



The uneven distribution of refugial endemics across the European Alps suggests a threefold role of climate in speciation of refugial populations

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Abstract

A little more than 10% of the vascular plant flora native to the European Alps is endemic to this area. It has long been noticed that the distribution of endemics across the Alps is very uneven. While most endemics are found along the southern edge of the Alps, with some also on its western, eastern, and northeastern edges, the northern edge of the Alps more or less between Lake Geneva in the west and Lake Traun in the east harbours almost no endemics. The distribution of endemics in the Alps has often been related to the location of glacial refugia. Accordingly, the virtual absence of endemics from the northern edge of the Alps has been explained with the unsuitability of climatic conditions for glacial survival of alpine plants there. After discussing evidence for the existence of glacial refugia for alpine species along the northern edge of the Alps and north of the Alps, I will examine how these refugia differed from refugia along the southern edge of the Alps. I conclude that the uneven distribution of endemics in the Alps is best explained by the different climate through time north and south of the Alps. These climatic differences affected the spatial structure and extent of refugia, the length of isolation of refugial populations, and selective conditions in refugia.

Keywords Alps · Climate · Endemics · Natural selection · Non-adaptive evolution · Refugia

Introduction

Following Aeschimann et al.'s (2004) *Flora Alpina*, the European Alps harbor 3983 native vascular plant taxa (species and subspecies), of which 417 are considered to be endemic to the Alps. It has long been known (Candolle 1875; Chodat and Pampanini 1902; Pawłowski 1970; Favarger 1972; Tribsch and Schönswetter 2003; Tribsch 2004; Aeschimann et al. 2011a, b; Taberlet et al. 2016) that these endemics are not evenly distributed across the Alps, but that a much higher number of endemics is found along the southern edge than along most of the northern edge of the Alps.

According to Tribsch and Schönswetter (2003), the distribution of endemic species in the Alps was first related

to the location of glacial refugia by Candolle (1875) and Chodat and Pampanini (1902), and a causal link between their distribution in glacial refugia and their evolutionary divergence and eventually speciation has commonly been assumed. Genetic divergence and subspeciation or speciation in glacial refugia are believed to result from various processes, including geographical isolation, genetic drift in small populations, and adaptive evolution in response to changing abiotic and biotic conditions, where the relative importance of these factors or their combination has been assessed differently by different authors (Hewitt 1996, 2000, 2004; Tribsch and Schönswetter 2003; Tribsch 2004; Hampe and Petit 2005; Carstens and Knowles 2007; Casazza et al. 2008, 2010, 2016b; Stewart et al. 2010; Hampe and Jump 2011; Mee and Moore 2014; Woolbright et al. 2014; Stewart and Stringer 2012; Gentili et al. 2015a, b; Kiedrzyński et al. 2017; Kadereit 2022).

High densities of endemics in particular refugial areas have also been linked to the geomorphological, edaphic, and climatic heterogeneity of these areas (Médail and Verlaque 1997; Médail and Diadema 2009; Casazza et al. 2008, 2010, 2016a; Nieto Feliner 2011, 2014). As such heterogeneity

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clearly has implications for population size, geographical isolation and variation in selective regimes, environmental heterogeneity should not be considered a separate factor when investigating speciation in refugia the Alps. Also, habitat diversity does not appear to correlate with endemism (Gugerli et al. 2008; Taberlet et al. 2016).

Finally, time available for divergent evolution and speciation needs to be considered (Bennett 1997; Willis and Niklas 2004; Hewitt 2004; Lister 2004; Casazza et al. 2016a; Keppel et al. 2018). While it has been argued that periods of isolation in the Quaternary were never long enough for speciation to be completed (Willis and Niklas 2004; but see Kadereit and Abbott 2021), persistence of interglacial adaptation through glacials has been postulated for *Taxus baccata* L. by Mayol et al. (2015), and population differentiation has been postulated to persist and accumulate through several climatic cycles by, e.g., Pawłowski (1970), Hewitt (2004), Lister (2004), Smyčka et al. (2017), Jardim de Queiros et al. (2022), and Parisod (2022). Such persistence and accumulation of differentiation implies a certain degree of climatic stability through time in glacial refugia, and such climatic stability has been advocated as a major condition in areas of endemism in general (Jansson 2003; Hampe and Jump 2011; Harrison and Noss 2017; Cai et al. 2023).

Considering the possible role of glacial refugia for evolutionary divergence and speciation, the uneven distribution of endemics across the Alps has been explained by the unsuitability of glacial conditions north of the Alps for the survival and/or diversification of high-elevation species by, e.g., Tribsch (2004), Schönswetter et al. (2005), and Smyčka et al. (2017), where these authors referred to different areas north of the Alps. On the other hand, it has long been known that high-elevation alpine (and high-latitude arctic) species were widespread in Quaternary glacials in the lowlands of Central Europe (Birks and Willis 2008). Indeed, Birks and Willis (2008) suggested that the often small interglacial (or postglacial, i.e., extant) ranges rather than the often large glacial ranges of alpine species should be considered refugial ('warm-stage refugia').

On the background of these very contradictory views of the presence of glacial refugia for high-elevation plant species north of the Alps, the possible role of refugia for the evident uneven distribution of endemic vascular plant species across the Alps has been reconsidered. After delimiting the area along the northern edge of the Alps where endemics are rare or absent, I will, selecting those endemics which are distributed in refugial areas, examine which of them are most closely related to species from the Alps and which originated in the Quaternary. While this approach concentrates on such species which are relevant when considering the role of

refugia for the uneven distribution of endemics, it also aims at establishing that in the Alps Quaternary speciation possibly related to glacial refugia has taken place at all. I will then examine whether the frequency of endemics might be related to the distribution of species diversity, intraspecific genetic diversity or environmental diversity. After discussing evidence for the existence of glacial refugia for high-elevation species along the northern edge of the Alps and north of the Alps and discussing the properties of these refugia, I will examine how these refugia differed from refugia along the southern edge of the Alps. I will conclude that the uneven distribution of endemics distributed in glacial refugia in the Alps is best explained by climatic differences north and south of the Alps. These affected the spatial structure and extent of refugia, the length of isolation of refugial populations, and selective conditions in refugia. In turn, these three factors affected rates of speciation.

Materials and methods

The endemic taxa examined (excl. apomicts) were taken from Aeschimann et al.'s (2004) *Flora Alpina*. Taxon names used were those used in the respective publication dealing with a taxon even though this partly differed from Aeschimann et al. (2004) and partly differs from current usage. I only considered those endemics which today are distributed in areas regarded glacial refugia (henceforth referred to as 'refugial endemics') because only these are relevant when considering the role of refugia for the uneven distribution of endemics. For these endemics, Google Scholar was used to search for phylogenetic and/or phylogeographic literature to identify their closest relatives and to search for information on their estimated age of origin to establish that they are likely to have originated in the Alps in the Quaternary. This approach also served to establish that in the Alps, Quaternary speciation possibly related to glacial refugia has taken place at all. In my search of the literature I encountered additional endemics that were not listed in Aeschimann et al. (2004). However, other endemics may have been missed. Refugial endemics of unknown relationships were not considered further. To assess the distribution of endemics in refugia, I either followed the assessment provided in individual accounts, referred to Tribsch and Schönswetter (2003) for distributional information, or compared their distribution to the distribution of refugial areas as shown in Schönswetter et al. (2005). When necessary, *Flora Europaea* (Tutin et al. 1968; Tutin et al. 1972; Tutin et al. 1976; Tutin et al. 1980; Tutin et al. 1993) was used to obtain further information on geographical distribution.

