

Are Disjunct Alpine and Arctic-Alpine Animal and Plant Species in the Western Palearctic Really “Relics of a Cold Past”?

Thomas Schmitt, Christoph Muster, and Peter Schönswetter

Abstract The climatic fluctuations during the Pleistocene as well as the Holocene warming caused numerous disjunctions of cold-adapted, arctic-alpine, and alpine biota. However, the depths of the genetic splits among the disjunct parts of the species distributions vary considerably. The arctic ranges are usually weakly differentiated, and great similarity with at least some areas in more Southern regions is frequently found. Likewise, major mountain ranges in geographic proximity often share genetically similar populations. However, the genetic constitution of populations from more remote (predominantly Southern) mountain systems is strongly different from all other populations. This suggests recent vicariance events in the two former groups, but long-lasting isolation in the latter group, which apparently is mostly composed of relics of a more distant cold past.

1 Introduction

The world’s climate has undergone dramatic changes during the history of the planet. The most recent period of climatic instability, the Pleistocene, was characterized by particularly strong and more or less regular oscillations between warm and predominantly moist, and cold and more often dry periods (Williams et al. 1998). During the cold stages, thermophilic species (e.g., Mediterranean or temperate taxa)

T. Schmitt (✉)

Department of Biogeography, Trier University, D-54286 Trier, Germany
e-mail: thsh@uni-trier.de

C. Muster

Molecular Evolution and Animal Systematics, Institute of Zoology II,
University of Leipzig, Talstraße 33, D-04103 Leipzig, Germany
e-mail: muster@rz.uni-leipzig.de

P. Schönswetter

Department of Plant Biogeography, Faculty Centre Biodiversity, University of Vienna,
A-1030 Wien, Austria
e-mail: peter.schoenswetter@univie.ac.at

were restricted to Southern refugia in the Southern European peninsulas where they have survived in refugia and expanded their ranges during warm periods such as the interglacials or the postglacial (de Lattin 1967; Müller 1980; Hewitt 1996, 2000, 2004a,b; Taberlet et al. 1998; Schmitt 2007). For temperate species, this view has, however, been challenged by the recent combination of pollen data and genetic analyses (Steward and Lister 2001), suggesting that refugia of, e.g., the Common Beech (*Fagus sylvatica*), were situated much further North than previously suggested (Magri et al. 2006).

The cycles of area regression and expansion of species currently restricted to high mountain habitats and/or high latitudes were likely diametrical: these species were potentially widely distributed during cold stages and experienced range restrictions during warm periods (de Lattin 1967). Consequently, current distribution patterns of species adapted to high altitudes or high latitudes are often strongly disjunct and many of the isolated area fragments are small and widely separated from the core of their distribution area (Varga and Schmitt 2008).

The application of molecular techniques to reconstruct genealogical relationships above, at or even below the species level, has created a powerful tool to unravel the biogeographic history of taxa in space and time (Hewitt 1999, 2001, 2004a; Taberlet et al. 1998; Avise 2000; Schmitt 2007). We here review phylogeographic data on high mountain and high latitude species with disjunct distribution areas hitherto available for the Western Palearctic. In the following, we distinguish between two distributional types of species: (1) alpine, montane, and dinodal species of the European mountain system (EMS) of temperate regions sensu Ozenda (1988) and (2) arctic-alpine species. For each of these two above categories we summarize published studies and some unpublished results, and we search for congruencies as well as differences among the observed phylogeographic patterns. Based on the degree of genetic divergence between isolated “relic” taxa or populations and those from the main distribution areas, we aim to unravel if these entities represent relics of a cold past or are rather descendants of fairly young range expansions.

2 Species of the European Mountain System (EMS) of Temperate Regions

The distributions of species of the EMS as defined here include the Cordillera Cantábrica and range from there over the Pyrenees, Alps, and Apennines to the Carpathians and the mountains of the Northern and central Balkan Peninsula. They normally do not occur South of the Pyrenees or of the Italian Abruzzo, and are also lacking from the mountain ranges of the Southern Balkan Peninsula South of the Adamović line (Ozenda 1988). Few species of this category occur throughout the entire outlined area. While some of these mountain species are restricted to a part of the EMS where they are fairly frequent, others exhibit much wider but scattered distribution areas.

