

Patterns of endemism and comparative phylogeography confirm palaeo-environmental evidence for Pleistocene refugia in the Eastern Alps

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Climatic fluctuations during Quaternary glaciations had a significant influence on the distribution of taxa and on their intraspecific genetic structure. In this paper, we test hypotheses on Pleistocene refugia for mountain plants in the eastern part of the European Alps derived from palaeoenvironmental and geological results, with new data on distributional patterns of 288 vascular plant endemics and molecular phylogeographies of selected species. High numbers of endemics are found in calcareous regions at the southern and the eastern border of the Eastern Alps, which remained unglaciated during the Pleistocene. The distribution of local endemic taxa in general, and of silicolous taxa in particular, shows a clear relationship with hypothetical glacial refugia in the southern, southeastern, easternmost, and northeastern Alps. Molecular phylogeographic data from several silicolous alpine species (*Androsace alpina*, *Androsace wulfeniana*, *Eritrichium nanum*, *Phyteuma globulariifolium*, *Ranunculus glacialis*, *Saponaria pumila*) are not completely congruent. However, all genetically defined population groups are in congruence with hypothetical refugia. In general, results from distributions of endemic taxa and data from intraspecific phylogeography are compatible with previously hypothesized refugia suggesting that refugial situations have shaped the current patterns. The combination of patterns of endemism with molecular phylogeographic data provides an efficacious approach to reveal glacial refugia in vascular plants.

KEYWORDS: alpine plants, biogeography, comparative phylogeography, Eastern Alps, endemism, Europe, geology, glacial refugia, Last Glacial Maximum, Pleistocene.

INTRODUCTION

It has been early recognised that endemic taxa are not randomly distributed (Candolle, 1875). Range restriction as a consequence of survival in refugia has been regarded as a driving force generating distributional patterns of endemics. Furthermore, the disruption of formerly continuous distributional ranges often results in vicariant speciation (Major, 1988). A relationship of areas of high endemism with presumed refugia has been documented, e.g., for the Alps (Pawłowski, 1970), for Australia (Crisp & al., 2001) and for Africa (Linder, 2001). However, in most cases, regions were identified as refugia based on high levels of endemism or species richness and not based on independent data.

Intraspecific genetic patterns, as revealed through phylogeographic studies, are often strongly influenced by survival of populations during and after glacial periods. Dramatic climatic changes during the Pleistocene caused considerable migration, fragmentation and extinction of populations (Hewitt, 1996; Bennett, 1997; Comes & Kadereit, 1998; Dynesius & Jansson, 2000). Taxa, which had formerly continuous distributions, sur-

vived in disjunct and often geographically restricted refugia, possibly resulting in the evolution of genetically distinct lineages. Thus, Pleistocene refugia are regarded as an important aspect that helped to shape the present patterns of genetic diversity (Hewitt, 1996; Hugall & al., 2002; Schönswetter & al., 2002; Tribsch & al., 2002). Several comparative phylogeographical studies have demonstrated that the ice ages caused partly congruent genetic patterns in several plant and animal species (e.g., Soltis & al., 1997; Moritz & Faith, 1998; Taberlet & al., 1998; Sullivan & al., 2000).

Ideally, testable biogeographic hypotheses for refugia should be based on independent palaeontological, palaeoenvironmental, and geological evidence. Explicit studies using this approach have revealed strong relationships of the location of refugia with intraspecific patterns of phylogeography (Hugall & al., 2002; Nason & al., 2002) or endemism (Tallis, 1991; Crisp & al., 2001). No attempts yet have been made, however, to test whether intraspecific phylogeographical patterns are congruent with patterns of endemism. If so, these combined patterns should allow confirmation of the location of refugia.

In this paper we compare patterns of endemism of vascular plants in the eastern part of European Alps (Eastern Alps, Fig. 1) with intraspecific phylogeographical patterns based on molecular data. The Eastern Alps provide an appropriate study system, being one of the best studied mountain areas of the world, with good data on taxonomy, distribution and ecology of the flora, plus detailed geological information (e.g., Vetter, 1933; Möbus, 1997). Furthermore, the geological and geomorphological impact of the ice ages has been studied thoroughly (e.g., Penck & Brückner, 1909; Jäckli, 1970; Nagl, 1972; van Husen, 1987, 1997). The extent of the last glacial advances, especially during the Würm-glaciation, and the altitudinal fluctuations of the snowline are known in detail, providing geological evidence for potential glacial refugia. Additionally, several palaeontological studies have focused on the vegetational history of the Eastern Alps and adjacent forelands (e.g., Frenzel, 1964; Bortenschlager, 1972; Bennett & al., 1991; Foddai & Minelli, 1994; Lang, 1994; Burga & Perret, 1998; Moscariello & al., 2000). All these data are useful in helping to interpret organismic shifts and reconstruct the climate and past environments.

We first summarize palaeo-environmental, palaeontological, and geological data for the Eastern Alps. Based on this information, we delimit potential refugia within the Eastern Alps. We then test whether the hypothetical refugia are also centers of endemism and whether genetically differentiated groups of populations occur there.

HYPOTHETICAL PLEISTOCENE REFUGIA IN THE EASTERN ALPS

Although the term “refugium” should be used in a stringent way (Tallis, 1991), in many studies it is used in different senses (e.g., Hewitt, 1996; Taberlet & al., 1998; Stehlik, 2000). Usually it characterizes regions where biota have survived unfavorable climatic conditions. Thus, areas with glacial-age fossils are regarded as refugia, or steep dolomite or serpentine slopes hosting “refugial” populations of plants growing otherwise in high altitudes above tree line. If we focus on long-term survival, e.g., throughout the last glaciation and Holocene, only those populations that survived cold periods and gave rise to new populations in warm periods (and vice versa) should be regarded as refugial (see Haffer, 1982; Tallis, 1991). An ideal refugium, therefore, prevents extinction and functions as a genetic reservoir by providing habitats for survival of plant populations during slow and abrupt climatic changes.

We define a refugium as a geographical area of relative ecological stability that provided habitats during cold and warm, wet and dry stages during the Quaternary for survival of populations, more or less *in situ*. Thus, a refugium was (more or less) situated in the same place during all stages of the Quaternary, for example, in mountain ranges that never have been fully glaciated. In such refugia, local migrations in response to climatic changes were mainly vertical. Within a refugium, therefore, similar climatic and edaphic conditions must be present during climatic change to assure survival of populations.

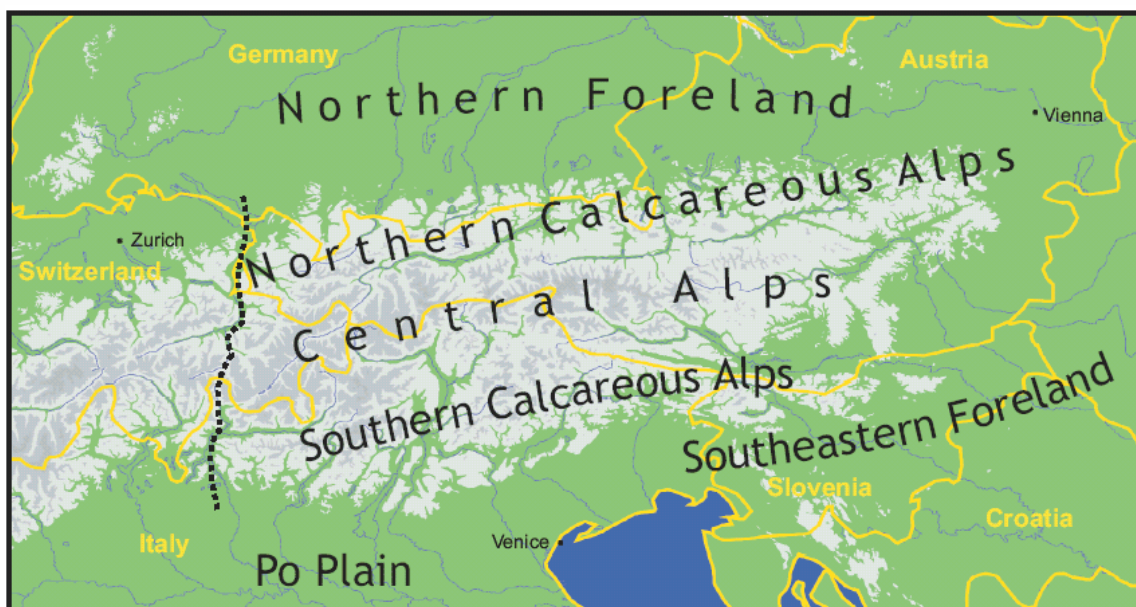


Fig. 1. The Eastern European Alps. Elevation: above 900 m (light grey), above 2100 m (dark grey); borders of countries are given by yellow lines; dashed line indicates border between the Western and Eastern Alps.

It has been predicted and demonstrated that mountain areas in general are important refugial areas (Bennett & al., 1991; Tzedakis, 1993; Hewitt, 1996; Taberlet & Cheddadi, 2002). Because of high habitat diversity in mountain areas, not only alternations of cold and warm periods, but also of wetter and drier periods, are easily buffered which guarantees long-term ecological stability. Lowland habitats without direct connections to mountains cannot be regarded as refugia for mountain plants, because the ecological conditions were not stable over time.

PALAEO-ENVIRONMENTAL, PALAEONTOLOGICAL, AND ECO- LOGICAL DATA

At the LGM (Last Glacial Maximum of the Würm glaciation), the majority of the Eastern Alps were covered with a continuous ice-sheet. Only peripheral parts to the South and to the East were locally glaciated (Jäckli, 1970; van Husen, 1987, 1997). The surface of the ice in the Central Alps was at 2300–2700 m altitude. Nunataks, i.e., mountain peaks protruding above the ice surface, were present more or less in all mountain ranges of the Eastern Alps with very few exceptions (van Husen, 1997). This implies that, in contrast to the situation during the Last Glacial Maximum (LGM) in Scandinavia, there were, at least theoretically, habitats available for plant life above the ice sheet throughout the Eastern Alps.

