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## RESEARCH PROJECT

# Molecular biogeography and population genetics of alpine plant species

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### Summary

1 There is a long-standing debate about the fate of the mountain flora of the Alps during Quaternary glaciation. Two main possibilities of glacial survival of alpine plant taxa have been proposed, namely the *tabula rasa* and the nunatak hypotheses. However, few molecular studies testing these two hypotheses in alpine plant species have been carried out so far.

2 According to the *tabula rasa* hypothesis, alpine plant species did not survive *in-situ*, but re-immigrated from one or a few large peripheral or periglacial refugia. In contrast, the nunatak hypothesis implies survival of alpine plant species on several small, isolated, high-alpine nunataks within the Alps. Early biogeographic studies suggested exact locations of peripheral refugia and nunataks, as well as precise migration routes. They provide clear hypotheses on the biogeography of alpine species, which could be tested with molecular techniques.

3 Two independent research projects are presented which have the aim to investigate the phylogeographic patterns of four alpine species.

4 *Erinus alpinus* is described to have re-immigrated into the Alps from a western peripheral refugium. This makes *E. alpinus* a model for a test of the *tabula rasa* hypothesis. The high alpine distribution of *Eritrichium nanum* covers many areas with postulated nunataks and seems suitable to test the nunatak hypothesis. *Rumex nivalis* does not fit to either of these two hypotheses. The species shows a decrease in population abundance in an east-western direction, which points to immigration from north-eastern peripheral refugia. However, the species' disjunct distribution and affinity to extreme habitats could also indicate glacial survival on nunataks. *Saxifraga oppositifolia* is common and widespread throughout the Alps. Molecular results from Northern Europe support both *in-situ* survival and re-immigration. It is not possible to propose an exact hypothesis on this species' biogeographic history in the Alps based on its present-day distribution. This ambiguity is probably shared by most common alpine species. The comparison of the

results on *S. oppositifolia* with those of the above three species may nevertheless enable an evaluation of the former's phylogeography in the Alps.

5 The proposed molecular projects will be among the first to investigate general biogeographic patterns of alpine plants and to provide population genetic data from many alpine populations on a large geographic scale.

**Keywords:** alpine species, glacial refugia, historical biogeography, nunataks, population genetics, postglacial colonisation

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## Introduction and biogeographic background

### MOLECULAR BIOGEOGRAPHY AND PHYLOGEOGRAPHY

The question how geological and climatic events have influenced the evolutionary diversification of organisms in space and time is the major topic of historical biogeography (Avice 1994; Comes & Kadereit 1998). The impact of historical biogeography on the understanding of present-day distribution areas and regional diversities has been strengthened by the use of diverse molecular techniques (e.g. Soltis *et al.* 1997; Taberlet *et al.* 1998). The genetic patterns observed are usually explained by geotectonical and paleoclimatical events at the end of the Tertiary (25–2.5 million years ago; Blondel *et al.* 1996) or by climatic changes during glacial, interglacial and postglacial periods of the Pleistocene (2.5–0.01 million years ago; Hewitt 1996).

In plants, many biogeographic studies have focused on postglacial spread out of peripheral or periglacial refugia or the possibility of long-term survival in refugia within glaciated areas (e.g. on nunataks). In particular, the exact locations of glacial refugia and the precise courses of postglacial re-immigration routes have been evaluated. Earlier studies mainly relied on floristic distribution patterns of plant species, but geographic mapping of radio-

dated pollen spectra and macrofossils has been an invaluable tool for evaluating changes in distribution area and abundance shifts in North America and Europe (Lang 1994; Burga & Perret 1998). However, fossil data alone do not allow more than a general interpretation of the biogeographic history of plant species, because they are strongly biased towards trees, wind-pollinated plants and wetland species. Fossils of alpine plant species are especially scarce (Lang 1994). In addition, the fossil record is limited in morphological and taxonomic resolution and does often not offer the possibility to assign material to species and specific evolutionary lineages or geographic subunits within species. Fossil analysis is *per se* descriptive and does not allow adequate sampling strategies to test particular biogeographic hypotheses or questions. Therefore, molecular genetic analysis is an attractive tool to investigate historical biogeography, phylogeography and microevolution (e.g. Ferris *et al.* 1995; Sewell *et al.* 1996; Strand *et al.* 1996; Bachmann 1997; Petit *et al.* 1997).

