a warm low mountain summit at the Carpathian–Pannonian interface. *Holocene* 26:1112–1125
- Geml J, Kauff F, Brochmann C, Taylor DL (2010) Surviving climate changes: high genetic diversity and transoceanic gene flow in two arctic–alpine lichens, *Flavocetraria cucullata*

- and *F. nivalis* (Parmeliaceae, Ascomycota). *J Biogeogr* 37: 1529–1542
- Górski P, Váňa J (2014) A synopsis of liverworts occurring in the Tatra Mountains (Western Carpathians, Poland and Slovakia): checklist, distribution and new data. *Preslia* 86: 381–485
- György Z, Vouillamoz JF, Höhn M. (2016) Microsatellite markers reveal common East Alpine-Carpathian gene pool for the arctic-alpine *Rhodiola rosea* (Crassulaceae). *Pl Syst Evol* 302:721–730
- Guttová A, Lackovičová A, Pišút I (2013) Revised and updated checklist of lichens of Slovakia (May 2013). *Biologia* 68: 845–850
- Hais M, Komprdová K, Ermakov N, Chytrý M (2015) Modelling the Last Glacial Maximum environments for a refugium of Pleistocene biota in the Russian Altai Mountains, Siberia. *Palaeogeogr Palaeoclimatol Palaeoecol* 438:135–145
- Hájek M, Horskák M, Tichý L, Hájková P, Dítě D, Jamrichová E (2011) Testing a relict distributional pattern of fen plant and terrestrial snail species at the Holocene scale: a null model approach. *J Biogeogr* 38:742–755
- Hájek M, Dudová L, Hájková P, Roleček J, Moutelíková J, Jamrichová E, Horskák M (2016) Contrasting Holocene environmental histories may explain patterns of species richness and rarity in a Central European landscape. *Quatern Sci Rev* 133:48–61
- Hájková P, Horskák M, Hájek M, Lacina A, Buchtová H, Pelánková B (2012) Origin and contrasting succession pathways of the Western Carpathian calcareous fens revealed by plant and mollusc macrofossils. *Boreas* 41:690–706
- Hájková P, Jamrichová E, Horskák M, Hájek M (2013) Holocene history of a *Cladium mariscus*-dominated calcareous fen in Slovakia: vegetation stability and landscape development. *Preslia* 85:289–315
- Hájková P, Horskák M, Hájek M, Jankovská V, Jamrichová E, Moutelíková J (2015). Using multi-proxy palaeoecology to test a relict status of refugial populations of calcareous-fen species in the Western Carpathians. *Holocene* 25:702–715
- Hedenäs L (2015) *Rhytidium rugosum* (Bryophyta) colonized Scandinavia from at least two glacial refugial source populations. *Bot J Linn Soc* 179:635–657
- Hedenäs L (2017) Phylogeography of Alpine populations of *Rhytidium rugosum* (Bryophyta) in a European context. *Alpine Bot* 127:197–209
- Hensen I, Kilian C, Wagner V, Durka W, Pusch J, Wesche K (2010) Low genetic variability and strong differentiation among isolated populations of the rare steppe grass *Stipa capillata* L. in Central Europe. *Pl Biol* 12:526–536
- Hill MO, Bell N, Bruggeman-Nannenga MA, Brugués M, Cano MJ, Enroth J, Flatberg KI, Frahm J-P, Gallego MT, Garilleti R, Guerra J, Hedenäs L, Holyoak DT, Hyvönen J, Ignatov MS, Lara F, Mazimpaka V, Muñoz J, Söderström L (2006) Bryological monograph. An annotated checklist of the mosses of Europe and Macaronesia. *J Bryol* 28:198–267
- Holmquist C (1962) The relict concept – is it merely zoogeographical conception? *Oikos* 13: 262–292
- Holub J (1999) *Dendrathera zawadskii* (herb.) Cvelev. In Čerňovský J, Feráková V, Holub J, Procházka F (eds) *Červená kniha ohrožených a vzácných druhův rostlin a živočichův SR a ČR 5, Vyššie rastliny [Red data book of rare and endangered vascular plant and animal species of Slovakia and Czech Republic 5, Vascular plants]*. Příroda, Bratislava, p 335 [in Czech]