The climatic snowline during the LGM was 1000–1500 m below the present level (Penck, 1905; Penck & Brückner, 1909; Nagl, 1972; Moscarillo & al., 2000) at between 1100 m in the northern and 1900 m in the central parts of the Eastern Alps (Fig. 2). Today the climatic snowline is between 2600 m in peripheral ranges and 3100 m in the central-most ranges (Nagl, 1972). In this study we assume that the downward displacement of vegetation belts during the LGM was more or less equivalent to the depression of the snowline. This was surely not the case throughout all of the Quaternary, because drier, continental periods alternated with moist ones (Tallis, 1991). When annual precipitation was higher, the tree line was closer to the snowline, and vice versa (Penck, 1905). However, information is not so detailed to be taken into consideration for the purpose of this study.

The current lower altitudinal limit for plants mainly growing in the subnival zone in the Eastern Alps (e.g., *Androsace alpina*, *Potentilla frigida*, *Saxifraga muscoides*) are centered below (but near) the climatic snowline (Reisigl & Pitschmann, 1958). Although high alpine vascular plants occur up to more than 4000 m, the upper limit of prospering populations in the centralmost parts

of the Eastern Alps is between 3400 and 3500 m (approximately 300 m above snowline; Reisigl & Pitschmann, 1958; Körner, 1999; A. Tribsch & P. Schönschwetter, pers. observ.).

Despite the possibility that alpine plants could have survived the LGM on nunataks within the Alps, the extent and importance of nunatak survival are still under discussion (Stehlik, 2000; Gugerli & Holderegger, 2001; Tribsch & al., 2002; Stehlik, 2003). In principle, there were thousands of ice-free nunatak areas, at least on exposed ridges and southern slopes even in heavily glaciated central parts of the Eastern Alps (central nunataks; Schönschwetter & al., 2002). Only a few regions (e.g., Salzburger Schieferalpen, Kitzbühler Alpen and Nonsberggruppe) were completely covered with ice during the LGM. We hypothesize that only peripheral nunatak regions with ice-free areas at altitudes lower than 300 m above the LGM snowline could have acted as refugia. However, this is based on the assumption that during glaciations the upper limits of plant growth relative to the snowline were similar to current ones.

The majority of alpine species in the Eastern Alps show clear preferences for calcareous or siliceous bedrock; a few species are specialized to intermediate substrates such as calcareous schists. The northern and the southern margins of the Eastern Alps consist nearly exclusively of limestone ranges, whereas the central parts are dominated by silicates (Fig. 2; Vettors, 1933; Möbus, 1997). In general, calcicolous plants had large, unglaciated refugia available, whereas silicicolous species were confined to small refugia.

REFUGIAL HYPOTHESES IN THE EASTERN ALPS

Overlaying geomorphological (Fig. 1), geological (Fig. 2), and palaeo-environmental (given in Figs. 4 and 5) data in a Geographical Information System (GIS) allows designation of areas in the Eastern Alps that could have acted as refugia for groups of plants with different ecological demands. Terms describing elevation zones follow Reisigl & Keller (1994) and Adler & al. (1994). Forest communities of boreal type with a closed canopy dominated by conifers (*Abies alba*, *Larix decidua*, *Picea abies*, and *Pinus sylvestris*) are called upper montane. Vegetation below the tree-line dominated by krummholz (*Alnus alnobetula*, *Pinus mugo*) and scattered trees (*Larix decidua*, *Picea abies*, and *Pinus cembra*) with fragments of tall herb communities and grasslands is termed subalpine. Vegetation types dominated by dwarf shrubs (*Rhododendron* spp., *Vaccinium* spp.) with scattered krummholz and grasslands are called lower alpine. Closed grasslands are termed upper alpine (middle alpine

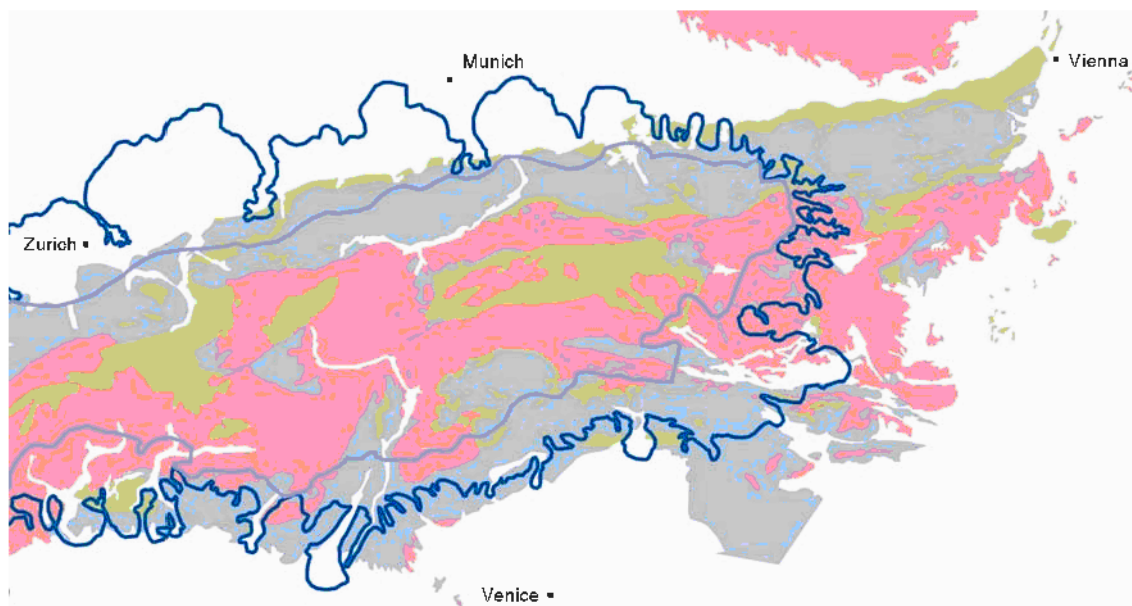


Fig. 2. Geological map of the Eastern Alps with maximum extent of the glaciers (dark blue line) and climatic snowline (light blue line) during the Last Glacial Maximum (LGM; see also Fig. 4). Siliceous bedrock is given in red, intermediate bedrock in green, and calcareous bedrock in blue. Other substrates (Tertiary and Quaternary sediments) are left white.

plus upper alpine in the sense of Reisigl & Keller, 1994). Fragmented grasslands and cushion communities of high altitudes (but below the climatic snowline) are termed subnival, and communities above the snowline with only scattered individuals of vascular plants are designated as nival.

Refugia for upper montane conifer forests.

— The importance of the Alps as refugium for upper montane tree communities is documented in several palaeontological studies (Bennett & al., 1991; Ravazzi, 2002). Assuming that the precipitation regime during the LGM was similar to the present, *Larix decidua*, *Picea abies*, *Pinus cembra* and *P. sylvestris* could grow up to 600–800 m in the Italian part of the southern Alps (Ravazzi, 2002). Frenzel (1964) documented, based on palynological data, that boreal tree species (*Abies alba*, *Alnus* sp., *Betula* sp., *Picea abies*, *Pinus cembra*, *Pinus* sect. *Diploxylon*) were present along the eastern border of the Austrian Alps during the LGM. Niklfeld (1972) estimated the LGM tree line to be at 450 m (\pm 150 m) in the northeastern Alps. Consequently, the treeline in the Eastern Alps during the LGM was between 200 and 800 m, and tree growth should have been possible at the southern and eastern borders of the region (Fig. 3).

Refugia for subalpine krummholz and lower alpine dwarf shrub communities.

— It can be argued that subalpine and lower alpine conditions were present at elevations up to 1200 m in the south and up to 600 m in the northeast (Figs 4, 5), approximately up to 300 m higher than the corresponding tree line. *Alnus*

alnobetula, *Pinus mugo* and *Salix* spp., but also dwarf shrubs such as *Rhododendron* spp. and *Vaccinium* spp., possibly lived in such elevations during the LGM. Refugia for subalpine and lower alpine species growing on siliceous bedrock existed only locally in the southern Alps north of Brescia (Fig. 5, S6), in larger areas of the easternmost Alps (S1), and in the adjacent western Alps to the north of the Po plains (S8). For calcareous communities, potential refugia were located in the northeastern calcareous Alps and along the southern border of the Alps (Fig. 4, C1–C7).

Refugia for upper alpine grasslands and subnival plants.

— At present, the elevation limit for upper alpine grasslands is 100–200 m below the climatic snowline (Reisigl & Pitschmann, 1958). One could thus assume that during the LGM, the climatic snowline also limited the growth of corresponding species. In addition to peripheral refugia, therefore, peripheral nunataks may also have acted as glacial refugia for species of the upper alpine belt.

Refugia for subnival plant species embrace mainly mountain ranges higher than c. 2400 m that host fragmentary subnival plant communities today. Thus, mainly peripheral nunataks up to c. 300 m above the LGM snowline can be considered as glacial refugia for these plants (Figs. 4, 5).