Results and discussion

The uneven distribution of endemic species across the Alps

Based on the distribution of endemics as mapped by Aeschimann et al. (2011a, b) and Tribsch and Schönswetter (2003), the area along the northern edge of the Alps that extends more or less from the Haut-Savoie in the West to the Oberösterreichische Voralpen in the East (Fig. 1) is very poor in endemics. While the western limit of this area has not been looked at in great detail recently, but may lie in the area of Lake Geneva (see Vierhapper 1924, 1925; quoted in Aeschimann et al. 2011a; Merxmüller 1954; ‘ligne du lac Léman au lac Majeur’ of Aeschimann et al. 2011a), the eastern limit is well known through the work of Merxmüller (1952, 1953, 1954), Niklfeld (1972), Tribsch and Schönswetter (2003), and Tribsch (2004). Merxmüller (1952) and Niklfeld (1972) identified the river Traun in the Oberösterreichische Voralpen as the eastern border (‘Traunlinie’, ‘ligne Traun – Lieser’ of Aeschimann et al. 2011a; Fig. 1) of those parts of the northern Alps poor in endemics. Interestingly, these eastern and western limits also coincide with break zones identified by Thiel-Egenter et al. (2011) and also by earlier authors (see Thiel-Egenter et al. 2011 for discussion) for the distribution of calcifuge species. From the ‘Oberösterreichische Voralpen’ toward the east (‘northeastern calcareous Alps’, ‘northeasternmost Prealps’ and ‘easternmost Central Alps’ following Tribsch (2004)), and particularly in the ‘southern’ and ‘southeastern calcareous Alps’ (following Tribsch (2004)) and the southwestern (Maritime



Fig. 1 Ice extent in the Alps in the Last Glacial Maximum based on Ivy-Ochs (2015). Map of the Alps: OpenStreetMap https://umap.openstreetmap.fr/de/map/alpen-relief_955504#7/46.108/12.953. The area between the two straight lines on the northern edge of the Alps harbours essentially no endemics. For numbers of endemic species in different parts of the Alps, see Aeschimann et al. (2011a, b), Tribsch and Schönswetter (2003), and Tribsch (2004)

and Ligurian) Alps (Médail and Quezel 1997; Casazza et al. 2008, 2010, 2016a), the number of endemics is much higher. This general pattern also becomes evident when considering the distribution (in the Alps) of monophyletic species-rich lineages such as *Moehringia* L. sect. *Moehringia* (Fior and Karis 2007; Aeschimann et al. 2004), *Primula* L. sect. *Auricula* Duby (Zhang et al. 2004; Boucher et al. 2016a) or *Saxifraga* L. sect. *Saxifraga* subsect. *Arachnoideae* (Engl. & Irmsch.) Tkach et al. (Gerschwitz-Eidt et al. 2023) where most or all endemics are distributed in the southern Alps. The same applies to, e.g., the diploid and polyploid species of *Knautia* L. from the Alps—the genus is considered to be of East Mediterranean origin (Resetnik et al. 2014; Frajman et al. 2016)—and to *Phyteuma* L., a more widespread genus reconstructed to have originated in the Alps (Schneeweiss et al. 2013).

There exist a number of endemics in the endemic-poor area north of the Alps considered here. Thus, Tribsch and Schönswetter (2003), for their ‘northeastern foreland of Austria’, ‘northern foreland of Germany’ and ‘Bodenseegebiet’ list *Biscutella laevigata* L. subsp. *kernerii* Mach.-Laur. (best combined with subsp. *subaphylla* Mach.-Laur. according to Tremetsberger et al. 2002), *Onosma helvetica* (A. D.C.) Boiss. subsp. *austriaca* (Beck) Teppner, *Tephroseris helenitis* (L.) B. Nord. subsp. *salisburgensis* Cufod., *Armeria purpurea* W.D.J. Koch and *Cochlearia bavarica* Vogt. All these, apart from *Biscutella laevigata* subsp. *kernerii*, clearly are not most closely related to alpine species, and the status of *Onosma helvetica* subsp. *austriaca* (considered a disjunct occurrence of the more widespread *O. pseudoarenaria* Schur by Kolarčík et al. 2014) has been questioned (Fischer et al. 2005). *Tephroseris helenitis* subsp. *salisburgensis*, not recognized taxonomically by Kadereit et al. (2021), has been hypothesized to be of postglacial origin (Pflugbeil et al. 2021), and *Cochlearia bavarica* is a hybrid taxon of probably very young age (Heubl and Vogt 1985; Koch et al. 1996; Koch 2002). Another few endemics have been identified to the west of the area considered by Tribsch and Schönswetter (2003). *Pulmonaria helvetica* Bolliger, endemic to the northern edge of the Alps in Switzerland and the Jura Mts., also is a hybrid taxon of likely postglacial origin (Grünig et al. 2021). Interestingly, *Arenaria gothica* Fr. from Lac de Joux in the Jura Mts. (Info Flora 2022) and *Saxifraga oppositifolia* L. subsp. *amphibia* (Sünd.) Braun-Blanq. from Lake Constance (Krause et al. 2017), both discussed by Kadereit (2022), are limited to the shores of lakes covered by ice in the last glacial and may be of only postglacial origin. *Armeria purpurea*, if indeed endemic to Lake Constance, can be added to this list. The two Lake Constance taxa appear to be extinct (Dienst et al. 2004). *Arenaria bernensis* Favarger, endemic to the western Prealps in Switzerland, may be a rare example for the possibly

Quaternary origin of a refugial endemic east of Lake Geneva (Berthouzoz et al. 2013).

Not all refugial endemics of the Alps are part of alpine lineages and/or of Quaternary age

If the refugial endemics in the Alps originated in glacial refugia, they should have originated in Quaternary times as closest relatives of species from the Alps. Although it will remain unknown whether refugial endemics originated in the area where they are found today, a number of studies which modeled the Last Glacial Maximum (LGM) distribution of refugial endemics in the Alps have shown that the most likely LGM distribution ranges of such endemics were geographically close to or included their current ranges (Schorr et al. 2012, 2013; Casazza et al. 2013; Pan et al. 2020; Guerrina et al. 2022; Adamo et al. 2023). Much has been published on the phylogeography and phylogeny of plant taxa—subspecies, species or larger lineages—from the Alps. However, information on phylogenetic relationships of refugial endemics and their likely time of origin is limited. Partly, taxa have not been analyzed at all; partly, sampling of potential closest relatives is not complete; partly, DNA sequence information generated was not sufficient to resolve relationships; and partly molecular dating, clearly problematical when using, for lack of fossils, secondary calibration in young lineages (Schenk 2016), was not attempted. With respect to the last point, all age estimates reported should be treated very carefully.

Apart from the fact that closer inspection led to the conclusion that some refugial endemics listed by Aeschmann et al. (2004) do not deserve to be recognized taxonomically (*Carex norvegica* Retz. subsp. *pusteriana* (Kalela) Chater: Więclaw et al. (2017); *Galium melioidorum* (Beck) Fritsch: Grossfurthner (2018); *Oxytropis campestris* (L.) DC. subsp. *tirolensis* (Sieber ex Fritsch) Leins & Merxm.: Schönswetter et al. (2004a); several species/subspecies of the *Papaver alpinum* L. complex: Schönswetter et al. (2009); *Veronica chamaedrys* L. subsp. *micans* M.A. Fischer: Bardy et al. (2010)), the literature available clearly shows that not all refugial endemics of the Alps originated as closest relatives of species distributed in the Alps, and that not all are of Quaternary age. Thus, there exist phylogenetically isolated and clearly pre-Quaternary refugial endemics such as *Berardia subacaulis* Vill. (Garcia-Jacas et al. 2016; Guerrina et al. 2022), *Gentiana froelichii* Rchb. (Favre et al. 2022), *Physoplexis comosa* (L.) Schur (Cellinese et al. 2009; Schneeweiss et al. 2013), *Saxifraga florulenta* Moretti (Patsiou et al. 2014; Ebersbach et al. 2017), *Valeriana celtica* L. (Bell and Donoghue 2005) and *Viola argenteria* Moraldo & Forneris (Casazza et al. 2016b; Marcussen et al. 2022). Irrespective of their partly

high age, however, evidence for a role of Quaternary climatic oscillations in the evolution and distribution of such species has been found. Thus, the subspecific differentiation of *Valeriana celtica* has been suspected to be of Quaternary age (Weberling et al. 1971), postglacial range contraction has been shown for *Berardia subacaulis* (Guerrina et al. 2022), and dispersal from a glacial refugium in *Saxifraga esculenta* has been hypothesized by Szövényi et al. (2009).