2.1 *Alpine Species*

During the last few years, an ample body of literature has accumulated exploring the phylogeography of alpine plants of the EMS. A review of hitherto available studies on Alpine plants was presented by Schönswetter et al. (2005). Therefore, we here consider only studies on species that show disjunctions among mountain ranges. For this group of alpine species, it could be shown by various examples in plants and animals that (1) the Alps often own more than one genetic lineage, (2) mountain areas in geographic proximity to the Alps may share genetic lineages with the adjacent regions of the Alps, and (3) more remote mountain areas mostly show strongly differentiated genetic lineages underpinning long geographic separation of these remote mountain areas and old relic status of their populations.

In the Alpine-Pyrenean disjunct *Phyteuma globulariifolium*, the populations from the Pyrenees were found to be genetically indistinguishable from Western Alpine plants, whereas a deep split was found in the Alps separating an Eastern and a Western group along River Etsch/Adige (Schönswetter et al. 2002). In the highly disjunct *Androsace halleri*, the most internal cpDNA haplotype is found in the Cordillera Cantábrica and in the Eastern Pyrenees, whereas the haplotypes from Massif Central and Alsace are derived by one and two mutational steps, respectively, indicating eastward range expansion (Dixon et al. 2007). A similar pattern was suggested in an amplified fragment length polymorphism (AFLP) study of *Pritzelago alpina* (Kropf et al. 2003), where populations from the Cordillera Cantábrica formed the sister group to the remaining populations. Some lineage diversification was observed in the Pyrenees, whereas one lineage was shared among Northeastern Alps, Tatras, and Southern Carpathians. A further clear example of colonization of the Carpathians from the Alps is provided by *Senecio carniolicus* (Suda et al. 2007), where diploid, tetraploid, and hexaploid cytotypes were found in the Eastern Alps, whereas the Carpathian populations (Tatras, Southern Carpathians) were uniformly hexaploid. In the Alpine-Carpathian *Hypochaeris uniflora*, Mráz et al. (2007) detected three strongly differentiated lineages in the Alps and the Western and the Eastern Carpathians, indicating long-term isolation of these three regions from each other. Most of the Alpine range was apparently colonized post-glacially from an Eastern Alpine refugium. By applying AFLP fingerprinting and chloroplast DNA data to *Campanula alpina* distributed in the Alps and Carpathians (mountains of the Balkan Peninsula were not sampled), Ronikier et al. (2008a) detected a deep split between the Alps and the Carpathians. Further splits separated Southwestern, Southeastern, Northeastern, and Northwestern parts of the Carpathian arch, indicating that the phylogeographical pattern of *C. alpina* has been mainly shaped by vicariance events. Virtually no AFLP differentiation was found among Pyrenean, alpine, and Tatra populations of *Oxytropis campestris* (Schönswetter et al. 2004a). In *Bupleurum stellatum*, mainly distributed in the Western Alps and the Southern part of the Central Alps, a deep split was found within the continuous distribution area roughly halfway between Lago di Garda and Lago di Como (Schönswetter and Tribsch 2005). The isolated population(s) from

Corsica clustered with high statistical support within the Eastern main group instead of the geographically closer Western group. The presence of several private AFLP fragments in the Corsican population, however, indicated that more time has elapsed since the dispersal event than in cases like *P. globulariifolium* and *O. campestris*. A strongly idiosyncratic genetic structure was revealed by a cpDNA study of *Pulsatilla vernalis* (Ronikier et al. 2008b), distributed over the EMS, parts of the Northerly adjacent lowlands, and Southern Fennoscandia. Two haplotype families separated by several mutational steps were found, both of which occurred throughout the species' distribution area except for the northernmost parts. Interestingly, the centralmost haplotype is essentially found over the entire distribution area, but was lacking from the Alps and Southern Finland. Specific microsatellite variation indicates the occurrence of periglacial lowland refugia North of the Alps, acting as source for post-glacial colonization of Scandinavia. The presence of different fixed haplotypes in Eastern and Western Scandinavia, however, suggests independent post-glacial colonization of these two areas, with possible founder effects.