The largest refugium for silicicolous species of upper alpine plant communities was the easternmost part of the Central Alps (Fig. 5, S1), where large areas remained unglaciated. Some regions (e.g., northern bor-

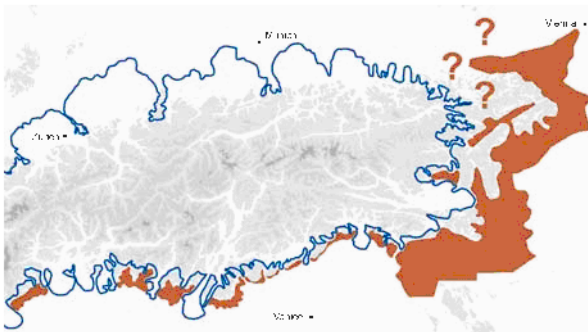


Fig. 3. Hypothetical Last Glacial Maximum refugia for upper montane forests (red-brown) in the Eastern Alps obtained from palaeo-environmental and palynological evidence (see text) along with maximum extent of the LGM glaciers (blue line).

der of the northeastern Alps, Pohorje, Bucklige Welt and parts of Fischbacher Alpen) do not support alpine vegetation today and thus cannot be considered as refugia. There are small areas at the southern margin of the ice

shield, however, which possibly also played a role as refugia (Fig. 5, S3, S4, S6, S7, S8). For sub-nival plants restricted to siliceous bedrock, peripheral nunatak regions in Ankogelgruppe, Goldberggruppe and Kreuzeckgruppe could be regarded as a potential refugium (Fig. 5, S2), as are those in the southeastern Ötztaler Alpen, eastern Ortlergruppe and southern Sarntaler Alpen (Fig. 5, S5). Other potential peripheral nunatak refugia extend the previously designated refugia in Niedere Tauern (S1), Karnische Alpen (S3), Adamello (S6), Bernina and adjacent ranges (S7), and in Misox and Alpi Ticinesi (S8).

Refugia for upper alpine plants depending on calcareous bedrock were mainly located in the Northeast and along the southern margin of the Eastern Alps (Fig. 4, C1 to C7). In some parts of the southern Alps (Dolomiten, Karnische Alpen), refugia very likely included peripheral nunataks. Mountain ranges lower than 1800 m in the northern and northeastern Alps and 2000 m in the easternmost part of the Alps do not harbor upper alpine plant communities today and therefore cannot be designated as refugia. Near the northern margin of the

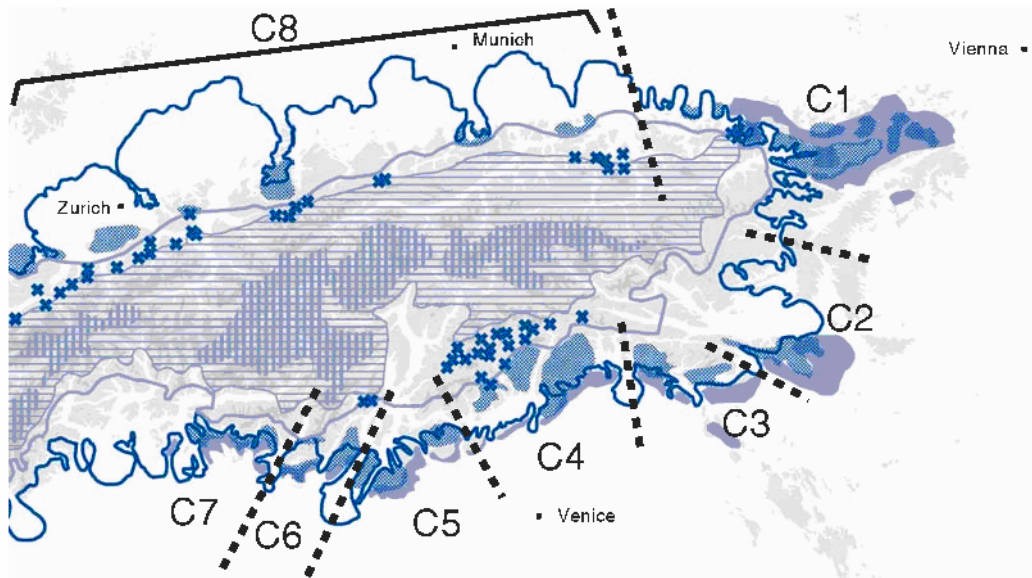


Fig. 4. Hypothetical Last Glacial Maximum refugia for calcicolous subalpine to lower alpine (blue), upper alpine (checked blue) and subnival plants (blue crosses) in the Eastern Alps along with geological and palaeoclimatological information of the Last Glacial Maximum (LGM; compilation from Penck, 1905; Penck & Brückner, 1909; Jäckli, 1970; van Husen, 1987). The maximum extent of the ice sheet is given as a dark blue line. The light blue line marks the LGM snowline. The horizontally lined region indicates areas that were more than 300 m above the LGM snowline. Nunataks in this area are termed “central nunataks”, those outside of this area “peripheral nunataks”. The vertically lined areas mark the most heavily glaciated regions (ice surface more than 700 m above the LGM snowline). Refugia: C1, north-eastern Calcareous Alps (Oberösterreichische Voralpen, Ybbstaler Alpen, Türrnitzer Alpen, Gutensteiner Alpen, Rax-Schneeberg, Müzzsteger Alpen, Hochschwab, Ennstaler Alpen, eastern Totes Gebirge, calcareous parts of Grazer Bergland); C2, southeasternmost Calcareous Alps (Karawanken, Steiner Alpen); C3, Alpi Giulie; C4, Karnische Alpen and Dolomiten; C5, Monte Baldo, Monti Lessini, and Prealpi Bellunesi; C6, Alpi Giudicarie, southern Brenta; C7, Alpi Bergamasche; C8, several peripheral parts of the Northern Calcareous Alps (Berchtesgadener Alpen, Bayerische Voralpen, Wettersteingebirge, Allgäuer Alpen, Säntis, northern Glarner Alpen).

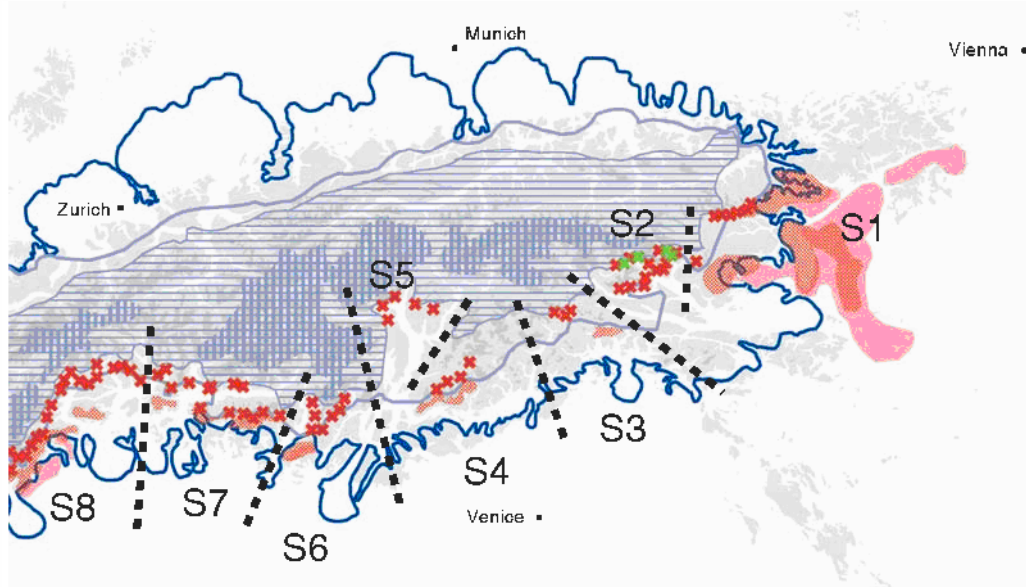


Fig. 5. Hypothetical Last Glacial Maximum refugia for silicicolous subalpine to lower alpine (red), upper alpine (checked red) and subnival plants (red crosses) in the Eastern Alps, and hypothetical refugium for subnival plants centered on intermediate substrates (green crosses), along with geological and palaeoclimatological information as given in Fig. 4. Refugia: S1, easternmost Central Alps (Pohorje, Fischbacher Alpen, Koralpe, Saualpe, Gleinalpe, Seetaler Alpen, eastern Gorktaler Alpen, eastern Niedere Tauern, southern Ennstaler Alpen); S2, southeastern Hohe Tauern (southern Ankogelgruppe, Kreuzeckgruppe, southeastern Goldberggruppe); S3, eastern Karnische Alpen; S4, southern Dolomiten (Alpi di Val di Fiemme); S5, southeastern Ötztaler Alpen, eastern Ortlergruppe, southern Sarntaler Alpen; S6, northern Alpi Giudicarie, southern Adamello; S7, Alpi Orobie, southwestern Bernina, southern Misox; S8, southern Alpi Ticinesi, southeastern Alpi Pennine.

the middle Alps, small areas between the glacier tongues remained unglaciated (Fig. 4, C8). Accordingly, Merxmüller (1954) hypothesized that these regions have acted as potential refugia. With employment of a strict definition of refugia, only a few quite small areas qualify. Potential peripheral nunatak refugia for species restricted to calcareous bedrock are found discontinuously in the Northern Calcareous Alps (Fig. 4, C8), in southern Brenta (C6) and in Karnische Alpen and Dolomiten (C4).

The refugia designated here are not identical with an earlier study by Stehlik (2000), because of the strict definition of a refugium and a different approach. The map provided by Stehlik (2000; see also Stehlik, 2003) is mainly based on hypotheses formulated in classical biogeographic literature from the first half of the last century.

Refugia for alpine plants centered on intermediate substrates. — A potential refugium with intermediate substrates such as calcareous schist (Fig. 2) is located in the eastern Goldberggruppe and in the southern Ankogelgruppe (in Fig. 5, S2). However, infrequent and locally restricted intermediate substrates are also found in other regions of the Eastern Alps (Niedere Tauern, within S1; Karnische Alpen, within S3; Allgäuer Alpen, within C8), which also could have served as refugia for corresponding plant species.