Some refugial endemics of the Alps appear to have their closest relatives in geographically very distant areas such as the Eurasian and North American Arctic (*Braya alpina* Sternb. & Hoppe: Warwick et al. 2004; Chen et al. 2020) or temperate Asia (*Callianthemum* C.A. Mey.: Kadereit et al. 2019), of which the latter appears to have arrived in Europe in the Quaternary. Others are most closely related to species widespread outside the Alps (*Cerastium carinthiacum* Vest: Skubic et al. (2018); *Chaerophyllum elegans* Gaudin: Piwczyński et al. (2015); *Odontites luteus* (L.) Clairv. subsp. *lanceolatus* (Gaudin) P. Fourn.: Pinto-Carrasco et al. (2017); *Tephrosieris integrifolia* (L.) Holub subsp. *serpentinii* (Gáyer) B. Nord. (Kadereit et al. 2021); *Teucrium lucidum* L.: Salmaki et al. (2016)), of which the latter two appear to have originated in the Quaternary. Several endemics (Table 1) have clear relationships to southern European species or lineages, although it is not always clear whether the Alps were colonized from these southern European areas or vice versa. Many more of those taxa considered to belong to the ‘South European Mountain’ and ‘Mediterranean’ floristic groups of Aeschmann et al. (2011b), the two largest groups of their floristic classification of the flora of the Alps, probably have relationships to southern European taxa. *Ranunculus villarsii* DC. and *R. venetus* Huter ex Landolt (Paun et al. 2005: Quaternary; Emadzade and Hörandl 2011: just before onset of Quaternary) are part of a species group widespread in the European Alpine System (EAS), and *Alyssum neglectum* Magauer et al. is the closest relative of *A. montanum* L. (Magauer et al. 2014) found across the EAS, both representing a pattern of relationships known from many more taxa (Christ 1867; Engler 1879; Ozenda 1985, 2009; Kadereit 2017).

However, of those species and subspecies endemic to the Alps for which satisfactory data are available, the majority do have their closest relatives in the Alps, and the origin of many of these has been dated to the Quaternary. Undated and dated examples are found in Table 2. In many of the undated examples, limited genetic divergence may imply young and possibly Quaternary age.

In summary, it is very clear that a substantial number of refugial endemics of the southern Alps are the result of Quaternary subspeciation or speciation of lineages distributed in the Alps.

Table 1 Refugial endemics most closely related to taxa or lineages outside the Alps. In the absence of ancestral area reconstructions, it is not always obvious whether the Alps were colonized from areas outside the Alps or vice versa

Taxon	Closest relative (s)	Geographical distribution of closest relative(s)	Estimated age of refugial endemic	References
<i>Alyssum cognense</i> Španiel, K. Kaplan, Juillerat & Bäumler	<i>A. spruneri</i> Jord. & Fourr. subgroup 'serbicum'	Central Balkans	Quaternary	Cetlová et al. (2021), Španiel et al. (2022)
<i>Androsace haussmannii</i> Leyb.	<i>A. komovensis</i> Schönswetter & Schneew.	Montenegro	Pre-Quaternary	Schönswetter and Schneeweiss (2009), Boucher et al. (2016a)
<i>Asperula rupicola</i> Jord.	<i>A. aristata</i> L.f. subsp. <i>oreophila</i> (Briq.) Hayek, <i>A. wetsteinii</i> Adamovic	Central Apennine, Dinaric Alps	Quaternary	Gargiulo et al. (2015)
<i>Brassica repanda</i> (Willd.) DC. subsp. <i>repanda</i> & <i>saxatilis</i> (DC.) Heywood	relationships unresolved	Most other subsp. SW Europe	–	Gómez-Campo (2003), Lega et al. (2012), Kadereit (2022)
<i>Cerastium subtriflorum</i> (Rehdb.) Pacher	<i>C. sylvaticum</i> Waldst. & Kit.	NW Balkans	–	Skubic et al. (2018)
<i>Erodium rodiei</i> (Braun-Blanq.) Potton	part of sect. <i>Absinthioidea</i> (Brumh.) Guitt. subsect. <i>Petraea</i> Brumh.	SW Europe, NW Africa	Quaternary	Alarcón et al. (2012)
<i>Eryngium spinalba</i> Vill.	<i>E. bourgatii</i> Gouan, <i>E. dilatatum</i> Lam.	SW Europe	–	Kadereit et al. (2008)
<i>Euphorbia austriaca</i> A. Kern.	<i>E. 'beskidensis'</i> , <i>E. carpatica</i> Wol., <i>E. illirica</i> Lam., <i>E. illirica</i> subsp. <i>sojakii</i> (Chrtek & Křísa) Dubovik	Carpathians	–	Frajman et al. (2016)
<i>Euphorbia kernerii</i> Huter ex A. Kern.	<i>E. triflora</i> Schott, Nyman & Kotschy, <i>E. thessala</i> (Formánek) Degen & Dörf.	Balkans	Quaternary	Frajman and Schönswetter (2017)
<i>Euphorbia saxatilis</i> Jacq.	sister to a Balkans clade	Balkans	Quaternary	Frajman and Schönswetter (2017)
<i>Helianthemum lunulatum</i> DC.	<i>H. pomeridianum</i> Dunal	Algeria, Morocco	Probably pre-Quaternary	Aparicio et al. (2017)
<i>Leucanthemum burnatii</i> Briq. & Cavill. in Burnat	sister <i>L. virgatum</i> Clos, <i>L. laciniatum</i> Huter, Porta & rigo, <i>L. tridactylites</i> A. Kern. & Huter ex Rigo	Mostly Italy	Quaternary	Wagner et al. (2019)
<i>Lilium pomponium</i> L.	<i>L. pyrenaicum</i> Gouan	Pyrenees	–	Ikinci et al. (2006)
<i>Linaria tonzigii</i> Lona	sister <i>L. capraria</i> Moris & De Not., <i>L. purpurea</i> (L.) Miller, <i>L. repens</i> (L.) Miller	Italy (<i>L. repens</i> widespread)	Quaternary	Biella et al. (2021)
<i>Macneilia graminifolia</i> (Ard.) Dillenb. & Kadereit subsp. <i>graminifolia</i>	various species from Italy and SE Europe	Italy and SE Europe	–	De Luca et al. (2022)
<i>Rhaponticum helenifolium</i> Godr. & Gren.	<i>R. cynaroides</i> Less.	Pyrenees	–	Hidalgo et al. (2006)
subsp. <i>helenifolium</i> & <i>bicknellii</i> (Briq.) Greuter				
<i>Sempervivum dolomiticum</i> Facechini	<i>S. cantabricum</i> J.A. Huber	Cordillera Cantabrica	Quaternary	Klein and Kadereit (2015)

Table 1 (continued)