In comparison with plants, much fewer animal species with disjunct alpine distributions have been analysed so far. A good example, resembling patterns already found in several plant species, was provided by allozyme polymorphisms in the butterfly *Erebia epiphron* (Schmitt et al. 2006). The lineage of *E. epiphron* from the Northern Alps is shared with the Jeseník population in Northern Czech Republic, thus strongly supporting a glacial link between the Northern Alps and the more Eastern Sudety Mountains. However, being currently separated by hundreds of kilometres from the Alps in a geographically small mountainous area, the *E. epiphron* populations in the Jeseník apparently represent a relic of a formerly wider distribution of the species. A link between the Western Alps and the Pyrenees is suggested by a genetic lineage shared by both regions. The Eastern Pyrenees, however, host an endemic lineage of this species underlining the independent evolution of one genetic entity most probably at the Southeastern slopes of the Pyrenees. Interestingly, the same area hosts a strongly differentiated lineage of the plant *A. halleri* (Dixon et al. 2007). Two further genetic groups in *E. epiphron* are endemic to the Southern and Eastern Alps (Fig. 1).

In summary, whereas some phylogeographic studies on species of the EMS provided evidence for highly dynamic scenarios involving unintuitive links among geographically widely separated mountain ranges (such as the link between the Eastern Alps and Corsica in *B. stellatum*, Schönswetter et al. 2005), others suggested vicariance events caused by disruptions during warm stages of the Pleistocene, resulting in splits of varying depths (shallow: e.g., *O. campestris*, Schönswetter et al. 2004a; deep: e.g., *H. uniflora*; Mráz et al. 2007).

2.2 Montane Species

Montane species show strong ecologic affinities to the forest belt habitats of the EMS and therefore occur at lower altitudes than the alpine species. However, this biogeographical group is much less studied than the one of alpine disjunct species.

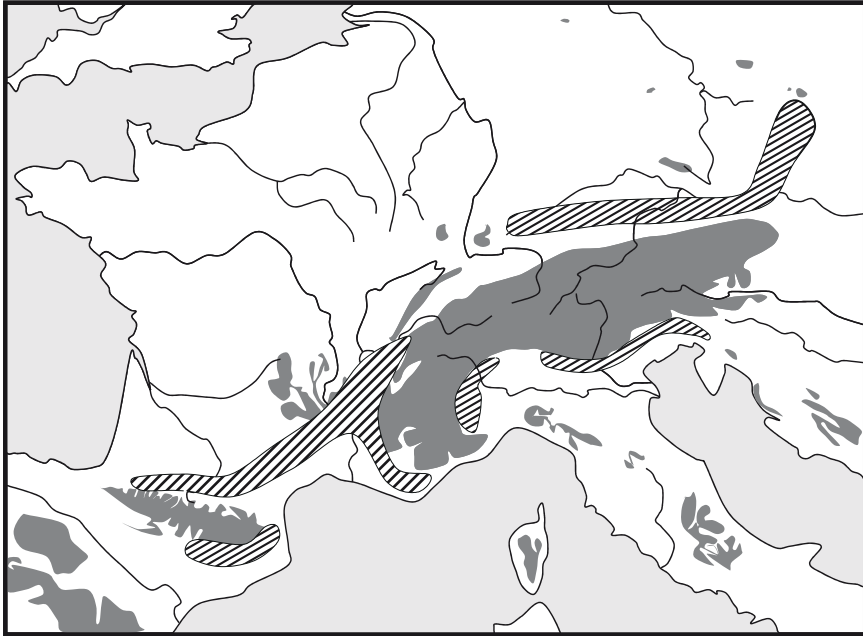


Fig. 1 Hypothetical distribution patterns of the alpine disjunct butterfly *Erebia epiphron* in Western Europe during the last glaciation. Redrawn from Schmitt et al. (2006)

A good example for a widespread montane species is represented by the butterfly *Erebia euryale*, which is a character species of the mountain forest biome of Southern Europe (Sonderegger 2005). Schmitt and Haubrich (2008) analysed allozyme patterns of 11 populations from four EMS (Pyrenees, Alps, Southern Carpathians, Rila) and found four well-supported groups (i.e., Pyrenees, Western Alps, Eastern Alps and Southeastern Europe, represented by Southern Carpathians and Rila). The genetic diversity of the populations was the highest in the Southeastern European group and decreased step-wise towards the West. Interestingly, the populations from Bulgaria and Romania were almost identical; therefore, the authors assume that they were not separated during the last ice age. In contrast, the differentiation among the three Western Alpine populations was considerable. Consequently, (1) the most important refugial area for this species has been located in Southeastern Europe including at least parts of the Carpathians and the Bulgarian mountains, (2) important refugial areas existed at the Southeastern or Eastern edge of the Alps, (3) scattered populations survived along the Southwestern Alps, and (4) relatively small populations have persisted at the foothills of the Pyrenees (Fig. 2). More studies in species of this distribution type are urgently needed to clarify whether the phylogeographic structure found in *E. euryale*, a character species of the European mountain forest biome, is representative for this biome as a whole or not.