A NUMERICAL APPROACH TO DESCRIBING DISTRIBUTION OF ENDEMICISM IN THE EASTERN ALPS

Many classical biogeographical studies dealing with the Alps have focused on endemic taxa and their distribution. To our knowledge Candolle (1875) and Chodat & Pampanini (1902) were the first who recognized a correlation of the existence of glacial refugia and the occurrence of endemic taxa. Merxmüller (1952, 1953, 1954) focused on distribution patterns of calcicolous taxa and their manifold disjunctions between the southern and northern Alps. Pawłowski (1970) recognised the southwestern, the southeastern and southern, as well as the northeastern Calcareous Alps as major centers of endemism. Niklfeld (1972) stressed the importance of the eastern edge of the northeastern Calcareous Alps for the persistence of montane taxa.

For identifying and confirming the hypothetical refugia in the Eastern Alps outlined above, we compare the altitudinal and bedrock preferences and regional distribution of a defined subset of endemic taxa of Eastern Alps. The study area is given in Fig. 6A (see Appendix for details). The area was divided into 115 study OGU (Operational Geographic Units), 99 of them covering the Eastern Alps *sensu stricto*, and 16 adjacent regions (Fig.

6A; Appendix 1). The OGU were defined mainly by geomorphological features in common use (mainly mountain ranges). The list of endemic taxa in the Eastern Alps was derived from taxonomic, floristic, and biogeographic literature listed in Appendix 2. For methodological reasons, taxa described as “taxonomically insufficiently known” were also included, when they were listed as an accepted taxon and when reliable distributional information was available. Apomictic groups or problematic species or groups of related species with mostly unknown distribution were excluded (e.g., *Alchemilla* spp., *Carduus defloratus* s.l., *Centaurea jacea* agg., *Centaurea maculosa* agg., *Hieracium* spp., *Potentilla collina* agg., *Ranunculus auricomus* agg., *Rosa* spp., *Rubus* spp., *Taraxacum* spp., *Thymus* spp., and a few others). A species or subspecies was considered endemic to the study region when its distributional range was restricted to this area. A taxon was also included when its continuous distributional area extended from the Eastern Alps to small adjacent regions. This was the case for some taxa extending to the West (e.g., Swiss Calcareous Alps) or to the Southeast (e.g., Velebit). Subendemic taxa, which occur disjunctly in other areas (e.g., Carpathians), were excluded. These data were used to construct a presence/absence matrix of occurrence (see Appendix 2). In addition, bedrock (1, not classified; 2, calcicolous; 3, intermediate; 4, silicicolous; see Appendix 2) and main elevational preferences (1, subnival to nival; 2, upper alpine to subnival; 3, upper alpine; 4, lower alpine; 5, subalpine; 6, upper montane forests; 7, deciduous forests; 8, special habitats) were derived from the literature (see Appendix 3) and from personal observations. Because of gaps in the floristic mapping the list does not contain all endemics of the Eastern Alps, and it perforce also includes some “doubtful” taxa. Nonetheless, the list is adequate for answering the questions posed.

Endemic taxa, altitude and bedrock. — From the 288 taxa endemic to the Eastern Alps region, 216 (75.0%) were confined to calcareous, 40 (13.9%) to siliceous (Table 1) and 7 (2.4%) to intermediate bedrock (Table 2). Twenty-five taxa (8.7%) showed no preference or were limited to special habitats (e.g., wetlands). The assignment to altitudinal vegetation belts (see Appendix 2) showed that the majority of endemic taxa were found above the tree line. Only one endemic species (0.3%) was restricted to deciduous woodland at low altitudes, 35 taxa (12.2%) were centered in upper montane forests, and 29 (10.1%) in the subalpine vegetation belt. Forty-nine taxa (17.0%) had their main occurrences in the lower alpine zone, and 89 (30.9%) taxa in the upper alpine zone. Thirty-two (11.1%) taxa were mainly found in the transition between the upper alpine and subnival zones. Fifty-three taxa (18.4%) were not classified

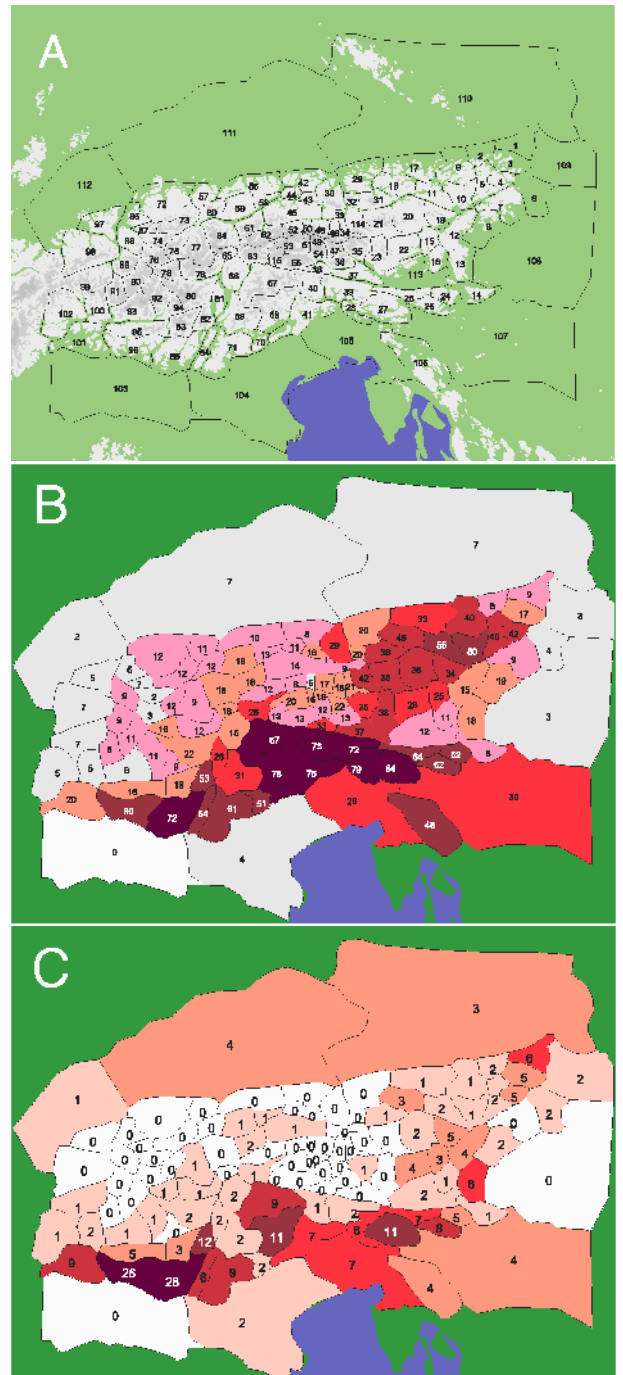


Fig. 6. Patterns of endemism in the Eastern Alps, I. **A**, delimitation of Operational Geographic Units (OGUs) upon which the floristic data are based (see Appendix 1). **B**, overall pattern based on all 288 taxa. **C**, pattern of narrow endemism based on all taxa present in less than five OGUs. Increasing color intensity indicates higher numbers (shown) of endemic taxa.

because they grow on elevation-independent specific substrates or habitats such as wetlands, vertical rock crevices, or riverbanks. A high level of endemic taxa in

high altitudes compared to the lowlands is a general phenomenon in Eurasian mountain systems (Favarger, 1972; Dhar, 2002). A likely explanation is that hardy alpine plants were better able to survive climatic changes during the Quaternary than lowland taxa. The high number of calcicolous endemic species might be explained by the predominance of calcareous refugia. High levels of endemism on calcareous bedrock are also found in other mountains of Eurasia, e.g., in the Caucasus (Kikvidze & Oshava, 2001). It is impossible to exclude, however, that other factors such as higher habitat diversity may also cause higher endemism in calcareous regions.

The pattern of overall endemism (Fig. 6B) was similar, but more detailed, to that presented by Pawlowski (1970). High numbers of endemics were found in the southern parts of the Eastern Alps and in the northeastern Alps. Endemic taxa that only occur in small distributional areas (narrow endemics; Fig. 6C) corresponded fairly well with the overall pattern of endemism (Fig. 6B). It was hypothesized that narrow endemics have had no or only restricted postglacial dispersal (Vogel & al., 1999), being still confined to refugia (see also Tribsch, 2003). A few narrow endemics, however, are also restricted to central parts of the Eastern Alps, where no refugia had been hypothesized.

There are 41 endemic taxa of mainly upper montane conifer forests that most likely survived the ice age along the southern and eastern margin of the Eastern Alps. Figure 7A shows a clear relationship of woodland endemics with unglaciated regions. These results are in accordance with the refugia given above (Fig. 3; Fig. 4, C1 to C7; Fig. 5, S1).

Seventy-eight endemic taxa were mainly found in subalpine to lower alpine elevations. Endemism was highest in the South and in the Northeast (Fig. 7B), which is in congruence with the potential refugia. Only twelve taxa are confined to silicates, one, *Sanguisorba dodecandra*, is an endemic of S7 refugium (see below). All other silicolous species can be related to refugium S1 or are local endemics of the Central Alps. The remaining taxa are confined to calcareous bedrock and presently occur in one or more refugia (C1 to C7; Fig. 4). Based on Fig. 7B, one could argue that some species extended their distribution towards the center of the Alps after glaciation.