Taxon	Closest relative (s)	Geographical distribution of closest relative(s)	Estimated age of refugial endemic	References
<i>Psilathera ovata</i> (Hoppe) Deyl	sister <i>Echinaria</i> Desf. or part of clade with <i>Echinaria</i> & <i>Sesleria</i> Scop. s.str.	Mostly S and SE Europe		Kuzmanović et al. (2017)
<i>Sesleriella sphaerocephala</i> (Ard.) Deyl	relationships to <i>Echinaria</i> , <i>Sesleria</i> s.str. <i>Psilathera ovata</i> , <i>Mibora</i> Adans., <i>Oreochloa</i> Link unclear	Widespread mostly in Europe		Kuzmanović et al. (2017)
<i>Tephrosieris balbisiana</i> (DC.) Holub	sister to <i>T. crispa</i> (Jacq.) Rchb., <i>T. helentis</i> (L.) B. Nord., <i>T. longifolia</i> (Jacq.) Griseb. & Schenk, <i>T. papposa</i> (Rchb.) Schur	<i>T. balbisiana</i> : Maritime Alps and Spain	Quaternary	Kadereit et al. (2021), Adamo et al. (2023)
<i>Viola culminis</i> F. Fen. & Moraldo, <i>V. calcarata</i> subsp. <i>villarsiana</i> (Roem. & Schult.) Merxm., <i>V. dubyana</i> Burnat ex Gremli, <i>V. valderia</i> All.	part of <i>Calcarata</i> species complex of <i>V. sect. Melanium</i> Ging	Italy, Sicily, Sardinia, Corsica	Quaternary	Hühn et al. (2023)

The uneven distribution of refugial endemics in the Alps is not correlated with the distribution of species diversity, intraspecific genetic diversity, or environmental diversity

It is conceivable that the rarity of endemics along the northern edge of the Alps as opposed to their relatively high frequency in the south is proportional to the overall distribution of species, intraspecific genetic, and/or environmental diversity. However, following Gugerli et al. (2008) and Taberlet et al. (2016), this does not seem to be the case. Thus, Gugerli et al. (2008) showed that potential habitat diversity across the Alps generally follows species richness patterns, while Taberlet et al. (2016) demonstrated that species richness does not correlate with areas of endemism. This in turn implies that areas of endemism do not correlate with habitat diversity. Gugerli et al. (2008) also found that highest intraspecific genetic diversity in the Alps occurs along their northern edge, and Taberlet et al. (2016) showed that intraspecific genetic diversity is negatively correlated with species endemism.

The nature of glacial refugia north of the Alps

Various evidence indicates the existence of glacial refugia north of the Alps, i.e., in lowland areas between the ice shields of the Alps and Scandinavia. Birks and Willis (2008) provided a list of 70 ‘alpiners’, defined as species that today occur mainly above the altitudinal or beyond the latitudinal treeline (thus including both alpine and arctic species), for which LGM or Weichselian Late Glacial (LG) macrofossils or pollen or spores have been found in northern and Central Europe. However, except for one, all species listed by Birks and Willis (2008) today are distributed in both the Alps (or other parts of the EAS) and in northern Europe, including, for some species, Scotland. As Birks and Willis (2008) clearly stated that ‘Little is known, however, of the LGM distributions of the bulk of the alpiners that occur in the Pyrenees and the Alps today because no taxonomically detailed macrofossil analyses have, as far as we know, been done on LGM or LG deposits in Iberia or near the Alps’, it is essentially unknown whether these fossils, in Central Europe, are derived from populations fleeing the Scandinavian ice shield rather than the ice shield of the Alps. Irrespective of this, these fossils certainly illustrate that LGM growing conditions in northern and Central Europe were suitable for plant species which today grow in the Alps and the Arctic. Birks and Willis (2008) also provided a map (based on Väre et al. 2003) of the extant occurrence of alpine species in the potential forest zone of Central Europe, and interpreted these occurrences as ‘cryptic Holocene refugia’. Probably

Table 2 Refugial endemics most closely related to taxa or lineages in the Alps and estimated time of their origin where available

Taxon	Closest relative (s)	Estimated age of refugial endemic	References
Undated			
<i>Achillea clusiana</i> Tausch	<i>A. atrata</i> L.	–	Ehrendorfer and Guo (2006)
<i>Alyssum wulfenianum</i> Willd. subsp. <i>wulfenianum</i> & <i>ovirens</i> (A. Kern.) Magauer	Subsp. <i>wulfenianum</i> nested in subsp. <i>ovirens</i>	–	Magauer et al. (2014)
<i>Arenaria bernensis</i> Favarger	<i>A. multicaulis</i> L.	–	Berthouzot et al. (2013)
<i>Biscutella laevigata</i> L. subsp. <i>lucida</i> (DC.) Archang.	<i>B. laevigata</i> subsp. <i>laevigata</i> W Alps	–	Parisod and Besnard (2007)
<i>Biscutella prealpina</i> Raffaelli & Baldoin	<i>B. laevigata</i> subsp. <i>laevigata</i> S Alps	–	Tremetsberger et al. (2002)
<i>Campanula elatinooides</i> Moretti and <i>C. elatines</i> L.	Sister to each other	–	Park et al. (2006)
<i>Campanula morettiana</i> Rchb. and <i>C. raineri</i> Perpent	Sister to each other	–	Park et al. (2006)
<i>Carex austroalpina</i> Becherer	<i>C. ferruginea</i> Scop.	–	Hendrichs et al. (2004)
<i>Centaurea rhaetica</i> Moritz	<i>C. nervosa</i> Willd., <i>C. nigrescens</i> Willd., <i>C. bugellensis</i> (Soldano) Soldano (<i>C. uniflora</i> group)	–	López-Alvarado et al. (2014)
<i>Doronicum glaciale</i> (Wulf.) Nyman subsp. <i>calcareum</i> (Vierh.) Hegi (+ subsp. <i>glaciale</i>)	<i>D. stiriacum</i> (Vill.) Dalla Torre, <i>D. clusii</i> (All.) Tausch s.s.	–	Pachschwöll et al. (2015)
<i>Euphorbia variabilis</i> Ces and <i>E. valliniana</i> Belli	sister to each other	–	Heimer and Frajman (2023)
<i>Euphrasia christii</i> Gremli	<i>E. alpina</i> Lam., <i>E. cisalpina</i> Pugsley, <i>E. sinuata</i> Vitek & Ehrend., <i>E. inopinata</i> Ehrend. & Vitek (<i>E. minima</i> Lam.)	–	Pan et al. (2019)
<i>Fritillaria involucrata</i> All., <i>F. tubaeformis</i> Gren. & Godr.	sister to each other	–	Day et al. (2014)
<i>Gentianella engadinensis</i> (Wettst.) Holub	<i>G. anisodonta</i> (Borbás) Á. Löve & D. Löve	–	Greimler et al. (2011)
<i>Helictotrichon setaceum</i> (Vill.) Henrard subsp. <i>setaceum</i> & <i>petzense</i> , <i>H. sempervirens</i> (Vill.) Pilger	<i>H. parlatorei</i> (J. Woods) Pil. species group	–	Ley et al. (2018)
<i>Knautia mollis</i> Jord. and <i>K. collina</i> Jord.	Sister to each other	Possibly Quaternary	Resetnik et al. (2014)
<i>Leontodon montaniformis</i> Widder	<i>L. montanus</i> Lam.	–	Samuel et al. (2006)
<i>Oreochloa seslerioides</i> K. Richt.	<i>O. disticha</i> (Wulf.) Link	–	Kuzmanović et al. (2017)
<i>Papaver alpinum</i> L.	Intraspecific differentiation in Alps	–	Bittkau and Kadereit (2002), Schönswetter et al. (2009)
<i>Pinguicula arvetii</i> P.A. Genty	<i>P. leptoceras</i> Rchb.	–	De Castro et al. (2016)
<i>Hornungia alpina</i> (L.) O. Appel subsp. <i>austroalpina</i> (Trpin) O. Appel	<i>H. alpina</i> subsp. <i>alpina</i> (subsp. <i>austroalpina</i> possibly diphyletic)	–	Winkler et al. (2010)
<i>Rhizobotrya alpina</i> Tausch	<i>Kernera saxatilis</i> (L.) Rchb.	–	Kropf et al. (2003), Walden et al. (2020)