Fig. 2 Hypothetical distribution pattern of the montane disjunct butterfly *Erebia euryale* in Europe during the last glaciation. Note that these centres only refer to the ones detected in this survey; thus, further centres of survival are possible and reliable, e.g., in peninsular Italy. Redrawn from Schmitt and Haubrich (2008)

2.3 *Dinodal Mountain Species*

Species of headwaters of mountain areas are often classified as belonging into an own biogeographic unit, the dinodal (Malicky 1983, 2000). Due to their water dwelling larvae, many Trichoptera species are considered part of this group. The most extensive genetic study of mountain species in this unit was performed on the mitochondrial COI gene of the caddisfly *Drusus discolor* (Pauls et al. 2006), which occurs in the mountain areas of Southern and central Europe.

No close relationships among mountain systems were detected (i.e., strongly differentiated endemic genetic lineages were detected in the Cantabrian Mts., Pyrenees, Massif Central, Eastern Sudety Mts., Tatra, Eastern and Southern Carpathians, as well as the high mountain systems of the Balkan Peninsula). Thus, long-lasting isolation and survival of populations in all these mountain systems over several glacial and interglacial cycles is the most likely scenario, and the strong liaison of the *Drusus* larvae with cold headwater mountain streams might have successfully impeded the exchange of individuals between different high mountain systems throughout time. Genetic differentiation and structuring in *D. discolor* had some similarities with the one observed in the mountain forest species

E. euryale (Schmitt and Haubrich 2008), i.e., a Western and an Eastern Alpine lineage, an endemic Pyrenean group, and endemic lineages in Southeastern Europe.

Interestingly, in *D. discolor* all relic populations from the low mountain ranges of central Germany (i.e., Rothaargebirge, Rhön, Harz, Thüringer Wald, Fichtelgebirge, Erzgebirge) share the same genetic lineage endemic to this region. This underlines the inference of an independent centre of survival and differentiation in this region, followed by post-glacial retraction to these mountain areas from lower areas. The same phenomenon was observed for the Jura, Vosges, and Black Forest populations. Finally, the populations from the Bohemian Massif harbour the Eastern Alps lineage, thus giving evidence for a Würm glacial link between these two adjacent regions.

The phylogeographic patterns observed in *D. discolor* show two interesting characteristics: (1) Different high mountain systems do not share closely related lineages, thus rejecting the hypothesis of continuous lowland areas between such widely separated mountains during glaciations; (2) Lower mountain ranges being in some geographic proximity to each other share haplotypes of the same genetic lineage, thus supporting the idea that the lower areas between them allowed high levels of gene flow at least during the last glaciation. Maybe the intermediate lowlands even are the refugia for such genetic lineages.

Another representative of headwaters of mountain areas is the freshwater flatworm *Crenobia alpina*. Allozyme electrophoresis and mtDNA sequencing of this species in the Eastern Alps and Germany unravelled a considerable number of strongly differentiated genetic lineages with their divergence maybe dating back as far as the late Tertiary. Most of these lineages most probably survived the glaciations of the Alps in small peripheral refugia to which some of them might still be restricted. Several of these refugia had their most likely location at the Northern margin of the Alps (Brändle et al. 2007).

3 Arctic-Alpine Species

Arctic-alpine distribution ranges comprise the arctic as well as the alpine belt of more Southern mountain ranges. Typically, arctic-alpine distributions are large and often encompass the entire Northern Hemisphere (circumpolar distribution); more restricted ranges are, e.g., amphi-Atlantic or amphi-Pacific (Abbott and Brochmann 2003). The last few years have seen increasing interest in phylogeographic studies of arctic-alpine higher plants, which are by now the doubtlessly best studied group. In the following, we focus on the relationships between the disjunct distribution areas of arctic-alpine taxa in the EMS and their main distribution area in the Arctic.