The highest number of endemic taxa is confined to the upper alpine to subnival zones (121 taxa), emphasizing the importance of high alpine habitats for endemics. Only four endemics are centered in the subnival zone. As shown in Fig. 7C, the pattern is not as clear as in the other groups discussed above. Again, nearly all taxa were found in the refugia at the southern and eastern border of the Alps. Many taxa also seem to have extended their distribution towards central parts of the Alps after glacia-

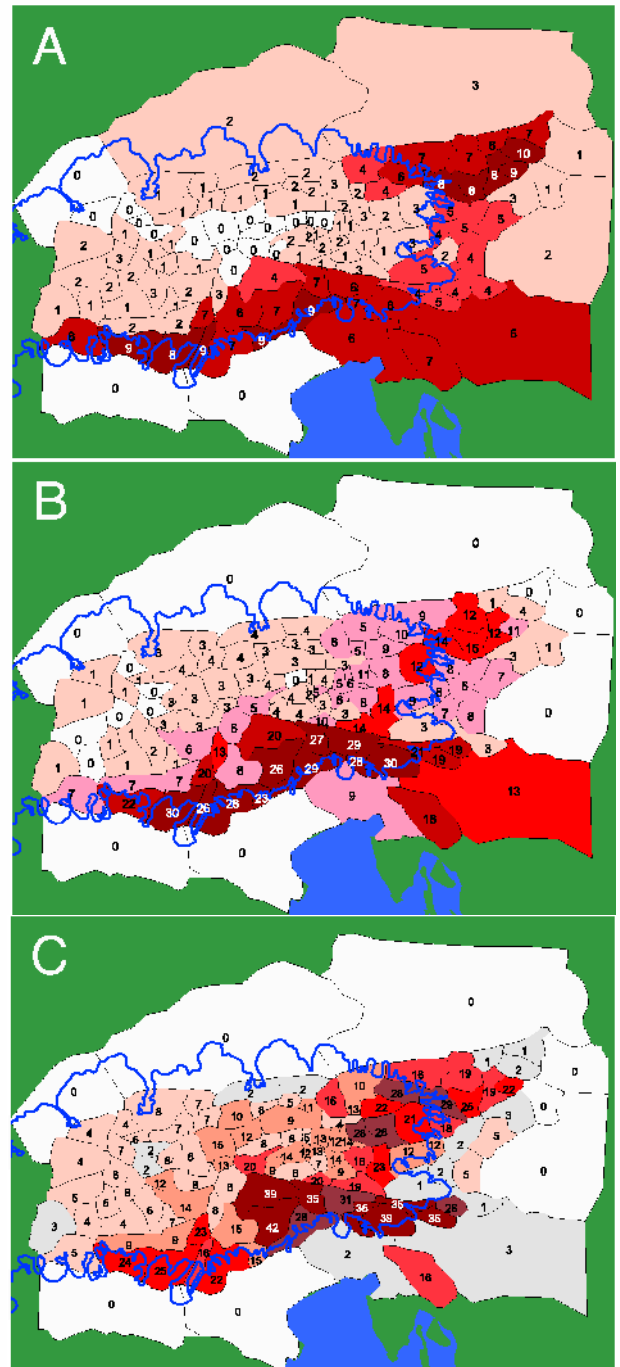


Fig. 7. Patterns of endemism in the Eastern Alps, II. A, endemism of taxa of upper montane forests. B, endemism of subalpine to lower alpine taxa. C, endemism of upper alpine to subnival taxa. For delimitation of operational geographic units (OGUs) see Fig. 6A and Appendix 1. Increasing color intensity indicates higher numbers (shown) of endemic taxa.

tion. Few taxa were restricted to regions outside the delimited refugia (see “Open questions” below).

All refugia on calcareous bedrock except refugium C8 were characterized by a high endemism (Fig. 8A).

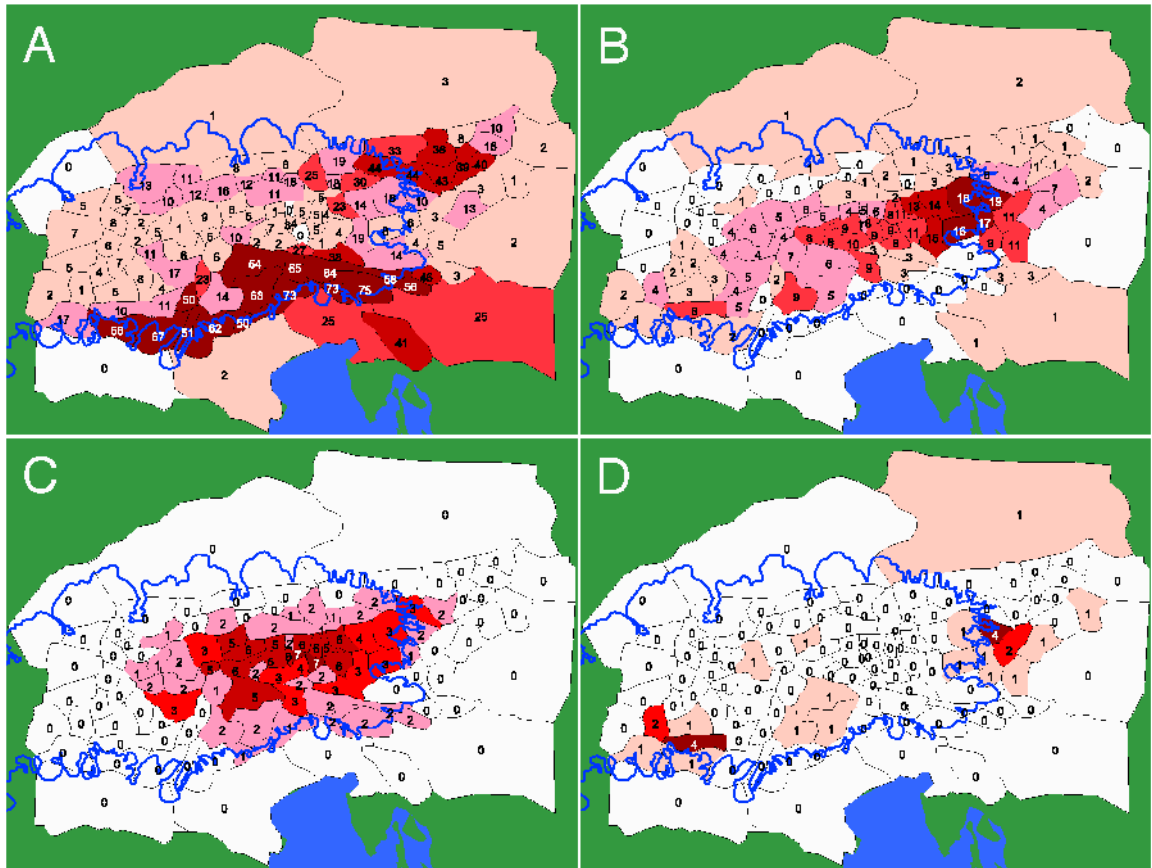


Fig. 8. Patterns of endemism in the Eastern Alps, III. A, endemism of taxa confined to calcareous bedrock. B, endemism of taxa confined to siliceous bedrock. C, endemism of taxa centered on intermediate substrates. D, narrow endemism of taxa confined to silicates and present in fewer than four OGUs. For delimitation of operational geographic units (OGUs) see Fig. 6A and Appendices 1 and 2. Increasing color intensity indicates higher numbers of endemic taxa.

This allowed confirmation of refugia in the Northeastern Calcareous Alps (C1) and at the southern margin of the Alps (C2, C3, C4, C5, C6 and C7; Fig. 4). Refugium C8 was not confirmed, because no narrow endemics are present there, although some parts of C8 were already regarded as Pleistocene refugia by Merxmüller (1954) based on disjunctly distributed taxa. Distributions of congeneric arachnid species (Muster, 2002) were also explained by refugia in the northern Alps.

We give special emphasis to patterns of endemism of silicolous plants, because the potential refugia are, besides the eastern refugium (S1), disjunct and restricted to small areas along the southern border of the Eastern Alps (S3 to S8; Fig. 5). As mentioned above, only 40 endemic taxa were confined to siliceous bedrock (Fig. 8B; Table 1). Most of them were found in the proposed refugia (Fig. 8B); some refugia are characterized by silicolous narrow endemic taxa (Fig. 8C). There are, however, a few exceptions: *Onobrychis arenaria* subsp. *taurica*, *Delphinium elatum* subsp. *tirolense*, and *Helictotrichon adsurgens* subsp. *ausserdorferi*. Although cited in standard literature, these taxa are not well stud-

ied taxonomically (W. Gutermann, pers. comm.). It is possible that these taxa do not deserve taxonomic recognition. Another exception is *Euphrasia inopinata*, which is only known from a few localities in the central Alps. Refugium S1 (Fig. 5) is confirmed by the presence of 13 endemics. Another eight taxa were centered in the presumptive refugia along the southern periphery of the Eastern Alps, of which six taxa could be related to only one refugium, i.e., *Androsace brevis* (S7), *Festuca ticiensis* (S8), *Sanguisorba dodecandra* (S7), *Saxifraga depressa* (S4), *Senecio incanus* subsp. *insubricus* (S7), and *Viola comollia* (S7; Fig. 5). *Minuartia cherlerioides* subsp. *ripii* (S4, S6, S7, S8), *Phyteuma hedraianthifolium* (S6, S7), and *Primula daonensis* (S6, S4; Fig. 5), and are present in more than one refugium. Refugium S8 (Fig. 5), extending further west into the southern and southeastern Penninic Alps outside the study area, possesses some silicolous narrow endemics, e.g., *Campanula excisa*, *Phyteuma humile*, and *Senecio halleri*. In conclusion, refugia S1, S4, S7 and S8 were confirmed by the occurrence of endemic species, while refugium S6 did not have exclusive endemics, but shared

Table 1. List of endemic silicicolous plant taxa of the Eastern Alps and adjacent areas. The presence (+) and absence (-) of the taxa is given for each refugium.