Table 2 (continued)

Taxon	Closest relative (s)	Estimated age of refugial endemic	References
Dated			
<i>Androsace brevis</i> (Hegetschw.) Cesati and A. wulfeniana Steber ex Koch	Sister to each other	ca. 2.98 mya	Schönswetter et al. (2003a), Schneeweiss et al. (2004), Boucher et al. (2012)
<i>Androsace adfinis</i> Biroli, A. <i>briganitiaca</i> Jord. & Fourr., A. <i>puberula</i> Jord. & Fourr.	Monophyletic group, A. <i>briganitiaca</i> is allopolyploid hybrid derivative of A. <i>adfinis</i> and A. <i>puberula</i>	ca. 1.7 mya or younger	Dixon et al. (2009)
<i>Androsace pubescens</i> DC.	A. <i>helvetica</i> (L.) All.	Quaternary	Boucher et al. (2012), Schneeweiss et al. 2017
<i>Callianthemum kernerianum</i> A. Kern. and C. <i>anemonoides</i> (Zahlbr.) Heynh.	Most likely sister to each other	Quaternary	Kadereit et al. (2019)
<i>Facchinia</i> Rohb.	Speciation mostly in Alps	Quaternary	Dillenberger and Kadereit (2017)
<i>Jovibarba globifera</i> (L.) J. Parn.	Subspecific differentiation	Quaternary	Klein and Kadereit (2015)
<i>Leucanthemum virgatum</i> (Destr.) Clos & L. <i>lithopolitanicum</i> (E. Mayer) Polatschek	Sister to each other	Quaternary	Konowalik et al. (2015), Wagner et al. (2019)
<i>Primula</i> L. sect. <i>Auricula</i> Duby	Several species pairs/species groups in Alps	Mostly Quaternary (Zhang et al. 2004; Kadereit et al. 2004), partly older (Boucher et al. 2016b)	Zhang et al. (2004), Kadereit et al. (2004), Boucher et al. (2016a, b)
<i>Pulsatilla alpina</i> (L.) Delabre	Subspecific differentiation	Quaternary	Sramkó et al. (2019)
<i>Ranunculus traunfelfneri</i> Hoppe and R. <i>bilobus</i> Bertol.	Both most closely related to R. <i>alpestris</i> from S and SW Alps	Quaternary (split between the two endemics)	Paun et al. (2008)
<i>Saxifraga</i> L. sect. <i>Saxifraga</i> subsect. <i>Arachnoideae</i> (Engl. & Irmsch.) Tkach et al.	Speciation mostly in Alps	Mostly Quaternary	Gerschwitz-Eidt et al. (2023)
<i>Sempervivum montanum</i> subsp. <i>stiriacum</i> , S. <i>pitonii</i>	Sister to each other	Quaternary	Klein and Kadereit (2015)
<i>Soldanella minima</i> Hoppe subsp. <i>austriaca</i> (Vierh.) Lüdi	S. <i>minima</i> subsp. <i>minima</i>	Quaternary	Slovák et al. (2022)

at least those occurrences close to the Alps are likely to be derived from refugial populations of alpine origin.

When considering the glacial distribution of arctic–alpine disjuncts (for reviews see Birks 2008; Schmitt et al. 2010), their wide presence between the Scandinavian and Alps ice shields has been inferred or postulated, based on phylogeographic data, for *Arabis alpina* L. (Ehrich et al. 2007), *Carex atrofusca* Schkur (Schönschwetter et al. 2006a), *Cherleria sedoides* L. (Scotland-Alps; Valtueña et al. 2015), *Dryas octopetala* L. (Skrede et al. 2006), *Gentiana nivalis* L. (Alvarez et al. 2012), *Minuartia biflora* (L.) Schinz & Tell. (Schönschwetter et al. 2006b), *Sibbaldia procumbens* L. (Scotland-Alps; Allen et al. 2015), *Saxifraga oppositifolia* L. (Winkler et al. 2013), and *Salix herbacea* L. (Alsos et al. 2009). Long-distance dispersal between the Alps and Scandinavia rather than continuous distribution in glacial times between these areas has been found in *Comastoma tenellum* (Rottb.) Toyok. (Schönschwetter et al. 2004b), *Ranunculus glacialis* L. (Schönschwetter et al. 2003b) and *Trollius europaeus* L. (Després et al. 2002), although a Central European population of the last species was found to be the closest relative of populations from the Alps. Independent colonization of Scandinavia and the Alps from distant areas has been postulated for *Ranunculus pygmaeus* Wahlenb. (Schönschwetter et al. 2006b). The very wide distribution of arctic–alpine species in Europe has also become evident from the analysis of the flora of Upper Teesdale (England), a very well-studied glacial relic site (Pigott 1956; Godwin and Walters 1967; Birks 2015).

Occurrences of alpine species in Germany (and Central Europe) north of the Alps have been looked at in considerable detail by Thorn (1957, 1960). Thorn (1957; see this reference for discussion of earlier authors) provided a list of 30 ‘dealpine’ species for Germany (and Central Europe). In his definition of dealpine Thorn (1957) followed Schustler (1923; quoted in Thorn 1957), who considered species dealpine when they occur mainly at alpine or even nival elevations but have scattered occurrences in Central Europe beyond the northern edge of the Alps. Such occurrences were interpreted as glacial relics by Schustler (1923). In 1960, Thorn provided a list and map of 72 species from lowland Central Europe beyond the edge of the Alps (Alpenvorland) which he considered glacial relics. Most of these species are found in the Black Forest (and Vosges in France), Swabian Alb, Franconian Alb, Upper Palatine and Bavarian Forest, Thuringian-Franconian Highlands and West and East Sudetes, with the northernmost occurrences of alpine species in the Harz. For the edge of the Bavarian Alps (Bayerisches Alpenvorland), Bresinsky (1965) identified ca. 60 species which he considered dealpine. His definition includes species distributed from alpine to lowland elevations. However, for lack of secure knowledge, Bresinsky

(1965) abstained from interpreting lowland occurrences of such species as relic occurrences.