- Horáček I, Ložek V, Knitlová M, Juříčková L (2015) Darkness under candlestick: glacial refugia on mountain glaciers. *Forgotten times and spaces: New perspectives in palaeoanthropological, palaeoetnological and archeological studies*, Masaryk University, Brno, pp 363–377
- Horskák M, Chytrý M, Pokryszko BM, Danihelka J, Ermakov N, Hájek M, Hájková P, Kintrová K, Kočí M, Kubešová S, Lustyk P, Otýpková Z, Pelánková B, Valachovič M (2010) Habitats of relict terrestrial snails in southern Siberia: lessons for the reconstruction of palaeoenvironments of full-glacial Europe. *J Biogeogr* 37:1450–1462
- Horskák M, Hájek M, Spitale D, Hájková P, Dítě D, Nekola JC (2012) The age of island-like habitats impacts habitat specialist species richness. *Ecology* 93:1106–1114
- Horskák M, Chytrý M, Hájková P, Hájek M, Danihelka J, Horskáková V, Ermakov N, German DA, Kočí M, Lustyk P, Nekola JC, Preislerová Z, Valachovič M (2015) European glacial relict snails and plants: environmental context of their modern refugial occurrence in southern Siberia. *Boreas* 44: 638–657
- Höhn M, Gugerli F, Abran P, Bisztray G, Buonamici A, Cseke K, Hufnagel L, Quintela-Sabaris C, Sebastiani F, Vendramin GG (2009) Variation in the chloroplast DNA of Swiss stone pine (*Pinus cembra* L.) reflects contrasting post-glacial history of populations from the Carpathians and the Alps. *J Biogeogr* 36:1798–1806
- Hroneš M (2011) Variabilita komplexu vrby laponské (*Salix lapponum*) v horách střední Evropy [Variability of the *Salix lapponum* complex in Mountains of the Central Europe]. Master's thesis. Faculty of Science, Palacký University Olomouc [in Czech]
- Hultén E, Fries M (1986) *Atlas of north European vascular plants*. Koeltz Scientific Books, Königstein
- Chytrý M, Horskák M, Sýrovátka V, Danihelka J, Ermakov N, German DA, Hájek M, Hájek O, Hájková P, Horskáková V, Kočí M, Kubešová S, Lustyk P, Nekola JC, Preislerová Z, Resl P, Valachovič M (2017) Refugial ecosystems in central Asia as indicators of biodiversity change during the Pleistocene–Holocene transition. *Ecol Indicators* 77:357–367
- Jadwiszczak KA, Drzymulska D, Banaszek A, Jadwiszczak P (2012) Population history, genetic variation and conservation status of the endangered birch species *Betula nana* L. in Poland. *Silva Fenn* 46:465–477
- Jankovská V, Pokorný P (2008) Forest vegetation of the last full-glacial period in the Western Carpathians (Slovakia and Czech Republic). *Preslia* 80:307–324
- Janská V, Jiménez-Alfaro B, Chytrý M, Divišek J, Anenkhonov O, Koroľyuk A, Lashchinskyi N, Culek M (2017) Palaeodistribution modelling of European vegetation types at the Last Glacial Maximum using modern analogues from Siberia: Prospects and limitations. *Quatern Sci Rev* 159:103–115
- Jamrichová E, Hájková P, Horskák M, Rybníčková E, Lacina M, Hájek M (2014) Landscape history, calcareous fen development and historical events in the Slovak Eastern Carpathians. *Veg Hist & Archaeobot* 23:497–513
- Jamrichová E, Petr L, Jiménez-Alfaro B, Jankovská V, Dudová L, Pokorný P, Kołaczek P, Zernitskaya V, Čierníková M,

- Břízová E, Hájková P, Hájek M (2017) Pollen-inferred millennial changes in landscape patterns at a major biogeographical interface within Europe. *J Biogeogr* 44:2386–2397
- Jüriado I, Liira J, Csencsics D, Widmer I, Adolf C, Kohv K, Scheidegger Ch (2011) Dispersal ecology of the endangered woodland lichen *Lobaria pulmonaria* in managed hemiboreal forest landscape. *Biodivers & Conservation* 20:1803–1819