Endemic taxon	Refugium ¹									
	S1	S2	S3	S4	S5	S6	S7	S8	CA ²	Out ³
<i>Androsace brevis</i>	-	-	-	-	-	-	+	-	-	-
<i>Androsace wulfeniana</i>	+	-	-	+	-	-	-	-	-	-
<i>Cochlearia excelsa</i>	+	-	-	-	-	-	-	-	-	-
<i>Delphinium elatum</i> subsp. <i>austriacum</i>	+	+	-	-	-	-	-	-	+	-
<i>Delphinium elatum</i> subsp. <i>tiroliense</i>	-	-	-	-	-	-	-	-	+	-
<i>Doronicum catarractarum</i>	+	-	-	-	-	-	-	-	-	-
<i>Draba pacheri</i>	+	+	-	-	-	-	-	-	-	-
<i>Euphrasia inopinata</i>	-	-	-	-	-	-	-	-	+	-
<i>Festuca eggleri</i>	+	-	-	-	-	-	-	-	-	-
<i>Festuca pseudodura</i>	+	+	+	+	-	-	-	-	+	-
<i>Festuca ticinensis</i>	-	-	-	-	-	-	-	+	-	-
<i>Festuca varia</i>	+	-	-	+	-	-	-	-	+	-
<i>Helictotrichon adsurgens</i> subsp. <i>ausserdorferi</i>	+	+	-	-	+	-	-	-	+	-
<i>Jovibarba globifera</i> subsp. <i>arenaria</i>	+	+	+	-	-	-	-	-	+	-
<i>Minuartia cherlerioides</i> subsp. <i>riionii</i>	-	-	-	+	-	+	+	+	+	-
<i>Onobrychis arenaria</i> subsp. <i>taurica</i>	-	+	-	-	-	-	-	-	+	-
<i>Onosma helvetica</i> subsp. <i>austriaca</i>	-	-	-	-	-	-	-	-	-	+
<i>Pedicularis aspleniifolia</i>	+	+	-	-	+	-	-	-	+	+
<i>Phyteuma globulariifolium</i> subsp. <i>globulariifolium</i>	+	+	+	+	+	-	-	-	+	-
<i>Phyteuma hedraianthifolium</i>	-	-	-	-	+	-	+	-	+	-
<i>Primula daonensis</i>	-	-	-	+	-	+	-	-	+	-
<i>Primula glutinosa</i>	+	+	+	+	+	+	-	-	+	+
<i>Primula villosa</i> subsp. <i>villosa</i>	+	-	-	-	-	-	-	-	-	+
<i>Pulmonaria stiriaca</i>	+	-	-	-	-	-	-	-	-	+
<i>Rhinanthus carinthiacus</i>	+	-	-	-	-	-	-	-	-	-
<i>Salix mielichhoferi</i>	+	+	+	+	-	-	-	-	+	-
<i>Sanguisorba dodecandra</i>	-	-	-	-	-	-	+	-	-	+
<i>Saxifraga blepharophylla</i>	+	+	-	-	-	-	-	-	+	-
<i>Saxifraga depressa</i>	-	-	-	+	-	-	-	-	-	-
<i>Saxifraga paradoxa</i>	+	-	-	-	-	-	-	-	-	-
<i>Saxifraga styriaca</i>	+	-	-	-	-	-	-	-	-	-
<i>Saxifraga stellaris</i> subsp. <i>prolifera</i>	+	-	-	-	-	-	-	-	-	+
<i>Sempervivum montanum</i> subsp. <i>stiriacum</i>	+	+	+	-	-	-	-	-	+	+
<i>Sempervivum pittonii</i>	+	-	-	-	-	-	-	-	-	-
<i>Sempervivum wulfenii</i> subsp. <i>wulfenii</i>	+	+	+	-	+	+	+	+	+	+
<i>Senecio incanus</i> subsp. <i>insubricus</i>	-	-	-	-	-	-	+	-	-	-
<i>Soldanella montana</i> subsp. <i>montana</i>	+	-	-	-	-	-	-	-	-	+
<i>Tephrosieris serpentina</i>	+	-	-	-	-	-	-	-	-	-
<i>Valeriana celtica</i> subsp. <i>norica</i>	+	-	-	-	-	-	-	-	-	+
<i>Viola comollia</i>	-	-	-	-	-	-	+	-	-	-

¹See Fig. 5 and Appendix 1 for code and location of refugia.²Occurrence in the siliceous Central Alps outside refugia.³Occurrence outside the siliceous Central Alps in the northern and southern Calcareous Alps and in the adjacent forelands.**Table 2. List of endemic plant taxa of the Eastern Alps centered on intermediate substrates. See Table 1 for explanations.**

Endemic taxon	Refugium									
	S1	S2	S3	S4	S5	S6	S7	S8	CA	Out
<i>Braya alpina</i>	-	+	-	-	-	-	-	-	+	-
<i>Comastoma nanum</i>	-	+	-	-	-	-	-	-	+	-
<i>Doronicum glaciale</i>	+	+	+	+	+	-	-	-	+	+
<i>Oxytropis campestris</i> subsp. <i>tiroliensis</i>	-	+	-	-	-	-	-	-	+	-
<i>Oxytropis triflora</i>	+	+	-	-	-	-	-	-	+	+
<i>Saxifraga rudolphiana</i>	+	+	-	-	-	-	-	-	+	-
<i>Sesleria ovata</i>	+	+	+	+	+	-	-	-	+	+

Table 3. Summary of evidence confirming hypothetical refugia (as given in Figs. 4 and 5) by analyses of patterns of endemism or phylogeography. ++ = good congruence of data with potential refugia; + = weak congruence; - = no congruence.

Siliceous refugium	Source of evidence		Calcareous refugium	Source of evidence	
	Endemism	Phylogeography		Endemism	
S1	++	++	C1	++	
S2	+	+	C2	++	
S3	-	-	C3	++	
S4	++	++	C4	++	
S5	-	-	C5	++	
S6	+	+	C6	++	
S7	++	+	C7	++	
S8	++	++	C8	-	

two endemics with neighboring refugia. Refugia S2, S3 and S5 were not confirmed by the present analysis of endemics (Table 3).

In spite of the wide distribution of intermediate substrates, the seven endemics growing mainly on this type of bedrock were restricted to the central and eastern parts of the Eastern Alps (Fig. 8C). All of them are centered in the Hohe Tauern region and the Zillertaler Alpen, where calcareous schist is the predominant bedrock over large areas (Fig. 2; Table 2). Four endemic taxa were present in refugium S1 (Fig. 5). All seven taxa occur in S2, but no taxon was confined to this region. In other potential refugia in the northern calcareous Alps or the Karnische Alpen, only a subset of taxa is present. Hence, most probably refugia S1 and S2 acted as Pleistocene refugia for endemic taxa of intermediate substrates.

Open questions. — The influence of different taxonomic treatments and national traditions in specific and infraspecific concepts on the results of this study is most likely low. The majority of endemic taxa are well circumscribed. We estimate that between 10 and 20% of the endemic taxa, most of them narrow endemics, need taxonomic revision. However, excluding these taxa from analysis would not change the overall picture.

Not all of the endemic taxa of the Eastern Alps exhibit a distributional pattern that is in good congruence with the hypothetical refugia, but are confined to central parts of the Alps. However, all of them (1) belong to taxonomically difficult groups (e.g., *Euphrasia* spp.), (2) are of doubtful taxonomic status (e.g., *Pulsatilla oenipontana*), or (3) are polyploids that could be of postglacial allopolyploid origin (e.g., *Festuca bauzanina*, *Draba ladina*; see Widmer & Baltisberger, 1999). An interesting taxon is *Euphrasia inopinata*, a diploid relative of the widespread tetraploid *Euphrasia minima*. This taxon is known only from a few localities in the central part of the Eastern Alps. *Euphrasia inopinata* differs from *E. minima* in minor and overlapping morphological characters (Vitek, 2000). It seems possible that *E. inopinata* is more widespread, not having been recorded in other regions.

Although apomictic taxa were not included in the study, two endemic dandelions of the otherwise exclusively arctic sect. *Arctica*, *Taraxacum handelii* and *T. reichenbachii*, deserve special attention, since they are confined to the Tyrolian Central Alps and have already been regarded as evidence for Central Alpine nunatak survival (Wendelberger, 1954).

Apart from the few endemics that do not occur in the above-defined refugia, there are several, mostly rare arctic-alpine taxa, that only occur in the central parts of the Eastern Alps (Noack, 1922), e.g., *Carex atrofusca*, *Equisetum arvense* subsp. *boreale*, *Galium triflorum*, *Juncus biglumis*, *Linnaea borealis*, *Silene suecica* (*Viscaria alpina*), *Minuartia biflora*, *Potentilla multifida*, *Potentilla nivea*, *Ranunculus pygmaeus*, *Rorippa islandica* s.str., *Sparganium hyperboreum*. Two contrasting hypotheses were invoked to explain this pattern: survival on nunataks (e.g., Jerosch, 1903) or postglacial immigration (e.g., Noack, 1922). The occurrence of rare arctic-alpine taxa at high alpine and montane to subalpine altitudes in formerly strongly glaciated areas (e.g., Engadine) was regarded as evidence against the nunatak hypothesis (Noack, 1922). Further studies are needed to decide which processes (e.g., present ecological factors, nunatak survival, or postglacial immigration) shaped the distributional patterns of these arctic-alpine taxa.