Of those species listed by Thorn (1957, 1960) and Bresinsky (1965) as dealpine or glacial relics, a number have been subjected to phylogeographic analyses often aiming at clarifying their relic status. Mainly based on patterns of genetic variation, such as the degree of genetic differentiation among hypothetical glacial relic populations and/or the occurrence of rare alleles, extra-alpine populations of *Arabis alpina* (Ehrich et al. 2007), *Arabidopsis lyrata* (L.) O’Kane & Al-Shebaz subsp. *petraea* (L.) O’Kane & Al-Shebaz (Clauss and Mitchel-Olds 2006; Wernisch 2007), *Carduus defloratus* L. (Vaupeul 2013), *Cicerbita alpina* (L.) Wallr. (Michel et al. 2010), *Draba aizoides* L. (Widmer and Baltisberger 1999; Vogler and Reisch 2013), *Gentiana pannonica* Scop. (Ekrťová et al. 2012), *Pulsatilla vernalis* Mill. (Ronikier et al. 2008; Kiedrzyński et al. 2017), *Saxifraga paniculata* Mill. (Reisch et al. 2003; Reisch and Poschlo 2004) and *Swertia perennis* L. (Urbaniak et al. 2018) were interpreted as glacial relics. When assuming that *Biscutella laevigata* grew in the Alps in a diploid form before the LGM (Parisod and Besnard 2007), the diploid sublineages outside the Alps of this enigmatic taxon (Manton 1934, 1937) also can be considered glacial relics (Tremetsberger et al. 2002). Evidence for the status of populations as glacial relics was considered inconclusive for *Saxifraga aizoides* (Lutz et al. 2000) and *Tofieldia calyculata* (L.) Wahlenb. (Vlasta and Münzbergová 2022), and postglacial colonization of extra-alpine areas beyond the edge of the northern Alps has been postulated for *Polygala chamaebuxus* L. (Windmaier et al. 2016), *Polygonum viviparum* L. (Bauert 1996) and *Rosa pendulina* L. (Fér et al. 2007; but see Danek et al. 2016). Following Reisch et al. (2002), there is no evidence for glacial relic endemism of *Sesleria albicans* Kit. ex Schultes, considered a prime example for glacial relic species in Central Europe by Ellenberg (1996).

Ideas about the distribution of trees during the LGM have changed greatly within the last three decades, based on new or reconsidered fossils as well as phylogeographic or species distribution modeling evidence (Gavin et al. 2014). It has become quite clear that at least boreal tree species, most likely in small populations in locally favorable conditions, existed in Central Europe and partly north of the Alps at that time (Willis et al. 2000; Stewart and Lister 2001; Bhagwat and Willis 2008; Birks and Willis 2008; Provan and Bennett 2008; Svenning et al. 2008; Tzedakis et al. 2013). This might provide indirect evidence that growing conditions north of the Alps should also have been good enough for herbaceous alpine plant species. Glacial survival in areas north of the Alps has been inferred from phylogeographic studies even of herbaceous temperate species such as *Galium pusillum*

agg. (Kolář et al. 2013, 2015; Knotek and Kolář 2018), *Hippocrepis comosa* L. (Leipold et al. 2017), *Melica nutans* L. (Tyler 2002), *Meum athamanticum* Jacq. (Huck et al. 2009), *Polygonatum verticillatum* (L.) All. (Kramp et al. 2009), *Sanguisorba minor* Scop. (Tausch et al. 2017), *Saxifraga rosacea* Moench subsp. *sponhemica* (C.C. Gmel.) D.A. Webb (Walisch et al. 2015) and, in western Europe, *Meconopsis cambrica* (L.) Vig. (Valtueña et al. 2012). Ohlemüller et al. (2012), in a simulation study, also identified large areas north of the main European mountain ranges as suitable for the growth of temperate plant species during the LGM.

Closer to the Alps, the analysis of distribution patterns of flowering plants led Merxmüller (1952–1954) to infer refugia along the northern edge of the Alps. Genetic evidence in support of Merxmüller (1952–1954) has been provided for, e.g., *Androsace lactea* L. (Schneeweiss and Schönswetter 2010), *Helleborus niger* L. (Záveská et al. 2021), *Polygala chamaebuxus* (Windmaier et al. 2016), *Hornungia alpina* (L.) O.Appel (Winkler et al. 2010) and *Ranunculus alpestris* L. (Paun et al. 2008).

Schönswetter et al. (2005), considering the entire Alps, found that of the several potential calcareous refugia along the northern edge of the Alps identified through the combination of geological and palaeoenvironmental data, only three (their refugia V: northern-Alpine peripheral refugium in central Switzerland; VI: northern-Alpine peripheral refugium in eastern Switzerland; VII: northern-Alpine peripheral refugium in southern Germany) could be verified on the basis of phylogeographic studies of *Erinus alpinus* L. and *Rumex nivalis* Hegetschw. (Stehlik 2002; Stehlik et al. 2002). In an earlier study, using the distribution of endemics and the results of phylogeographic studies of alpine plant species, Tribsch and Schönswetter (2003) aimed at identifying refugial areas in the eastern Alps (containing the eastern part of the northern Alps discussed here). A hypothetical refugial area for species of upper alpine and subnival distribution comprising several peripheral parts of the northern calcareous Alps (Berchtesgadener Alpen, Bayerische Voralpen, Wettersteingebirge, Allgäuer Alpen, Säntis, northern Glarner Alpen; their area C8) could not be confirmed because of the absence of narrow endemics from this area.

In conclusion, it seems beyond reasonable doubt that suitable areas for glacial survival of high-elevation species from the Alps were available north of the Alps in much the same way as south of the Alps. If the distribution of populations in refugial areas should be causally linked to their evolutionary divergence resulting in subspeciation or speciation, this implies that northern and southern refugia differed in properties relevant for speciation.

Differences between northern and southern glacial refugia and their potential influence on speciation

Climate

Climatic conditions in glacials were very different north and south of the Alps (Birks and Willis 2008). While in the north, climate favored steppe shrub tundra vegetation (and steppe tundra vegetation further north), most likely very similar to interglacial ecological conditions at alpine elevations (Körner 2021), vegetation south of the Alps, below a narrow montane forest zone, was xeric *Artemisia*–*Poaceae*–*Chenopodiaceae* steppe. When refugial populations persisted (in interglacials or the Holocene) in their glacial refugial areas, they are believed to have been exposed to strong selection (Hewitt 1996, 2000, 2004; Ackerly 2003; Hampe and Petit 2005; Stewart et al. 2010; Stewart and Stringer 2012; Mee and Moore 2014). Along these lines, Gerschwitz-Eidt et al. (2023) suggested, for a subgroup of alpine saxifrages, that some speciation in this lineage may be the result of a two-step process, in which glacial climate resulted in geographical isolation in glacial refugia in a first step, and subsequent interglacial climate resulted in adaptive divergence of populations persisting in the refugial area in a second step (see also Kadereit 2022).

Space

Looking at fossil evidence, the often rather wide distribution of glacial relics (dealpines) in Central Europe, and the possibly very wide glacial distribution of arctic–alpine species in Central Europe, it seems very likely that glacial refugia of alpine species north of the Alps will have been very large areas probably containing many populations linked through gene flow. This hypothesis is supported by the fact that ecological conditions in glacials in Central Europe may have been very similar to interglacial ecological conditions at alpine elevations. Much in contrast to this, as mentioned earlier, glacial vegetation south of the Alps, below a narrow montane forest zone, has been characterized as steppe (Birks and Willis 2008) or xeric *Artemisia*–*Poaceae*–*Chenopodiaceae* steppe (Birks 2015). The latter was considered too dry for high-elevation open tundra-like vegetation by Birks (2015). This might imply that much in contrast to the vast size of glacial refugia north of the Alps, glacial refugia south of the Alps may have been spatially very limited where the southern latitudinal limits were imposed by climate. Probably more importantly, there existed large topographical differences at the northern and southern edges of at least the LGM ice shield of the Alps. Looking at this ice shield (Fig. 1), it is obvious that LGM glaciation, dependent on climate, reached into the lowland

in most parts north of the Alps. Much in contrast to this, the edge of the LGM ice shield was located in mountainous areas in most parts of the southern Alps. In addition to the latitudinal limitation of southern alpine refugia, this will have resulted in their further topographical fragmentation. For the Maritime and Ligurian Alps (Casazza et al. 2008, 2010, 2016a), the effects of small scale refugia on the degree of among population differentiation have been shown for, e.g., *Gentiana ligustica* R. Vilm. & Chopinet (Diadema et al. 2005), *Saxifraga florulenta* (Szövényi et al. 2009), *Primula latifolia* Lapeyr. and *P. marginata* Curtis (Schorr et al. 2013) and *Viola argenteria* (Casazza et al. 2016b). In summary, glacial refugia for high-elevation species north of the Alps are likely to have been classical macrorefugia, and those south of the Alps may have had similarities with microrefugia (or cryptic refugia; for discussion of terms see Birks 2015).