A close relationship between the central and Northern European populations of a species appears intuitively self-evident and has often been suggested by classical biogeographers (e.g., Vierhapper 1918; Holdhaus 1954; de Lattin 1967; Ozenda 1988). Good examples for such a connection are *Ranunculus glacialis* (Schönswetter et al. 2003), *Arabis alpina* (Ehrich et al. 2007), and *Veronica alpina* (Albach et al. 2006),

which all colonized the North Atlantic region from source populations in the Alps. *Dryas octopetala* likely colonized Northern Europe from source populations located between the Scandinavian ice shield and the Alps (Skrede et al. 2006). In contrast, the Scandinavian populations formed monophyletic groups in *Minuartia biflora* (Schönschwetter et al. 2006b) and *Carex atrofusca* (Schönschwetter et al. 2006a), indicating that Northern European and Alpine populations have been separated for a certain period of time. In *Carex bigelowii* (Schönschwetter et al. 2008), the single Alpine (meta-)population has strong links to the phylogeographical group dominant in the Hercynic mountains, the Tatras, Scandinavia, Iceland, and Scotland. The Hercynic populations were genetically variable, while only a few clones were detected in the Alps, indicating a strong founder effect. Whereas the lack of phylogeographic structure within the four detected phylogeographic groups of *Juncus biglumis* did not allow tracing the closest relatives for Alpine and Scandinavian populations (Schönschwetter et al. 2007), *Ranunculus pygmaeus* populations from the two latter areas have their closest relatives on the Taymyr Peninsula in Northern Siberia and in the Urals, respectively, (Schönschwetter et al. 2006b). In *Comastoma tenellum* (Schönschwetter et al. 2004b), two unrelated lineages were found in the Alps. The by far most common one was endemic to the Alps, while the second, encountered only in two Eastern Alpine populations, exhibited unresolved relationships to Carpathian and Scandinavian populations. Thus, this species has apparently colonized the Alps at least twice.

Similar arctic-alpine distribution patterns like in plants are also observed in many animal species. Holdhaus (1954) listed several dozens of invertebrate species with this distribution pattern in Europe in his seminal monograph on the legacy of the Pleistocene glaciations preserved in contemporary animal distributions. However, while most molecular studies are from plants, mitochondrial sequence variation has been studied in not more than three arthropod taxa of this disjunction type until now.

An illustrative example is provided by wolf spiders of the *Pardosa saltuaria* group (Muster and Berendonk 2006). This is a complex of six closely related species (Wunderlich 1984; Marusik et al. 1996) whose taxonomic status needs revision in the light of the recent genetic findings. The species group is patchily distributed from the Western Palearctic over Siberia to the Altai (Fig. 3a). Focussing on the European range, Muster and Berendonk (2006) found three clades of deep mitochondrial divergence, i.e., a Pyrenean clade, a Balkan clade, and a “Northern clade.” The latter included Scandinavia, the Alps, the Carpathians, the Giant Mountains, and the Bohemian Forest. Recent results from a nuclear rDNA marker (spanning ITS1, 5.8S rDNA, ITS2) generally confirmed this pattern of genetic divergence (Muster et al. unpublished). A detailed population genetic analysis using the information of both loci (mitochondrial and nuclear) in a coalescent-based Bayesian Markov chain Monte Carlo (MCMC) framework (Hey and Nielsen 2007) revealed a pattern of extensive but differential late glacial gene flow among Northern clade areas (Muster et al. 2009). The inferred gene flow was mainly unidirectional with a prevailing direction from the North to the South.