The haploid chloroplast genome is often used to investigate biogeographic questions. It is non-recombinant, mostly maternally inherited and has a low mutation rate (McCauley 1995). As a consequence, cpDNA

markers are more likely to reflect historical processes (e.g. fragmentation or expansion of the distributions, refugial isolation, genetic divergence, founder effects, migration routes) over longer time periods than biparentally inherited nuclear markers such as allozymes or RAPDs. Since intraspecific genetic variation of cpDNA has been found, these genetic polymorphisms can be used to characterise populations. In addition, effective population size for chloroplast genes is only half that of nuclear genes in an outcrossing plant species (Ennos 1994). Hence, the probability of genetic reassortment of cpDNA in glacial refugia through genetic drift should be greater than in nuclear markers, leading to substantial genetic differentiation among refugial source populations and their descendants. Nevertheless, cpDNA haplotype variation as observed in RFLPs or sequence analysis is often relatively low (Schaal *et al.* 1998; Newton *et al.* 1999), and its geographic resolution may be limited. Thus, many biogeographic questions can not be addressed using cpDNA data, especially at the regional scale. Highly resolving dominant markers like AFLPs, ISSRs and RAPDs offer realistic alternatives (Weising *et al.* 1995; Mueller & Wolfenbarger 1999).

#### PRESENT STATE OF BIOGEOGRAPHIC RESEARCH ON ARCTIC OR ALPINE PLANT SPECIES

Most molecular studies on historical biogeography or phylogeography of European plant species have dealt with genetic patterns at a continental scale. Taberlet *et al.* (1998) concluded that there is little congruence between the phylogeographic patterns of the taxa investigated so far, although the proposed postglacial colonisation routes exhibit some similarities. In contrast, high congruence between several herbaceous plants of Western North America has been found (Soltis *et al.*

1997). The north-south direction of mountain ranges in North America and the availability of refugia in the South may have caused common biogeographic and evolutionary histories between species.

The more complex situation in Europe, with centres of glaciation in Scandinavia and in the Alps and the mountain ranges of the Alps and the Pyrenees as migration barriers in longitudinal direction, is reflected by the controversy between two different scenarios of glacial survival of arctic and/or alpine plant species: the nunatak hypothesis and the *tabula rasa* hypothesis. Whereas Dahl (1987) and Abbott *et al.* (1995) invoked unglaciated areas in northern Europe, where plant species have survived the ice-ages (nunatak hypothesis), Nordal (1987), Birks (1996) and Gabrielsen *et al.* (1997) considered the total extinction of pre- or interglacial populations with subsequent re-colonisation from peripheral refugia after the retreat of glaciers (*tabula rasa* hypothesis) to be more likely. Indications of *in-situ* survival are the relatively high amount of endemism in formerly glaciated areas in Norway, the presence of numerous amphiatlantic species in Scandinavia, which do not occur in the Alps, the similarity between the subalpine-alpine floras of Iceland, the British Isles and Scandinavia (Dahl 1987) and high amounts of cpDNA-RFLP variation (Abbott *et al.* 1995). In contrast, Nordal (1987) stressed that the isolation of postglacial plant populations for 10,000–15,000 years is sufficient to create the amount of endemism observed in Norway. He concluded that immigration by long-distance dispersal after the ice-ages and subsequent evolutionary differentiation are the most probable explanations for the present genetic diversity. Birks (1996) showed that present-day ecological factors (regional climate, geology, elevation) can explain the local species richness in Scandinavia