- Juričková L, Horáčková J, Ložek V (2014) Direct evidence of central European forest refugia during the last glacial period based on mollusc fossils. *Quatern Res* 82:222–228
- Kajtoch Ł, Cieślak E, Varga Z, Wojciech PW, Mazur MA, Sramkó G, Kubisz D (2016) Phylogeographic patterns of steppe species in Eastern Central Europe: a review and the implications for conservation. *Biodivers & Conservation* 25:2309–2339
- Kärnefelt I, Thell, A, Randlane T, Saag A (1994) The genus *Flavocetraria* Kärnefelt & Thell (*Parmeliaceae*, Ascomycotina) and its affinities. *Acta Bot Fenn* 150:79–86
- Karpiuk T, Bezusko L, Bezusko A (2015) Paleochorological studies of *Selaginella selaginoides* (L.) P. Beauv. ex Mart. et Schrank and *Diphasiastrium alpinum* (L.) Holub in the younger dryas within plain part of Ukraine. *Bull Taras Shevchenko Natl Univ Kyiv* 69:16–19
- Każmierczakowa R, Zarzycki K, Mirek Z, Adamowski W, Babczyńska-Sendek B (2014) *Polska czerwona księga roślin: paprotniki i rośliny kwiatowe [Polish Red Data book of Plants: Pteridophytes and flowering plants]*. Instytut Ochrony Przyrody PAN, Kraków [in Polish]
- Kliment J, Turis P, Janišová M (2016) Taxa of vascular plants endemic to the Carpathian Mts. *Preslia* 88:19–76
- Koch M (2002) Genetic differentiation and speciation in prealpine *Cochlearia*: allohexaploid *Cochlearia bavarica* Vogt (Brassicaceae) compared to its diploid ancestor *Cochlearia pyrenaica* DC. in Germany and Austria. *Pl Syst Evol* 232:35–49
- Koch MA, Dobeš C, Bernhardt KG, Kochjarová J (2003) *Cochlearia macrorrhiza* (Brassicaceae): a bridging species between *Cochlearia* taxa from the Eastern Alps and the Carpathians? *Pl Syst Evol* 242:137–147
- Koch MA, Kiefer C, Ehrlich D, Vogel J, Brochmann C, Mummenhoff K (2006) Three times out of Asia Minor: the phylogeography of *Arabis alpina* L. (Brassicaceae). *Molec Ecol* 15:825–839
- Konstantinova NA, Vilnet AA, Stefanut S (2014) On the distribution and variability of *Bucegia romanica* Radian. *Arctoa* 23:137–144
- Košuthová DA, Šibík J (2013) Ecological indicator values and life history traits of terricolous lichens of the Western Carpathians. *Ecol Indicators* 34:246–259
- Košuthová A, Steinová J, Spribile T (2013) Niche shift in lichens: are they real or the result of cryptic speciation? A case study in the boreal lichen *Cladonia botrytes*. *Acta Biol Cracov* 55:42
- Košuthová A, Svitková I, Pišút I, Senko D, Valachovič M, Zaniewski P, Hájek M (2015) Climatic gradient within temperate Europe and small-scale species composition of lichen-rich dry acidophilous Scots pine forests. *Fungal Ecol* 14:8–23
- Kučera J, Váňa J, Hradílek Z (2012) Bryophyte flora of the Czech Republic: updated check list and Red List and a brief analysis. *Preslia* 84:813–850
- Kučera J, Zmrhalová M, Shaw B, Košnar J, Plášek V, Váňa J (2009) Bryoflora of selected localities of the Hrubý Jeseník Mts summit regions. *Čas Slez Muz* 58:115–167
- Lambracht E, Westberg E, Kadereit JW (2007) Phylogeographic evidence for the postglacial colonization of the North and Baltic Sea coasts from inland glacial refugia by *Triglochin maritima* L. *Flora* 202:79–88
- Lavrinenko OV, Lavrinenko IA (2015) Communities of the class *Oxycocco-Sphagnetea* Br.-Bl. Et R. Tx. 1943 in the East European tundras. *Veg Russ* 26:55–84
- Lendvay B, Höhn M, Brodbeck S, Mindrescu M, Gugerli F. (2014) Genetic structure in *Pinus cembra* from the Carpathian Mountains inferred from nuclear and chloroplast microsatellites confirms post-glacial range contraction and identifies introduced individuals. *Tree Genet Genomes* 10:1419–1433