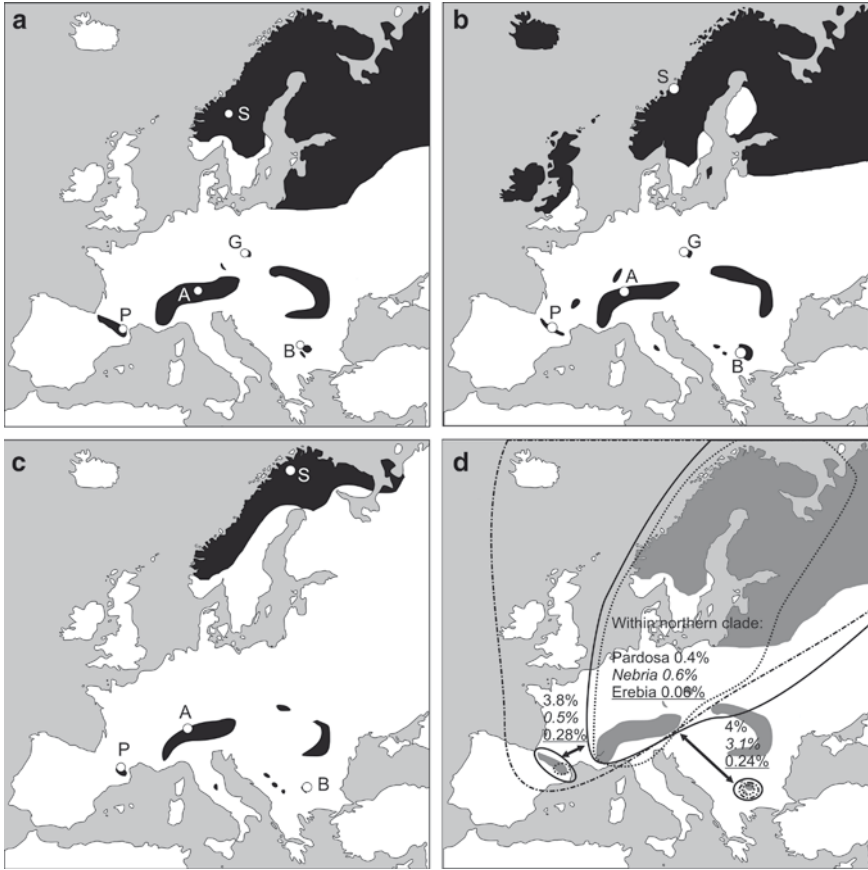


Fig. 3 European distribution areas and sampling localities of three arctic-alpine invertebrates: the wolf spiders of the *Pardosa saltuaria* group (a) redrawn from Muster and Berendonk (2006), the ground beetle *Nebria rufescens* (b) modified from Holdhaus and Lindroth (1939), and the butterfly *Erebia pandrose* (c) modified from Varga (1971). The white dots indicate the sampling locations. Abbreviations: A Alps; B Balkans; G Giant Mountains; P Pyrenees; S Scandinavia. In Fig. 3d the geographic extension of major mitochondrial clades is shown, together with the Kimura 2 parameter distance (in %) between clades and within the Northern clade. Solid line *Pardosa saltuaria* group, chain line *N. rufescens*, dotted line *Erebia pandrose*

In order to test the phylogeographic hypothesis derived from the wolf spider data, preliminary results from two further arctic-alpine arthropod taxa are presented here. The ground beetle *Nebria rufescens* (Fig. 3b) occupies an even larger arctic area than the *Pardosa* spiders and includes North America (Holdhaus 1954). The area of the butterfly *Erebia pandrose*, on the other hand, is mainly restricted to Europe (Fig. 3c), with a few populations in the mountains of Central Asia (Cupedo 2007). Within Europe, the distributions of these species are also different (Fig. 3a–c), with *N. rufescens* resembling more the boreomontane distribution type of de Lattin

(1967), as indicated by occurrences on the British Isles and in some rather low mountain ranges. In marked contrast, *E. pandrose* shows the typical arctic-alpine disjunction sensu de Lattin (1967), and even in Scandinavia the species' range is limited to the mountains and the far North, while it is restricted to the highest elevations in the Southern European mountains.

In a pilot study, Muster et al. (2009) sequenced the complete mitochondrial ND1 gene from five individuals of each of four (in *E. pandrose*) and five populations (in *N. rufescens*) as shown in Fig. 3. To allow the direct comparison of the level of genetic variation, the data set of the wolf spiders was reduced to the first five sequences of each of five similar areas. Both striking similarities and idiosyncratic differences in the resulting genetic structures were found. First, the overall level of sequence divergence was highly different (K2P-distance: *Pardosa* 2.4%, *Nebria* 1.3%, *Erebia* 0.2%) despite the fact that identical genes in co-distributed species were investigated. Analysis of molecular variance (Excoffier et al. 1992, 2005) clearly showed that the populations in the Southern mountains contributed disproportionately to the overall genetic differentiation of these taxa.

Despite the different life histories and migration abilities in these three taxa, great similarities in the genetic structures existed (Fig. 4). Most importantly, the haplotypes from the Balkans formed a distinct and highly supported clade in all three study systems. Another common feature was the low divergence among Scandinavia, the Alps, and several rather low Central European mountain ranges (Hercynian Mountains), which always clustered in a “Northern clade” with little geographic structure (except for *N. rufescens*, where each area has its own unique mutations).