without invoking the nunatak hypothesis. Molecular data further indicate that there has been extensive gene flow among widely distributed populations of *Saxifraga oppositifolia* during the Weichselian glaciation (115,000–18,000 years AD) in Scandinavia, and that the present nordic populations were established after massive immigration from genetically variable periglacial populations (Gabrielsen *et al.* 1997). Given the high levels of migration inferred from the latter study, eventually occurring genetic differentiation of possible nunatak populations would have been genetically swamped by postglacial immigration. Gabrielsen *et al.* (1997) thus conclude that the nunatak hypothesis is superfluous to explain the present distribution of arctic-alpine species in Northern Europe.

The intra-specific biogeographic history of common alpine plant species (thereafter used in the sense of mountain plants growing in the Alps) has only rarely been investigated with molecular methods so far. The existing studies were either done on rare or special species such as glacial relics (Bauert *et al.* 1998; D. Lang *et al.*, unpubl. data), focussed on population traits such as clonal diversity or mating structures (Bauert 1996; Steinger *et al.* 1996; Escaravage *et al.* 1998; Gugerli *et al.* 1999; von Flüe *et al.* 1999) or were interested in vicariance and taxonomic relationships on the above-species level on large geographical scales (Hungerer & Kadereit 1998). The results of these studies do not allow any broad generalisations on the intra-specific phylogeography of alpine plant species to be drawn. There are some early non-genetic, but quite detailed studies on the biogeography of alpine plants. These also referred to specific problems of the *tabula rasa* and the nunatak hypotheses or stated precise migration routes from peripheral refugia into the central parts of the Alps (Chodat & Pampanini 1902; Bri-

quet 1906; Brockmann-Jerosch & Brockmann-Jerosch 1926). These authors' hypotheses on the origin and evolution of alpine plant species were further developed by Merxmüller (discussion on the origin of numerous alpine taxa; 1952, 1953, 1954), Favarger (1958) and Hess *et al.* (1967). The main biogeographic principles such as location of nunataks or peripheral refugia in present-day species-rich areas remained the same.

Chodat & Pampanini (1902) and Briquet (1906) stressed the *tabula rasa* hypothesis for the flora of the Alps during the ice-ages, corresponding to the view of Nordal (1987), Birks (1996) and Gabrielsen *et al.* (1997) for Scandinavia, that all present-day alpine plant species had to re-immigrate from peripheral refugia outside the glaciated parts of the Alps. Chodat & Pampanini (1902) postulated a south-alpine peripheral refugium in the region between the lakes of Garda and Como (Judicarie Alps) and a west-alpine peripheral glacial refugium for the flora of the middle part (Landolt 1992) of the Alps in the Grajic and Cottic Alps. The same authors claimed that species migrated from these refugia along the southern alpine foothills. Accordingly, the valley of Valais in Switzerland was colonised from the Piedmont, i.e. Penninic Alps, Valle d'Aosta and Cogne, while the Engadine was colonised from Val Venosta (Stelvio). Briquet (1906) postulated additional refugia. He suggested a peripheral refugium in the southern Lepontic Alps, a jurassic-rhodanic peripheral refugium (to the south of Lyon and in the northern Jura mountains), and some peripheral refugia at the edge of the Northern Alps (e.g. Alpstein, Pilatus, Stockhorn). Both Chodat & Pampanini (1902) and Briquet (1906) believed that the immigration of plants along main alpine valleys (Rhône, Tyrolean Inn) was impossible because of long persistence of slowly retreating glaciers.

