Chapter 3
Molecular Biogeography of the High Mountain Systems of Europe: An Overview

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Abstract The biogeography of alpine and arctic–alpine species is complex, much more complex than thought until relatively recently. Alpine species survived glacial periods mostly within refugia in close proximity to the mountains where they are found today. One mountain range can be colonised from several glacial refugia, while one refugium can be the source of colonisation of more than one mountain range. The zonal distributions in the glacial cold steppes are only of importance for arctic–alpine species. Their arctic ranges normally derive from there, while the southern mountains were colonised from there or from near-mountain refugia as in the cases of the alpine species.

Keywords Alpine disjunct species · Arctic–alpine disjunctions · Refugia · Range dynamics · Nunataks · Biogeography · Phylogeography

3.1 Introduction

Europe is a continent characterised by a larger number of different high mountain systems, especially in its southern parts. These mountains vary considerably in their size and in their height. By far the highest and largest mountain system in Europe is the Alps, if the even higher Caucasus that forms part of the border with Asia is not considered. The Pyrenees and the Scandes also represent large systems of continuous high mountains. This applies less to the Carpathians, which have larger stretches along their length of 1300 km without true high mountain habitats (i.e. the alpine zone or oreal, naturally not covered by forests). Furthermore, many generally

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small blocks of high mountain areas are scattered through the southern European peninsulas, like those of the Balkans, the Apennine Peninsula and Iberia. Finally, isolated and small high mountain systems are found elsewhere, such as the Massif Central, the Vosges, the Harz and some parts of the Sudety Mountains. Accordingly, Europe can be visualised as a highly diverse archipelago composed of mountain islands of very different sizes and very different degrees of isolation embedded in a matrix of lowland areas. This complexity of high mountains translates into a high diversity of their biogeographic structures (Fig. 3.1).

In this chapter, I therefore give a short overview of the biogeographic structures of the high mountains of Europe. On the one hand, I focus on the biogeographic structures within single mountain systems, on the other hand, I work out the different biogeographic links among different high mountain systems. A special focus of this chapter is on molecular analyses, these being highly suitable for unravelling biogeographic structures. Most of the examples presented refer to invertebrates and plants. Based on these genetic patterns, a comprehensive analysis of range dynamics in high mountain ecosystems in space and time is presented.

Before considering the more detailed biogeographic structures of high mountain species, we have to define two fundamental distribution types, the arctic–alpine and the alpine disjunct species. Arctic–alpine species are distributed in the alpine belt of high mountain systems in the South and in the Arctic realm and have long been interpreted as having resulted from the postglacial disjunction of an extended zonal distribution during the last ice age, with retreat to high altitudes in the South and high latitudes in the North (Scharff 1899; Holdhaus 1954). Alpine disjunct species are lacking in the tundra belt of the North, but are distributed in several of the southern high mountain systems in the subalpine and alpine belt. The distributional

Fig. 3.1 Centres of genetic endemism of alpine elements. The *bold line* indicates the Alps, the most important centre of alpine endemism in Europe. *Continuous lines* highlight further mountain ranges with high numbers of genetic endemism. *Broken lines* indicated mountain systems with frequent genetic endemism, while *dotted lines* mark those mountains with just few cases of genetic endemism. Map based on Google Maps

group of arctic–alpine species must not be mixed up with boreo-montane species, which have a somewhat similar distribution, but are confined to the montane and subalpine forests in the mountains and to the boreal forest belt in the North (Schmitt 2009); furthermore, these elements are also found in the forests of the lower European mountain ranges without an alpine belt. Similar differences exist between alpine disjunct and montane disjunct species. As boreo-montane and montane disjunct species are not true high mountain elements, they are not addressed in this chapter.