- Lisická E (2005) *The lichens of the Tatry Mountains*. Veda, Bratislava
- Lisická E, Lackovičová A (1998) On lichens in Slovakia. *Sauteria* 9:297–302
- Liška J (2012) Lichen flora of the Czech Republic. *Preslia* 84:851–862
- Liška J, Pišút I (1995) Lišajníky (Lichens). In Kotlaba F (ed) *Červená kniha ohrožených a vzácných druhů rostlin a živočichův SR a ČR 4 [Red data book of rare and endangered vascular plant and animal species of Slovakia and Czech Republic 4]*. Příroda, Bratislava, pp 120–156 [in Slovak and Czech]
- Litterski B, Ahti T (2004) World distribution of selected European *Cladonia* species. *Symb Bot Upsal* 34:205–236
- Ložek V (1973) *Příroda ve čivrtohorách [Nature in the Quaternary]*. Academia, Praha [in Czech]
- Magyari E, Jakab G, Rudner E, Sümegei P (1999) Palynological and plant macrofossil data on Late Pleistocene short-term climatic oscillations in north-eastern Hungary. *Acta Palaeobot Suppl* 2:491–502
- Magyari EK, Kuneš P, Jakab G, Sümegei P, Pelánková B, Schäbitz F, Braun M, Chytrý M (2014) Late Pleniglacial vegetation in eastern-central Europe: are theremodern analogues in Siberia? *Quatern Sci Rev* 95:60–79
- Meindl C (2011) *New aspects in plant conservation—phylogeography, population dynamics, genetics and management of steppe plants in Bavaria*. PhD thesis, Fakultät für Biologie und vorklinische Medizin, University of Regensburg, Regensburg
- Meusel H, Jäger EJ (eds) (1992) *Vergleichende Chorologie der Zentraleuropäischen Flora*. Band III. 2 parts: part 1 (text) pp ix + 333; part 2 (maps and references) pp ix + 266, including 556 maps. Gustav Fischer Verlag, Jena, Stuttgart, New York
- Molnár VA (2003) *Pflanzenraritäten im Karpatenbecken. Verborgene Schätze*. Universität Debrecen, FNW Lehrstuhl für Botanik
- Mráz P, Ronikier M (2016) Biogeography of the Carpathians: evolutionary and spatial facets of biodiversity. *Biol J Linn Soc* 119:528–559
- Nordal I, Jonsell B, Marcussen T (2005) *Viola rupestris*: molecular analyses to elucidate postglacial migration in Western Europe. *J Biogeogr* 32:1453–1459
- Ochyra R, Zsmajda P, Bednarek H, Bocheński W (1988) *Scorpidium scorpioides* (Hedw.) Limpr. In Tobolewski Z, Wojterski T (eds) *Atlas of the geographical distribution of*

- spore plants in Poland. Vol. 3. Series 5. Mosses (*Musci*). Państwowe Wydawnictwo Naukowe, Warszawa–Poznań pp 41–47
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Wagner H (2016) vegan: community ecology package. *R package version 2.3-3*. Available at <http://CRAN.R-project.org/package=vegan>
- Onuț-Brännström I, Tibell L, Johannesson H (2017) A worldwide phylogeography of the whiteworm lichens *Thamnolia* reveals three lineages with distinct habitats and evolutionary histories. *Ecol Evol* 7:3602–3615
- Pawlowska S (1966) Floristic statistics and the elements of the Polish flora. In Szafer W (ed) *The vegetation of Poland*. Pergamon Press and PWN – Polish Scientific Publishers, Oxford – London – Edinburgh – New York – Paris – Frankfurt – Warszawa, pp 138–240
- Pearson RG (1965) Problems of post-Glacial refugia. *Proc R Soc London* 161:324–330
- Plenk K, Bardy K, Höhn M, Thiv M, Kropf M (2017) No obvious genetic erosion, but evident relict status at the westernmost range edge of the Pontic-Pannonian steppe plant *Linum flavum* L.(Linaceae) in Central Europe. *Ecol Evol* 7: 6527–6539
- Prausová R, Marečková L, Kapler A, Farkas T, Indreica A, Šafářová L, Kitner M (2016) *Adenophora liliifolia*: condition of its populations in Central Europe. *Acta Biol Cracov Bot* 58: 83–105