COMPARATIVE PHYLOGEOGRAPHICAL PATTERNS IN THE EASTERN ALPS

Survival in isolated refugia during cold or warm stages of the Quaternary is regarded as a major evolutionary process causing differentiation and shaping divergent lineages. Concordances of distributional patterns of intraspecific lineages across several species have been used to localize major European refugia, which acted as main sources for the postglacial re-colonization of Europe (e.g., Taberlet & al., 1998; Hewitt, 2000).

However, there is increasing evidence that distinct evolutionary lineages could also be related to “northern refugia” (Stewart & Lister, 2001) some of them located within or close to the Alps. So far, corresponding “northern” lineages have been found in several animals (Bilton & al., 1998, small mammals; Volckaert & al., 2002, the fish *Cottus gobio*; Koskinen & al., 2002, the fish *Thymallus thymallus*; Surget-Groba & al., 2002, the lizard *Lacerta vivipara carniolica*).

Phylogeographical studies of endemic and widespread alpine plants are accumulating rapidly (Bauert & al., 1998, *Saxifraga cernua*; Stehlik & al., 2001, 2002a, *Eritrichium nanum*; Holderegger & al., 2002, *Saxifraga oppositifolia*; Koch, 2002, *Cochlearia* spp.; Kropf & al., 2002, *Anthyllis montana*; Schönswetter & al., 2002, *Phyteuma globulariifolium*; Stehlik, 2002, *Rumex nivialis*; Tribsch & al., 2002, *Saponaria pumila*; Schönswetter & al., 2003, *Androsace wulfeniana* and *A. brevis*). Most of them evidence refugia within or near the Eastern Alps. Some of these studies cover only minor parts of the Eastern Alps. Hence, a comparative phylogeographic analysis of the Eastern Alps can only rely on a few species, and the phylogeographical patterns hitherto found are far from being congruent.

To test whether intraspecific phylogeographical patterns in alpine to subnival co-distributed plant species of the Eastern Alps can be related to the hypothetical refugia outlined above, we compared phylogeographic data already published. As all species except one (*Rumex alpinus*) are silicicolous, we compared only data from six silicicolous alpine plant species. The taxa are *Androsace alpina* (Primulaceae, Schönswetter & Tribsch, 2001; Fig. 9A), *Androsace wulfeniana* (Primulaceae, Schönswetter & al., 2003; Fig. 9B), *Eritrichium nanum* (Boraginaceae, Stehlik & al., 2001, 2002a), *Phyteuma globulariifolium* (Campanulaceae, Schönswetter & al., 2002; Fig. 9D), *Ranunculus glacialis* (Ranunculaceae, Schönswetter & al., in press), and *Saponaria pumila* (Caryophyllaceae, Tribsch & al., 2002; Fig. 9C). Data were derived from Amplified Fragment Length Polymorphism (AFLP) fingerprinting (see Stehlik & al., 2001, and Schönswetter & al., 2002 for details), and in one case also from Restriction Fragment Length Polymorphism of PCR amplified fragments of the chloroplast DNA (cpDNA-PCR-RFLPs; Stehlik & al., 2002a).

Intraspecific phylogeographic patterns can help localize glacial refugia. Glacial survival in isolated refugia, which has likely occurred repeatedly during the Quaternary, is presumed to result in genetic divergence of populations or groups of populations (Hewitt, 1996). After deglaciation, refugial populations that have diverged during the glacial cycles re-invaded formerly glaciated parts of the Alps. In some alpine plants studied up to now, e.g., *Saponaria pumila* (Tribsch & al., 2002)

and *Erinus alpinus* (Stehlik & al., 2002b), a decrease in genetic diversity from peripheral refugia towards central parts of the Alps could be observed, indicating direction of historical migrations. In most other studies published, only groups of populations could be differentiated (Stehlik & al., 2001; Schönswetter & al., 2002) without exhibiting much internal structure or a clinal organization of genetic diversity. All of these populational groups, however, overlap with refugia that were hypothesized on the basis of palaeoclimatological and geological data and, altogether, confirm the significance of most of the hypothesized refugia, especially if similar phylogeographical patterns are found repeatedly (Taberlet & al., 1998; Stehlik & al., 2000; but see also Stehlik, 2003 for survival on nunataks).

The phylogeographical patterns varied among the studied taxa. However, they all show clusters of divergent populations that are in good congruence with the hypothetical refugia outlined above (Table 3). Thus, it is likely that there is a consistent genetic pattern indicating re-colonization of the Eastern Alps out of refugia at their margin (Tribsch & al., 2002). Based on these phylogeographic results of several taxa, refugia S1, S4 and S8 again can be confirmed (Fig. 10; Table 3). There is also weak evidence for areas S2, S6 and S7 to have acted as refugia, but no such evidence was found for the potential refugia S3 and S5. Refugium S2 was only of significance for *Saponaria pumila* (Tribsch & al., 2002). Refugia S6 and S7 in combination were of significance for *Phyteuma globulariifolium*. In the studies of *Eritrichium nanum*, the results could be interpreted as showing separate survival in refugia S6 and S7. Only two populations from refugium S6, however, were included.

In the studies of *Eritrichium nanum* (Stehlik & al., 2001, 2002a), the obtained phylogeographic pattern was interpreted as suggesting glacial survival on central nunataks. However, assuming survival on peripheral nunatak refugia in the Eastern Alps is an equally viable phylogeographic alternative (but see Stehlik, 2002, 2003 for contrasting comments).

CONCLUSIONS

Focusing on the Eastern Alps, we tested hypotheses on the location of glacial refugia based on palaeo-environmental data with patterns of endemism of vascular plants and phylogeographical data. Distributional (Figs. 8B, D; Table 1) and phylogeographical patterns (Fig. 10) were largely congruent and allowed confirmation of some of the hypothetical refugia for silicicolous alpine plants (see Fig. 5), in particular the easternmost Central Alps, the southwestern Dolomites, the Alpi Orobie and the southern Alpi Ticinesi (see Table 3). There is also evi-



Fig. 9. Four of the silicolous alpine plant species for which detailed phylogeographical information based on AFLP fingerprinting is available for their entire distributional area in the Alps. A, the high alpine to subnival cushion plant *Androsace alpina* (Primulaceae) is endemic to the European Alps, where it is widespread. Schönschwetter & al. (2001) detected a differentiation into at least three groups of populations with the populations at the southwestern margin of the distributional area being genetically most strongly differentiated. B, the rare endemic *Androsace wulfeniana* is restricted to two small areas in the Alps, the easternmost Central Alps of Austria and the southwestern Dolomites. Schönschwetter & al. (2003) detected strong divergence among nearly all of the investigated populations of this alpine cushion plant and a pronounced phylogeographical structure. In the formerly weakly glaciated easternmost Eastern Alps, there were obviously two isolated refugia for this species. The disjunct populations in the Dolomites were genetically depauperate but, judging from their high degree of genetic divergence, long isolated from the rest of the distributional area of the species. C, the alpine cushion plant *Saponaria pumila* (Caryophyllaceae) is growing in the Eastern Central Alps and, disjunctly, in the Southern Carpathians. As in *Androsace wulfeniana*, Tribsch & al. (2002) detected two refugia in the easternmost Eastern Alps and a third one in the southern Dolomites. Genetic diversity varied strongly among the investigated populations, and helped to trace migration routes, including long distance dispersal events, from the refugia towards central parts of the Alps. D, *Phyteuma globulariifolium* (Campanulaceae) occurs in the eastern Pyrenees and throughout the Alps. Schönschwetter & al. (2002) found a deep phylogeographical split running from north to south along the Brenner Pass and Etsch valley (Italy/Austria), congruent with a gap in the distribution of the species. The resulting two populational groups of this alpine to subnival species were further subdivided. The Pyrenean populations were not differentiated from Western Alpine ones and can thus be regarded as descendants of relatively recent long distance dispersal.

dence that the southeastern Hohe Tauern and parts of the Alpi Giudicarie acted as refugia. For plant species growing on intermediate substrate (Fig. 8C; Table 2) southwestern Hohe Tauern could have acted as a refugium. For plants growing on calcareous bedrock no phyloge-

graphical studies were available for the Eastern Alps. Based on distributional data of endemic taxa (Fig. 8A), refugia along the southern margin of the Eastern Alps and in the Northeastern Calcareous Alps were supported. Moreover, distributional data confirm that not only hardy

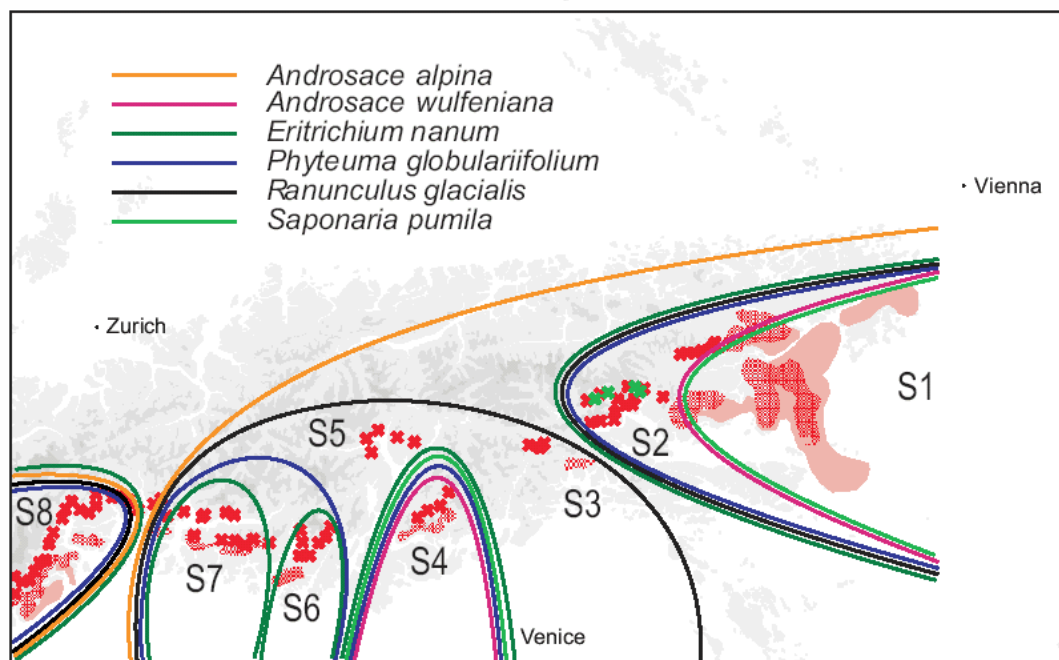


Fig. 10. Summary of phylogeographical data for silicolous taxa of the Eastern Alps. For each investigated taxon (see text) the delimitation of genetically defined groups of populations is given. The proposed refugia are given in Fig. 5.

alpine plants but also plants confined to upper montane woodland of boreal type (Fig. 7A) and plants of sub-alpine and lower alpine elevations (Fig. 7B) have refugia within the Alps, which is congruent with paleontological data (Fig. 3).