3.2   Different Genetic Lineages Within High Mountain Systems

Following the picture of an island archipelago of high mountain systems in the 'European Sea of Lowlands', the Alps are the largest 'island', or even a 'continent' surrounded by other mountain 'islands'. As such, the Alps harbour a large number of endemic high mountain species, some of them distributed throughout these mountains, others with rather narrow distributions in some parts of the Alps, with many of these distributions located in the south-western or south-eastern Alps (Varga and Schmitt 2008). Although some of these geographically restricted endemics are genetically impoverished (e.g. *Erebia sudetica inalpina*; Haubrich and Schmitt 2007), perhaps as a result of constantly low numbers of individuals and the hereby resulting genetic bottlenecks, others are genetically even more diverse than their lowland relatives (e.g. *Coenonympha darwiniana, C. macromma*; Schmitt and Besold 2010). This high genetic diversity might be the consequence of simple uphill—downhill shifts within one region as conditions changed from interglacial to glacial and vice versa without major genetic bottlenecks.

In most cases, more widely distributed Alpine species comprise several genetic lineages, which can be 'translated' into several centres of differentiation, i.e. refugia that later served as centres of dispersal. The classic pattern, repeated with little variation in numerous plant and animal species (e.g. Schönswetter et al. 2002, 2003a, b, 2004a; Stehlik et al. 2002a; Tribsch et al. 2002; Margraf et al. 2007; Thiel-Egenter et al. 2009), is of four genetic groups localised in the south-western, western, central and eastern Alps (Fig. 3.2a). This pattern is assumed to have evolved in four glacial refugia in the lower and thus unglaciated parts of the south-western Alps, south of the western and central Alps as well as east of the eastern Alps, i.e. in southern peripheral refugia. Some species show a pattern of fewer refugia, with just an eastern and a western genetic group (Fig. 3.2b), and thus only two centres of survival (e.g. Pauls et al. 2006; Haubrich and Schmitt 2007; Schmitt and Haubrich 2008). However, some species even had peripheral refugia north of the Alps (e.g. *Erebia epiphron*; Schmitt et al. 2006) or survived (additionally or even exclusively) on nunataks (i.e. ice-free areas surrounded by the Alpine glaciers), as proven for several plant species (e.g. Stehlik et al. 2001, 2002b; Holderegger et al. 2002; Stehlik 2002).

Fig. 3.2 Genetic structures in the Alps. **a** The most common pattern of genetic differentiation in the Alps is one of the four different lineages. **b** However, a reduction of this pattern, e.g. to just two lineages, is frequently observed. Maps based on Google Maps

In the Pyrenees, we also observe numerous species with more than one genetic lineage within these mountains. However, the most often observed number of different lineages in animals and plants found here is two (e.g. Kropf et al. 2002, 2003; Schmitt et al. 2006; Lauga et al. 2009), translating into only two glacial refugia (and differentiation centres) in close proximity to the Pyrenees and not four as in the much bigger Alps. Higher numbers of different lineages in the Pyrenees

are rare, but have been shown, e.g. for *Rhododendron ferrugineum* with five (Charrier et al. 2014) and *Cardamine alpina* with a number of lineages that is difficult to quantify (Lihová et al. 2008).

Similarly to the Pyrenees, two genetic lineages were frequently observed in the Carpathians, with one of these in the mountains' northern part and the second in the eastern and southern regions (e.g. Pauls et al. 2006; Mráz et al. 2007; Ronikier et al. 2008a; Ujvárosi et al. 2010; Theissinger et al. 2012). An additional endemic genetic lineage in the Apuseni mountains (island mountains in the Carpathian Basin) was obtained for the stonefly *Arcynopteryx dichroa* (Theissinger et al. 2012). In *Soldanella* species, two major lineages were distinguished, but in contrast to the above pattern, the northern lineage also included the eastern Carpathians and thus was geographically more extended. Furthermore, some geographically restricted endemic species are known in this group (Zhang et al. 2001), hence underlining that the biogeographic history of the high mountain elements of the Carpathians can be more complex than the two-refugia theory.

The Balkan Peninsula presents a complex pattern of numerous small blocks of high mountain systems in relatively close geographic proximity to each other. Unfortunately, this area is still poorly studied phylogeographically. Morphological studies in butterflies, however, strongly support an east-west split for several high mountain species (Varga 1975), speaking for long lasting separation of the mountain areas east and west of the Central Balkan Depression. This split was supported by a genetic study of the stonefly *Arcynopteryx dichroa* (Theissinger et al. 2012), but the butterfly species *Erebia ottomana* and *Coenonympha rhodopensis* showed relatively uniform genetic constitutions throughout the area, thus supporting the hypothesis that in these cases gene flow connected populations throughout the Balkan mountains during glacial periods (Louy et al. 2013, 2014a).