- Printzen Ch (2008) Uncharted terrain: the phylogeography of arctic and boreal lichens. *PI Ecol Divers* 1:265–271
- Printzen C, Domaschke S, Fernández-Mendoza F, Pérez-Ortega S (2013) Biogeography and ecology of *Cetraria aculeata*, a widely distributed lichen with a bipolar distribution. *MycKeys* 6: 33–53
- R Core Team (2016) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <https://www.R-project.org/>
- Ratyńska H, Czortek P (2014) Nowe stanowisko skalnicy torfowiskowej [New locality od *Saxifraga hirculus*]. *Tatry* 4:51
- Reisch C (2008) Glacial history of *Saxifraga paniculata* (Saxifragaceae): Molecular biogeography of a disjunct arctic-alpine species from Europe and North America. *Biol J Linn Soc* 93:385–398
- Reisch C, Poschold P, Wingender R (2003) Genetic variation of *Saxifraga paniculata* Mill. (Saxifragaceae): molecular evidence for glacial relict endemism in central Europe. *Biol J Linn Soc* 80:11–21
- Roleček J, Čomej II, Tokarjuk AI (2014) Understanding the extreme species richness of semi-dry grasslands in east-central Europe: a comparative approach. *Preslia* 86:13–34
- Roleček J, Hájek M, Karlík P, Novák J (2015) Reliktní vegetace na mezických stanovištích [Relict vegetation on mesic sites]. *Zprávy Českoslov Bot Společn* 50:201–245 [in Czech]
- Ronikier M (2011) Biogeography of high-mountain plants in the Carpathians: an emerging phylogeographical perspective. *Taxon* 60:373–389
- Ronikier M, Costa A, Fuertes Aguilar J, Nieto Feliner G, Küpfer P, Mirek Z (2008) Phylogeography of *Pulsatilla vernalis* (L.) Mill. (Ranunculaceae): Chloroplast DNA reveals two evolutionary lineages across central Europe and Scandinavia. *J Biogeogr* 35:1650–1664
- Růžička V, Zacharda M, Němcová L, Šmilauer P, Nekola JC (2012) Periglacial microclimate in low-altitude scree slopes supports relict biodiversity. *J Nat Hist* 46:2145–2157
- Rybniček K (1966) Glacial relicts in the bryoflora of the highlands Českomoravská vrchovina (Bohemian-Moravian Highlands); their habitat and cenotaxonomic value. *Folia Geobot Phytotax* 1:101–119
- Rybničková E, Rybniček K (2006) Pollen and macroscopic analyses of sediments from two lakes in the High Tatra mountains, Slovakia. *Veg Hist Archaeobot* 15: 345–356
- Rybničková E, Rybniček K (2014) Palaeovegetation in the Pavlovské vrchy hills region (South Moravia, Czech Republic) around 25,000 bp: the Bulhary core. *Veg Hist Archaeobot* 23:719–728
- Sabovljević M, Frahm JP (2011) Genetic diversity of the relict moss *Rhytidium rugosum* (Hypnales) in Europe inferred from the ITS region (nrDNA). *Biologia* 66:42–49
- Sabovljević M, Frahm JP, Schaumann F (2006) The origin of the German populations of *Hilpertia velenovskyi* (Pottiaceae, Bryopsida): inferences from variation in the nuclear ITS region. *Cryptog Bryol* 27:357–365
- Schmitt I, del Prado R, Grube M, Lumbsch HT (2009) Repeated evolution of closed fruiting bodies is linked to ascoma development in the largest group of lichenized fungi (Lecanoromycetes, Ascomycota). *Molec Phylogenet Evol* 52:34–44
- Schönswetter P, Paun O, Tribsch A, Niklfeld H (2003) Out of the Alps: colonization of Northern Europe by East Alpine populations of the glacier buttercup *Ranunculus glacialis* L. (Ranunculaceae). *Molec Ecol* 12:3373–3381
- Schönswetter P, Tribsch A, Niklfeld H (2004a) Amplified fragment length polymorphism (AFLP) suggests old and recent immigration into the Alps by the arctic-alpine annual *Comastoma tenellum* (Gentianaceae). *J Biogeogr* 31:1673–1681