However, although it seems very likely that expansion of high-elevation plant species further south than the edge of the south Alps was not possible in lowland areas due to climatic conditions there (Birks 2015), it is obvious that a large number of species from high elevations in the Alps also grow in southern European mountains. Accordingly, refugial areas of some high-elevation species south of the Alps also may have been very large.

Following Aeschimann et al. (2011b), 77 species found in the Alps are shared with the Dinarids, 66 with the Apennine, 44 with the Pyrenees, and 40 with the Carpathians, and many more occur in different combinations of these mountain ranges. The alpine flora of south European mountains has also been analyzed by Gentili et al. (2015a, b), who identified suitable habitats of high-elevation alpine species, and Vargas (2003) provided an early comparative analysis of seven plant species ranging from the Alps to south European mountain ranges. Detailed analyses of species distributed from the Alps via the Massif Central and the Pyrenees to the southern Spanish Sierra Nevada have been presented by Kropf et al. (2006, 2008). Examination of six species led to the conclusion that this distribution is clearly best explained by interglacial/postglacial disruption of a continuous range obtained by migration in four of these six species. On the other hand, the occurrence of *Phyteuma globulariifolium* Sternb. & Hoppe in the Pyrenees has been interpreted as the result of long-distance dispersal from the southwestern Alps by Schönswetter et al. (2002), and Sanz et al. (2017) concluded that the Sierra Nevada population of *Artemisia umbelliformis* Lam. most likely originated by long-distance dispersal from the Alps. For the Carpathians, most disjunctions with the Alps have been interpreted as the result of vicariance of a once continuous range with some instances of long-distance dispersal (Ronikier 2011; Mráz and Ronikier 2016). Habitat continuity in glacial times between the southwest Alps and the Apennine has been thought likely

by Zhang et al. (2004), Dillenberger and Kadereit (2013) and Moore et al. (2013), and genetic discontinuity between the Apennine and the Alps was detected by, e.g., Ansell et al. (2008) and Grassi et al. (2009), again pointing at vicariance of a once continuous range.

All this confirms the very close relationship between the flora of the Alps and those of the Pyrenees, Apennine, Carpathians, Dinarids, and Balkans already pointed out and discussed in some detail long ago by, e.g., Christ (1867) and Engler (1879), and more recently by Ozenda (1985, 2009), Aeschimann et al. (2011b), and Kadereit (2017).

For the many high-elevation species from the Alps which did not expand into southern mountain ranges in glacial times, it seems likely that glacial refugia on the southern edge of the Alps often will have covered substantially smaller areas than glacial refugia north of the Alps because refugia in the south were latitudinally limited by different climate in the south and because they were further fragmented by the location of the edge of the ice shield in mountainous areas. Although such smaller refugial areas do not qualify as one of three types of microrefugia as defined by Rull (2009), because these imply the existence of a macrorefugium, Birks (2015) suggested that a fourth type of microrefugium without the existence of a macrorefugium could be recognized. Whether considered microrefugia or not, small glacial refugia on the southern edge of the Alps are similar to microrefugia in several respects. Most importantly, in a spatial context, refugia were isolated (Cai et al. 2023) and effective population sizes may have been small, favoring evolutionary divergence through processes such as genetic drift (Stewart et al. 2010; Mee and Moore 2014; Woolbright et al. 2014).

Time

The overall duration of the Quaternary was the same north and south of the Alps. However, periods of geographical isolation of refugial populations, a likely prerequisite for speciation, might have differed in length in the north and south. Provided glacial refugia north of the Alps were indeed the vast lowland areas between the northern European ice shield and the ice shield of the Alps, geographical isolation among refugial populations will have been very limited in glacials, and opportunity for geographical isolation will only have arisen in interglacials provided populations at high elevations were geographically isolated. In support of limited geographical isolation in lowland refugia, gene flow among refugial populations in glacial times in Central Europe has been postulated for *Carduus defloratus* (Vaupel 2013), *Cicerbita alpina* (Michl et al. 2010), and *Saxifraga rosacea* subsp. *sponhemica* (Walisch et al. 2015). In contrast to lack of geographical isolation in the north, geographical isolation among populations occurred in the small and fragmented

glacial refugia south of the Alps. As, in sum, interglacials were much shorter than glacials since the so-called Mid-Pleistocene between about 1.25 and 0.7 million years ago (Birks 2019), overall time of isolation will have been longer south than north of the Alps. The possible evolutionary effect of this is similar to what has been concluded from a comparison of the phylogeographic structure of montane *Anthyllis montana* L. and alpine *Hornungia alpina*, where genetic differentiation in the former was found to be much stronger than in the latter (Kropf et al. 2003). Kropf et al. (2003) argued that this can be explained by long glacial vicariance in the former and short interglacial vicariance in the latter species.

A potential threefold role for climate in the evolution of refugial endemics

The above considerations show that climate, either (1) directly through natural selection or indirectly through affecting (2) the size of refugial areas and (3) the duration of geographical isolation, may have played a role in the evolution of refugial endemics. Their very uneven distribution in the Alps, with a virtual absence along much of the northern edge of the Alps and the existence of many endemics along the southern edge of the Alps, was the starting point of my argument. Potentially, climate will have had a direct influence on evolutionary divergence when populations persisted in southern refugia and were increasingly subjected to warming conditions and changes in associated abiotic and biotic factors which represented dramatically altered selective conditions. In support of this, Luqman et al. (2023) showed that populations of *Dianthus sylvestris* Wulfen in glacial refugia at the southern edge of the Alps evolved to their current adaptive optima from an alpine-like refugial state, although far less so than populations expanding from these refugia. The biology and evolution of such stable rear edge (Hampe and Petit 2005) populations or species have been discussed by, e.g., Ackerly (2003), Hampe and Petit (2005), Hampe and Jump (2011), Woolbright et al. (2014), Kiedrzyński et al. (2017), and Kadereit (2022). A potential indirect influence of climate is twofold. First, unsuitable climate may have limited the size of glacial refugia for high-elevation species along the southern edge of the Alps, and the location of the edges of glaciers in mountainous terrain will have further fragmented the spatial extent of refugia. Geographically isolated suitable climatic conditions have recently been hypothesized to be an important explanatory variable for the geographical distribution of species diversity (Coelho et al. 2013). Much in contrast to this, refugial areas in the north of the Alps most likely were of vast size. Such size difference may have favored evolutionary processes typical for isolated small populations (mainly genetic drift) in the south. Second,

climate affected the duration of geographical isolation differently in the south and north. While in the south, isolation arose in long glacials, it arose, if at all, in much shorter interglacials in the north. This will have increased the probability of evolutionary divergence in the south. It seems likely that a combination of all three factors will have played a role in the evolution of the endemics found along the southern edge of the Alps.

As pointed out above, the northeastern Alps ('northeastern calcareous Alps' and 'northeasternmost Prealps') have been identified as an area of endemism by several authors (e.g., Tribsch and Schönswetter 2003; Tribsch 2004; Essl et al. 2009). As climatic differences between the northeastern Alps and endemic-poor areas to the west are less obvious than the climatic differences between north and south of the Alps, the presence of an area of endemism in the northeastern Alps deserves special attention. Probably most importantly, vegetation along the eastern edge of the Alps appears to have been xeric steppe probably in much the same way as along the southern edge of the Alps (Frenzel 1964; Lang 1994), partly, in the area of the Wiener Becken, even containing stands of *Pinus nigra* J.F. Arnold (Niklfeld 1972). In support of this, the refugial area 'easternmost Central Alps' is located on the eastern edge of the Alps (Tribsch 2004). Interestingly, Janská et al. (2017) postulated high habitat suitability for typical steppe vegetation along the easternmost part of the northern edge of the Alps during the LGM.