The presented attempt, i.e., testing hypotheses on the location of refugia with patterns of endemism and intraspecific phylogeographic patterns independently is a novel one to our knowledge. Several previous studies, however, considered both aspects (see e.g., Schneider & al., 1998; Stehlik & al., 2000; Hugall & al., 2002), but a comparative approach comparing both patterns was never done. It would be highly interesting if in other regions (e.g., other mountain ranges and non-glaciated arctic and subarctic regions) similar congruencies between phylogeographical patterns, patterns of endemism, and potential glacial refugia are found. A similar approach could also contribute to the still controversial discussion, of whether main refugial areas in Eurasia are restricted to southern latitudes, as suggested by several authors (see, e.g., Taberlet & al., 1998; Hewitt, 2000), or if “northern cryptic refugia” (Stewart & Lister, 2001) are also found at more northern latitudes. Our study clearly supports that there were refugia for boreal woodlands at the southern and eastern margin of the Alps. The same situation might apply, e.g., for the Carpathians and other mountain ranges at similar latitudes. It should also be possible to test if northern refugia of deciduous forests were located further north than

previously believed, e.g., in Slovenian and Croatian mountains. This is indicated by the occurrence of some narrowly distributed taxa growing in deciduous forests there. For such studies comprehensive datasets on distribution of vascular plants and more phylogeographic data from woodland taxa are needed.

The overall pattern largely confirms hypotheses already published a long time ago (e.g., Chodat & Pampanini, 1902; Jerosch, 1903; Merxmüller, 1952, 1953, 1954; Pawłowski, 1970). The refugia are centers of endemism, and they are congruent with areas of endemism identified by historical biogeographical methods (Tribsch, 2003). They were also important refugial areas for more widespread taxa, observable today in genetically divergent areas.

Although the dataset of endemic taxa (Appendix 2) would be slightly modified by the availability of more detailed taxonomic and distributional data, we do not expect that the overall pattern of endemism described here will fundamentally change. There is no doubt that new taxonomic revisions, which are still urgently needed in many groups of the European mountain flora, and floristic mapping will improve our knowledge about taxonomy and distribution of vascular plants. Regional studies with a finely scaled grid system, such as that used in the mapping of the flora of Central Europe, will give a sharper picture of distribution patterns and also refugial areas. First approaches with large datasets including all alpine vascular plant species from Switzerland gave

highly stimulating results (Wohlgemut, 2002). Integrating distributional data internationally, however, is a prerequisite for such studies. Moreover, a comprehensive study of distributional data of animals (see e.g., Holdhaus, 1954, and Muster, 2002) would be highly interesting in the Eastern Alps. We expect similar patterns of endemism.

More phylogeographical studies of plants as well as of animals are needed from the Alps to complete the picture of the impact of the ice ages in shaping genetically divergent areas. These studies should include calcicolous plants such as *Rumex nivialis* (Stehlik, 2002) and *Erinus alpinus* (Stehlik & al., 2002b) as well as species with different habitat requirements, breeding systems, pollination syndromes and dispersal abilities. A comparative approach integrating many co-distributed species would be highly interesting.

How to deal with refugia and endemism (see also Tzedakis & al., 2002) as reservoirs for genetically variable and/or divergent populations provides a challenge for conservation policy (Moritz & Faith, 1998; Taberlet & Cheddadi, 2002). Our study has demonstrated that quite small areas were of great historical importance.

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- Appendix 1.** Delimitation of geographic entities upon which the floristic data are based (for geographical orientation see Fig. 6A): 1, Wienerwald; 2, Türritzer Alpen; 3, Gutensteiner Alpen; 4, Rax-Schneeberg; 5, Müritzsteger Alpen; 6, Bucklige Welt; 7, Fischbacher Alpen; 8, Grazer Bergland; 9, Ybbstaler Alpen; 10, Hochschwab; 11, Ennstaler Alpen; 12, Gleinalpe; 13, Korralpe; 14, Pohorje; 15, Seetaler Alpen; 16, Saualpe; 17, Oberösterreichische Voralpen; 18, Totes Gebirge; 19, Seckauer Tauern; 20, Rottenmanner and Wölzer Tauern; 21, Schladminger Tauern; 22, Gurktaler Alpen east; 23, Gurktaler Alpen west; 24, Karawanken east; 25, Karawanken west; 26, Steiner Alpen (Kamniške Alpe); 27, Alpi Giulie (Julijske Alpe) east; 28, Alpi Giulie west; 29, Salzkammergut-Berge; 30, Berchtesgadener Alpen; 31, Dachstein; 32, Tennengebirge; 33, Salzburger Schieferalpen; 34, Ankogelgruppe north; 35, Ankogelgruppe south; 36, Kreuzeckgruppe; 37, Gailtaler Alpen; 38, Lienzer Dolomiten; 39, Karnische Alpen (Alpi Carniche) main chain east; 40, Karnische Alpen main chain west; 41, Karnische Alpen south; 42, Chiemgauer Alpen; 43, Loferer and Leoganger Steinberge; 44, Kaisergebirge; 45, Kitzbühler Alpen; 46, Goldberggruppe north; 47, Goldberggruppe south; 48, Glocknergruppe north; 49, Glocknergruppe south; 50, Granatspitzgruppe north; 51, Granatspitzgruppe south; 52, Venedigergruppe north; 53, Venedigergruppe south; 54, Schobergruppe; 55, Villgratener Berge; 56, Bayerische Voralpen; 57, Ammergauer Alpen; 58, Rofangebirge; 59, Karwendel; 60, Wettersteingebirge; 61, Tuxer Alpen; 62, Zillertaler Alpen north; 63, Zillertaler Alpen south; 64, Stubai Alpen north; 65, Stubai Alpen south; 66, Sarntaler Alpen; 67, Dolomiten (Dolomiti) north; 68, Dolomiten southeast; 69, Dolomiten southwest (Alpi di Val di Fiemme); 70, Prealpi Bellunesi; 71, Monti Lessini; 72, Allgäuer Alpen; 73, Lechtaler Alpen; 74, Ferwallgruppe; 75, Samnaungruppe; 76, Silvrettagruppe; 77, Ötztaler Alpen north; 78, Ötztaler Alpen south; 79, Sesvennagruppe; 80, Ortlergruppe; 81, Nonsberggruppe; 82, Brenta; 83, Adamello-Presanella; 84, Monte Baldo; 85, Alpi Giudicarie; 86, Bregenzerwald; 87, Lechquellengebirge; 88, Rätikon; 89, Plessur-Alpen; 90, Albula-Alpen; 91, Plattagruppe; 92, Livigno-Alpen; 93, Bernina; 94, Sobretta-Gavia; 95, Alpi Orobie; 96, Prealpi Bergamasche; 97, Sântis; 98, Glarner Alpen; 99, Adula-Alpen; 100, Misox-Alpen; 101, Prealpi Ticinesi; 102, Alpi Ticinesi; 103, Po plain west (Lombardia); 104, Po plain centre (Veneto); 105, Po plain east and low Karst (Friuli-Venezia Giulia, Slovenia); 106, High Karst; 107, southeastern Prealps and foreland of Slovenia; 108, southeastern foreland of Austria and Hungary; 109, Wiener Becken (south of river Danube); 110, north-eastern foreland of Austria; 111, northern foreland of Germany; 112, Bodenseegebiet; 113, Klagenfurter Becken; 114, Radstädter Tauern; 115, Rieserfernergruppe.

Appendix 2.

List of endemic taxa of the Eastern Alps. Elevation class: 1, subnival to nival; 2, alpine to subnival; 3, upper alpine; 4, lower alpine; 5, subalpine; 6, upper montane forests; 7, deciduous forests; 8, special habitats. Bedrock preference: 1, not classified; 2, calcicolous; 3, intermediate; 4, silicicolous. Operational Geographic Units (OGUs) are vertically numbered from 1 to 115 (see Fig. 6A). 1 = presence of taxon in OGU. - = absence of taxon in OGU.

Table with columns: Endemic taxon, Elevation class, Bedrock preference, and 115 vertical columns representing OGUs. The table lists various plant species such as Achillea, Anemone, Campanula, and Galium, along with their distribution patterns across the OGUs.

Appendix 2 (continued).

Table with columns: Endemic taxon, Elevation class, Bedrock preference, and a grid of binary data (0s and 1s) representing distribution patterns across various elevations and bedrock types.

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