- Schönswetter P, Tribsch A, Niklfeld H (2004b) Amplified fragment length polymorphism (AFLP) reveals no genetic divergence of the eastern Alpine endemic *Oxytropis campestris* subsp. *tirolensis* (Fabaceae) from widespread subsp. *campestris*. *Pl Syst Evo* 244:245–255
- Schönswetter P, Popp M, Brochmann C (2006a) Central Asian origin of and strong genetic differentiation among populations of the rare and disjunct *Carex atrofusca* (Cyperaceae) in the Alps. *J Biogeogr* 33:948–956
- Schönswetter P, Popp M, Brochmann C (2006b) Rare arctic-alpine plants of the European Alps have different immigration histories: The snow bed species *Minuartia biflora* and *Ranunculus pygmaeus*. *Molec Ecol* 15:709–720
- Schönswetter P, Elven R, Brochmann C (2008) Trans-Atlantic dispersal and large-scale lack of genetic structure in the circumpolar, arctic-alpine sedge *Carex bigelowii* s.l. (Cyperaceae). *Amer J Bot* 95:1006–1014
- Szczecińska M, Sramko G, Wołosz K, Sawicki J (2016) Genetic diversity and population structure of the rare and endangered plant species *Pulsatilla patens* (L.) Mill in East Central Europe. *PLOS ONE*, 11:e0151730
- Skrede I, Eidesen PB, Portela RP, Brochmann C (2006) Refugia, differentiation and postglacial migration in arctic-alpine Eurasia, exemplified by the mountain avens (*Dryas octopetala* L.). *Molec Ecol* 15:1827–1840

- Sofronova EV, Ivanova EI, Mikhaleva LG, Poryadina LN (2014) Rare lichens, mosses, liverworts and fungi from the Republic Sakha (Yakutia), Russia. *Folia Cryptog Estonica* 51:89–102
- Soó R (1938–39) Északi reliktum növények Magyarország flórájában [Northern relic species in the flora of Hungary]. *Acta Geobot Hung* 2:151–199 [in Hungary]
- Stachurska-Swakoń A, Cieślak E, Ronikier M (2012) Phylogeography of subalpine tall-herb species in Central Europe: the case of *Cicerbita alpina*. *Preslia* 84:121–140
- Starosta J (2016) Taxonomická studie okruhu terčovníku *Physconia muscigena* [A taxonomic study of *Physconia muscigena* group]. Thesis, Charles University, Prague [in Czech]
- Stewart JR, Lister AM, Barnes I, Dalén L (2010) Refugia revisited: individualistic responses of species in space and time. *Proc Roy Soc London* 277:661–671
- Stoicovici L. 1984. Interspecific relationships of the glacial relics *Swertia perennis* L. and *Pedicularis sceptrum-carolinum* L. in a Rumanian fen. *Pl Ecol* 56:139–145
- Svenning JCH, Skov F (2010) Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecol Letters* 10:453–460
- Szafer W (1950) Flora dryasowa z Krościenka nad Dunajcem oraz uwagi o klimacie ostatniego zlodowacenia w Karpatach Zachodnich. *Bull Polish Inst Géol* 24:31–57
- Šmidová A, Münzbergová Z, Plačková I (2011) Genetic diversity of a relict plant species, *Ligularia sibirica* (L.) Cass. (Asteraceae). *Flora* 206:151–157
- Šoltés R (2004) Glaciálne relikty machorastov na Slovensku - charakteristika stanovišť, multivariantná analýza [Glacial relict bryophytes in Slovakia – habitat description and multivariate analysis]. *Biosozologia* 2:3–29 [in Slovak]
- Šoltés R (2014) *Výbraná skupina glaciálnych reliktov v bryoflore Slovenska* [Selected group of glacial relict bryophytes of Slovakia]. Inaugural dissertation, Technical University, Zvolen [in Slovak]
- Těšitel J., Vratislavská M, Novák P, Chorney II, Roleček J (2018) Merging of *Pedicularis exaltata* and *P. hacquetii* in the Carpathians: from local history to regional phylogeography based on complex evidence. *Folia Geobot*, this issue.