Of the endemics of the northeastern Alps listed by Tribsch and Schönswetter (2003; their refugial area C1), *Campanula beckiana* Hayek, probably *Campanula pulla* L., *Euphorbia austriaca* A. Kern. and *Euphorbia saxatilis* Jacq. have their closest relatives in southeast Europe and cannot be considered part of alpine lineages. Many other of the northeastern Alps endemics listed by Tribsch and Schönswetter (2003) have at least some (often few) occurrences along the eastern edge of the Alps when the Rax-Schneeberg area of Tribsch and Schönswetter (2003) is considered part of the xeric steppe area. This seems justified on the basis of the distribution of some taxa (Niklfeld 1972). The endemics listed by Tribsch and Schönswetter (2003) are: *Achillea clusiana* Tausch, *Biscutella laevigata* subsp. *austriaca*, *Callianthemum anemonoides* (Zahlbr.) Endl., *Campanula praesignis* Beck, *Dianthus alpinus* L., *Dianthus plumarius* L. subsp. *hoppei* (Port.) Hegi (a taxon not recognized in Aeschmann et al. 2004), *Doronicum glaciale* (Wulfen) Nyman subsp. *calcareum* (Vierh.) Hegi, *Draba stellata* Jacq., *Galium meliodorum* (a taxon not distinguishable from *G. lucidum* All. according to Grossfurthner (2018)), *Leontodon montaniformis* Widder, *Leucanthemum atratum* (Jacq.) DC., *Melampyrum angustissimum* Beck, *Melampyrum subalpinum* (Jur.) A.Kern., *Papaver alpinum* p.p., *Primula clusiana* Tausch,

Pulsatilla styriaca (Pritz.) Simonk., *Soldanella austriaca* Vierh., and *Thlaspi alpestre* Jacq. Also, in much of the northeastern Alps east of the Traunlinie, the edge of the LGM ice shield was located in mountainous area (Fig. 1; Ivy-Ochs 2015; Seguinot et al. 2018).

It is, thus, conceivable that these taxa originated in refugia along the eastern edge of the Alps where the role of climate might have been the same as hypothesized for the southern edge, and then spread westwards. Indeed, Niklfeld (1972) listed a number of taxa distributed in the *Pinus nigra* area along the eastern edge of the Alps which also grow along the northern edge of the northeastern Alps. Of the endemic species listed above, only *Doronicum glaciale* has been analyzed phylogeographically (Pachschwöll et al. 2015). Pachschwöll et al. (2015) reported that *D. glaciale* subsp. *calcareum*, distributed in unglaciated areas, cannot easily be separated from *D. glaciale* subsp. *glaciale* which is distributed in formerly glaciated areas to the west. They identified a primary contact zone between the two and postulated recent westward migration of subsp. *glaciale*.

However, Tribsch and Schönswetter (2003) also listed some endemics which today do not grow along the eastern edge of the Alps ((*Dianthus plumarius* subsp. *blandus* (Rchb.) Hegi, a taxon not recognized in Aeschmann et al. (2004), *Festuca versicolor* Tausch subsp. *brachystachys* (Hack.) Markgr.-Dann. and subsp. *pallidula* (Hack.) Markgr.-Dann., *Galium truniacum* (Ronninger) Ronninger, *Pulmonaria kernerii* Wettst.)). Understanding the origin of those taxa found along the northeastern but not the eastern edge of the Alps clearly requires further investigation.

These considerations for the NE Alps may also apply to the western limit of the north Alps area lacking endemics, i.e., to areas west of Lake Geneva (ligne du lac Léman au lac Majeur of Aeschmann et al. 2011a), as steppe vegetation bordered on the Alps to the west but not to the east of Lake Geneva (Lang 1994). Somewhat in accordance with this, Divíšek et al. (2022) identified the northwestern Alps as an LGM source area for steppe species limited to Central Europe. As regards the LGM ice shield west of Lake Geneva, however, this expanded into lowland areas as far south as the Chartreuse/Isère area (Fig. 1; Ivy-Ochs 2015; Seguinot et al. 2018).

Conclusion

Considering glacial refugia in the Alps, Smyčka et al. (2017) concluded that these constitute museums of phylogenetic diversity and served as islands of suitable conditions during glacial periods. Equally, Jardim de Queiros et al. (2022), for terrestrial organisms including vascular plants, hypothesized persistence through glacial climate cycles as a major component for the evolution of endemics in the Alps.

Both these explanations clearly emphasize climatic stability as a major factor in the origin and distribution of endemics, as postulated more generally by, e.g., Fjeldsø and Lovett (1997), Jansson (2003), Jetz et al. (2004), Hampe and Jump (2011), Svenning et al. (2015), Harrison and Noss (2017), and Cai et al. (2023).

For the specific setting examined here, i.e., the uneven distribution of endemics in the Alps, a more differentiated picture of the role of climate for the origin of endemics emerges. Thus, potentially climate influenced the size of refugia, the duration of geographical isolation and the selective conditions in refugia, and thus influenced both neutral and adaptive evolutionary processes. While a role of both neutral and adaptive processes has been postulated before (Hewitt 1996, 2000, 2004; Tribsch and Schönswetter 2003; Tribsch 2004; Hampe and Petit 2005; Carstens and Knowles 2007; Casazza et al. 2008, 2010, 2016b; Stewart et al. 2010; Hampe and Jump 2011; Mee and Moore 2014; Woolbright et al. 2014; Stewart and Stringer 2012; Gentili et al. 2015a, b; Kiedrzyński et al. 2017), southern Alps endemics may serve as good study systems for assessing the relative roles of these processes. Given the right data and analytical tools, their distinction may be possible (e.g., Luqman et al. 2021; for discussion of analytical approaches see Johri et al. 2022). As emphasized by de Lafontaine et al. (2018), it will be particularly interesting to investigate the role of natural selection, shown by Luqman et al. (2023) and also postulated by Hua and Wiens (2013) when concluding that speciation via climatic-niche divergence may have predominated during the climatic oscillations of the Quaternary. Probably, as postulated by Gerschwitz-Eidt et al. (2023), speciation at the southern edge of the Alps was a two-step process. While in a first step, often small populations became isolated in glacial refugia, adaptive divergence took place in interglacials (or the Holocene) when refugial populations persisted in their refugia. If such scenario could be confirmed, it would be obvious that glacial refugia were more than just sanctuaries where species were preserved from extinction as also concluded by Nieto Feliner (2011).

Here, it is hypothesized that the uneven distribution of refugial endemics in the Alps may be the result of uneven rates of origination north and south of the Alps. The possibility of uneven rates of extinction in these two areas was not considered. When assuming that climatic stability is a major factor in the origin and distribution of endemics (Fjeldsø and Lovett 1997; Jansson 2003; Jetz et al. 2004; Hampe and Jump 2011; Svenning et al. 2015; Harrison and Noss 2017; Cai et al. 2023), it is conceivable that the generally harsher climate along the northern edge of the Alps did not allow endemics to persist. However, based on the evidence presented above, the hypothesis that the properties of refugia north of the Alps did not favor the origin of

distinct genetic lineages, i.e., endemics, is favored. Also, the possible role of other factors for the uneven distribution of endemics in the Alps was not discussed. For example, as Smyčka et al. (2017) reported that high endemism in glacial refugia is found only on calcareous bedrock, bedrock as a factor affecting endemism clearly deserves further analysis.

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