3.3 Genetic Links Between High Mountain Systems

As Europe's most important high mountain system, the Alps have multiple biogeographic links to all neighbouring mountains (Fig. 3.3; Schmitt 2009). In a number of cases, in both animals and plants, identical genetic lineages exist in the south-western Alps and in the Pyrenees (e.g. Kropf et al. 2002; Martin et al. 2002; Schönswetter et al. 2002, 2004b; Gaudeul 2006; Schmitt et al. 2006; Reisch 2008). This often repeated pattern is in most cases thought to be the result of glacial distributions in the hilly areas of southern France and postglacial retreat into the adjoining mountain ranges, leading to a rather young vicariance event, which is still not mirrored in the genetic make-up of the now disconnected population groups. Quite similar phenomena, with similar biogeographic explanations, are known between the north-eastern Alps and the Tatra mountains (e.g. Kropf et al. 2003; Muster and Berendonk 2006; Schönswetter et al. 2006; Suda et al. 2007; Paun et al. 2008; Triponez et al. 2011; Schmitt et al. 2014) as well as the south-eastern Alps and the north-western Balkan mountains (Triponez et al. 2011; examples for

Fig. 3.3 Different high mountain systems share identical genetic lineages in many cases. *Bold arrows* indicate that such a sharing is very commonly observed. *Solid arrows* show that this pattern is frequent, while *dotted arrows* indicate relatively few known cases. The *arrows* indicate the dominating direction of exchange, with *two-sided arrows* assuming equilibrium of exchange between mountains. Map based on Google Maps

boreo-montane species: Ronikier et al. 2008b; Kramp et al. 2009). Although genetic data from the western Balkan mountains are generally scarce, it is worth noting that the south-eastern Alps—western Balkan mountains link is frequently supported by the existence of taxa that only occur in these two regions (e.g. Holdhaus 1954; Varga and Schmitt 2008; Schönswetter and Schneeweiss 2009; Tshikolovets 2011).

Focussing now on the smaller mountain ranges of Europe and their biogeographic links, we start with the Massif Central in France. This mountain range sometimes even possesses its own endemic genetic lineages, supporting the idea of independent glacial refugia in its geographic proximity without recent genetic exchange, neither with the western Alps nor with the Pyrenees (e.g. Pauls et al.

2006; Triponez et al. 2011; Kropf et al. 2012). Genetic links are known with the Pyrenees (e.g. Descimon 1995; Ronikier et al. 2008b (however, these two species are not typical alpine elements); Schmitt et al. 2014) and the western Alps (Kramp et al. 2009 (but referring to a boreo-montane species); Triponez et al. 2011). However, the latter link seems to be less frequent than the former, thus supporting the idea that the isolating power of the Rhone valley was stronger than that of the hilly regions between the Massif Central and the Pyrenees.

The Apennines, a long stretch of mountains with some interspersed insular high mountain areas, harbours some high mountain endemics, especially in its central and southern parts (e.g. the plants *Adonis distorta, Androsace mathildae, Aquilegia bertoloni, Soldanella calabrella*), hence supporting the evolutionary independence of this area. However, many taxa also show high similarity with counterparts in the south-western Alps and offer evidence of glacial gene flow between these mountain ranges during cold phases (Moore et al. 2013; Louy et al. 2014b). A particularly interesting case involves representatives of the beetle species complex *Oreina alpestris/speciosa*. In this example, the populations of the northern Apennines show much higher similarity with ones from the south-western Alps than with those of the central Apennines (Triponez et al. 2011), thus indicating several colonisation waves from the south-western Alps to the Apennines, with the older ones preserved in the more southern mountains, the younger ones more to the North.