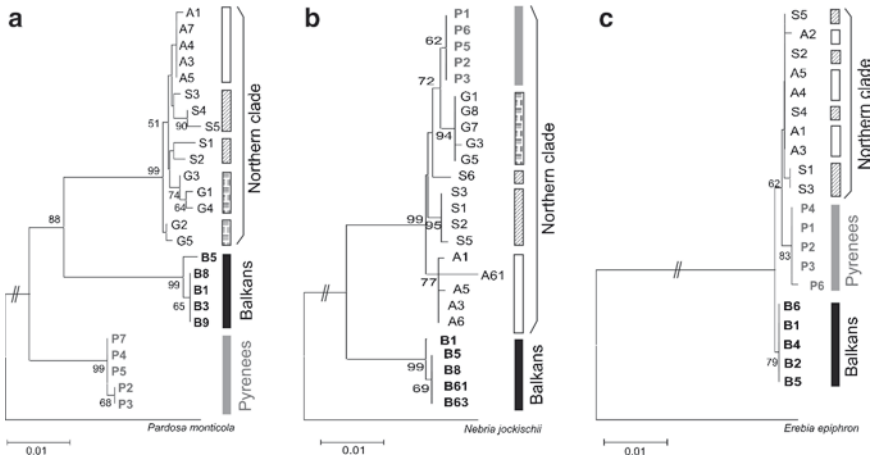


Fig. 4 Neighbour-joining trees showing the phylogenetic relationships of 25 individuals of the *Pardosa saltuaria* group (a), 25 individuals of *Nebria rufescens* (b), and 20 individuals of *Erebia pandrose* (c). All three trees are shown on the same scale, highlighting the different degree of overall sequence divergence. Bootstrap values >50% from 1,000 replicates are shown at the nodes. Letter abbreviations are the same as in Fig. 3

The position of the Pyrenees differed among the investigated taxa. While the Pyrenean haplotypes formed a clade as distinct from the Northern populations as the Balkan clade in *Pardosa* and *Erebia*, the Pyrenees clearly fell within the Northern clade in *Nebria*.

It is most likely that the populations from Scandinavia, the Alps, and the Hercynian Mountains are descendants of large populations that have dwelled in the periglacial tundra belt during the last glaciations, or at least that substantial levels of late glacial gene flow among mountain ranges occurred. Similarly, allozyme data from the diving beetle *Hydroporus glabriusculus* suggest a common late glacial origin of the British and the Scandinavian populations from source populations South of the Northern European ice sheet (Bilton 1994). In the *Nebria* beetles and in the arctic-alpine burnet moth *Zygaena exulans* (Schmitt and Hewitt 2004), such late glacial connections obviously existed also between the Alps and the Pyrenees. Thus, the traditional concept of enormous continuous distributions in the periglacial tundra belt during the glaciations (Holdhaus 1954; de Lattin 1967) could be partly corroborated. On the other hand, the Balkans and in some taxa also the Pyrenees have been isolated, and populations there consequently evolved independently for fairly long periods of time, probably since several glacial cycles. They thus represent old relic populations of high conservation importance. Altogether, the populations from disjunct parts of the distribution areas of arctic-alpine disjunct arthropods can be regarded as relics, which originated at very different time horizons.

4 Relics or not Relics: That's the Question

The genetic analyses of different species with alpine and arctic-alpine disjunct distribution patterns unravel a great variety of different biogeographical patterns and considerable differences in the time frames of the vicariance and/or dispersal events. Most often, separations in arctic-alpine species between the Northern populations and the high mountain systems in central and Southern Europe (often the Alps) are recent (i.e., post-glacial) phenomena. In alpine disjunct and in arctic-alpine species, adjoining high mountain systems often own the same genetic lineage (as, e.g., shown by multiple genetic links between the Western Alps and the Pyrenees, the Eastern Alps and the Carpathians, and the Southeastern Alps and the Dinaric mountain systems), thus underlining a recent (in most cases post-glacial) vicariance or dispersal event in the respective genetic lineage. A similar situation is often found in high and low mountain systems in geographic proximity (e.g., Northeastern Alps and Bayerischer Wald) or in neighbouring low mountains, e.g., in Germany. These areas thus harbour young relic populations that may result from large zonal distributions of such taxa in the tundra belt during the last ice age.

The most basal and thus oldest splits in arctic-alpine and alpine disjunct species are commonly found in the Southernmost European high mountain systems with typical alpine zonation. The Cordillera Cantábrica in this respect represents one important

mountain area for the survival of old genetic entities, but also the high mountain systems of the Balkan Peninsula and to some degree the Pyrenees show importance as areas for the survival of old lineages, which can be interpreted as relics of cold stages of a more distant past.

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