- Theodoridis S, Randin C, Szövényi P, Boucher FC, Patsiou TS, Conti E (2017) How do cold-adapted plants respond to climatic cycles? Interglacial expansion explains current distribution and genomic diversity in *Primula farinosa* L. *Syst Biol* 66:715–736
- Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM, Webb DA (1964–1993) *Flora Europaea*. Cambridge University Press, Cambridge
- Vitikainen O (1994) Taxonomic revision of *Peltigera* (lichenized Ascomycotina) in Europe. *Acta Bot Fenn* 152:1–96
- Vogler F, Reisch C (2013) Vital survivors: Low genetic variation but high germination in glacial relict populations of the typical rock plant *Draba aizoides*. *Biodivers & Conservation* 22:1301–1316
- Wagner HH, Werth S, Kalwij JM et al (2006) Modelling forest recolonization by an epiphytic lichen using a landscape genetic approach. *Landscape Ecol* 21:849–865
- Wagner V, Treiber J, Danihelka J, Ruprecht E, Wesche K, Hensen I (2012) Declining genetic diversity and increasing genetic isolation towards the range periphery of *Stipa pennata*, a Eurasian feather grass. *Int J Pl Sci* 173:802–811
- Wagner S, Liepelt S, Gerber S, Petit RJ (2015a) Within-range translocations and their consequences in European larch. *PLOS ONE* 10:0127516
- Wagner S, Litt T, Sánchez-Goñi MF, Petit RJ (2015b) History of *Larix decidua* Mill. (European larch) since 130 ka. *Quatern Sci Rev* 124:224–247
- Weeda EJ (1992) *Zandviooltje (Viola rupestris) in de duinen van Noord-Kennemerland*. Stichting Uitgeverij Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht
- Werth S, Gugerli F, Holderegger R, Wagner HH, Csencsics D, Scheidegger Ch (2007) Landscape-level gene flow in *Lobaria pulmonaria*, an epiphytic lichen. *Molec Ecol* 16:2807–2815
- Willing E (ed) (1978) (continuously updated): Herbarium collection of Eckhard Willing at the Herbarium Berolinense (B)
- Winkler M, Tribsch A, Schneeweiss GM, Brodbeck S, Gugerli F, Holderegger R, Abbott RJ, Schönswetter P. (2012) Tales of the unexpected: Phylogeography of the arctic-alpine model plant *Saxifraga oppositifolia* (Saxifragaceae) revisited. *Molec Ecol* 21:4618–4630
- Wirtz N, Printzen C, Lumbsch HT (2008) The delimitation of Antarctic and bipolar species of neuropogonoid *Usnea* (Ascomycota, Lecanorales): a cohesion approach of species recognition for the *Usnea perpusilla* complex. *Mycol Res* 112:472–484
- Wróblewska A (2008) From the center to the margins of geographical range: molecular history of steppe plant *Iris aphylla* L. in Europe. *Pl Syst Evol* 272: 49–65
- Wróblewska A, Brzosko E, Chudzińska E, Bordács S, Prokopiv AI (2010) Cytotype distribution and colonization history of the steppe plant *Iris aphylla*. *Ann Bot Fenn* 47: 23–33
- Wróblewska A (2013a) The phylogeographical and population genetic approach to the investigation of the genetic diversity patterns in self-incompatible clonal and polyploid *Linnaea borealis* subsp. *borealis*. *Bot J Linn Soc* 173:64–76
- Wróblewska A (2013b) High genetic diversity within island-like peripheral populations of *Pedicularis sceptrum-carolinum*, a species with a northern geographic distribution. *Ann Bot Fenn* 50:289–299
- Zobel M, Otto R, Laanisto L, Naranjo-Cigala A, Pärtel M, Fernández-Palacios LM (2011) The formation of species pools: historical habitat abundance affects current local diversity. *Global Ecol Biogeogr* 20:251–259