The mountains north of the Alps, if they have high mountain species *sensu stricto* at all, in most cases share their genetic lineages with the Alps, i.e. they are derived from the same refugia as the nearby Alpine populations (e.g. Pauls et al. 2006; Schmitt et al. 2006; Mardulyn et al. 2009; Triponez et al. 2011; Alvarez et al. 2012; Charrier et al. 2014). Exceptions to this rule are the caddisfly *Drusus discolor* with a genetic lineage restricted to Jura, Vosges and Black Forest (Pauls et al. 2006) and the butterfly *Erebia manto* with the genetically strongly differentiated taxon *vogesiaca* endemic to the Vosges (Schmitt et al. 2014).

The Cantabrian mountains, being the westernmost range with alpine zonation, also harbour some endemic lineages, thus underlining their independent biogeographic status (e.g. Kropf et al. 2003; Pauls et al.2006). In the majority of cases, however, close genetic links with the Pyrenees exist, indicating the presence of glacial refugia between both mountain ranges and resultant genetic intermixing (e.g. Kropf et al. 2002; Vila et al. 2011).

The Carpathians and Balkan high mountain systems have in many respects distinct alpine floras and faunas. Nevertheless, they sometimes share identical typical species, such as the butterflies *Erebia melas* and *Coenonympha rhodopensis* (Tshikolovets 2011). However, even identical genetic lineages were recorded in some cases, thus presenting evidence for a recent (most likely Würm glacial) exchange between both regions. This was for example shown for the mountain forests butterfly *Erebia euryale* (Schmitt and Haubrich 2008) and the boreo-montane plant *Ranunculus platanifolius* (Stachurska-Swakon et al. 2013). For the stonefly *Arcynopteryx dichroa*, distinct genetic lineages exist in both areas, but rare occurrences of the Carpathian haplotype group in the Bulgarian high

mountain systems call for a recent gene flow in North-South direction (Theissinger et al. 2012).

Although some similarities exist between the alpine faunas and floras of the Apennines and the Balkan high mountain systems (e.g. shared endemic plants such as *Aurinia rupestris, Leontopodium nivale, Saxifraga glabella*), the exchange between these two mountain areas might in most cases not be very recent, as in most of the examples referred to above (cf. Schönswetter and Schneeweiss 2009; Louy et al. 2013).

3.4 Arctic–Alpine Disjunction

In arctic–alpine species, i.e. species with occurrences in the high mountain ranges in the South and in the Arctic, wide zonal ice age distributions in the periglacial steppe region with postglacial retreats uphill and polewards have classically been assumed (Holdhaus 1954). Following this assumption, the disjunction between northern and southern populations dates only to the postglacial and should not have resulted in corresponding differentiations, so that mostly similar populations should be found in the North and the South. In support of this theory, highly similar genetic make-up of northern and southern populations has frequently been recorded (e.g. Schönswetter et al. 2003c, 2008; Albach et al. 2006; Muster and Berendonk 2006; Skrede et al. 2006; Ehrich et al. 2007; Reisch 2008; Schmitt et al. 2010).

In many arctic–alpine species, only part of the southern mountain populations is similar to the ones from the Arctic, while others are not. These patterns call for additional perialpine glacial refugia in close proximity to the mountain ranges (as exclusively in the alpine disjunct species) supplementing the extended zonal distributions. In most of these cases, the Alps and the Arctic share identical genetic lineages, which were thus apparently derived from this periglacial steppe region. Many species occurring in the Pyrenees and the Tatras also share these lineages (e.g. Muster and Berendonk 2006; Schmitt et al. 2010). However, lineages in the Alps do not always have a northern origin. For example, populations of *Gentiana nivalis* derived from the extended zonal ice age distribution were detected in the North, the Pyrenees and Carpathians, while three other lineages exist in the Alps, calling for three perialpine glacial refugia in addition to the zonal range (Alvarez et al. 2012). In the stonefly *Arcynopteryx dichroa*, the northern clade is limited in the South to the Black Forest, thus supporting the existence of an extended zonal range of the species, but its limited impact on the postglacial recolonisation of the southern mountains indicates that these were mostly colonised from glacial refugia in their foothills (Theissinger et al. 2012).

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