What are the genetic implications of the *tabula rasa* hypothesis? The peripheral refugia of Chodat & Pampanini (1902) and Briquet (1906) are geographically quite large areas. The number of surviving populations therein and their sizes were probably large. Principally, plant populations of different peripheral refugia should be genetically different due to long periods of isolation during the ice-ages. This differentiation is a result of restricted gene flow, genetic drift and, possibly, different selective pressures in peripheral refugia. As a result, lower genetic similarity among populations from different peripheral refugia than among populations descending from the same refugium and, perhaps, different private alleles should be found. In contrast, genetic similarity among populations along particular re-immigration routes into the Alps must be comparatively high. The present distribution of alpine species probably is the result of several subsequent immigration waves. Nevertheless, the sources of these waves should still be detectable by comparing the genetic variation of populations along migration paths with the genetic variation presently found in populations within peripheral refugia. Only a small fraction of the genetic variation of a peripheral refugium (source regions; Ellstrand & Elam 1993) might have migrated towards the middle parts of the Alps after glaciation. Just a genetic subsample would have reached the by then vacant localities in the Alps. This genetic "thinning", the result of recurring founder events during subsequent immigration waves, should become stronger with increasing distance from the source. Migration waves reached the central alpine regions last, and the absolute number of waves should be lower than in regions nearer to the peripheral refugia ("loi de la proximité"; Chodat & Pampanini 1902). Expectations of the *tabula rasa* hypothesis are therefore, that popula-

tions in the central parts of the Alps should be genetically less variable than populations nearer to peripheral refugia and that the genetic variation of populations at the distribution limit of a species should be lowest. During foundation of the central alpine populations, founder effects, genetic drift and inbreeding most probably played important roles, and, hence, the number of alleles and their frequencies in these populations should be different from present-day populations in peripheral refugia and populations along migratory routes.

Brockmann-Jerosch & Brockmann-Jerosch (1926) argued in favour of the nunatak hypothesis stating that it is not possible to deduce upon refugia of alpine plant species only on the basis of the locations of never glaciated areas. In fact, the present distribution of alpine plant species is often not in accordance with suggested migration routes out of peripheral refugia. Brockmann-Jerosch & Brockmann-Jerosch (1926) therefore believed in the existence of high-alpine, supraglacial, snow-free nunataks; in the central parts of the Alps the upper limit of the ice-sheet reached 2600 m a.s.l. (Hess *et al.* 1967). Populations on high-alpine nunataks could have acted as sources for re-colonisation of vacant areas after glaciation. A major argument in favour of the nunatak hypothesis is that areas with many geomorphologically induced nunataks are often areas with increased species diversity. Proposed high-alpine nunatak regions are the Monte Rosa, the valleys of Visp, the Simplon, the Rothorn-mountains near Arosa, high mountains of the Engadine and the Bernina (Brockmann-Jerosch & Brockmann-Jerosch 1926). Maps of the location of floristically deduced alpine nunatak regions in the middle part of the Alps are presently in preparation (Stehlik, in press).

High alpine nunatak populations were probably small and rare, surviving on small patches of ice-free slopes or mountain tops. They were exposed to high radiation and extreme wind conditions, which warranted snow-free conditions during the vegetation period. Regions with nunataks were discontinuously distributed with large geographic gaps between them. Populations on nunataks should thus be viewed as isolated. Long isolation, recurring bottlenecks and founder effects, followed by inbreeding and genetic drift, should have led to relatively low genetic variation in nunatak regions and to strong differentiation among populations on different nunataks (Ellstrand & Elam 1993). Nevertheless, populations on island nunataks could have stored ancient cpDNA haplotypes or gained private alleles. These genetic patterns should still be detectable among present-day populations descended from potential nunatak populations.

In general, it is expected that genetic similarities among populations should decrease with increasing geographic distance between them in both of the above hypotheses. However, the reasons for these decreases are different in the two hypotheses. In the *tabula rasa* hypothesis, genetic similarity should decrease linearly (recurring founder effects and thinning out of genetic variation along migration routes). In contrast, changes in genetic similarities among populations should be more discontinuous or even abrupt in the nunatak hypothesis.

### **The aim of the research projects**

Our projects consist of two completely independent studies. Nevertheless, they complement each other in an ideal way. The studied species were chosen in order to be representative of the alpine flora and to allow valid

generalisations on biogeographic patterns of alpine plant species (Meusel *et al.* 1965, 1978; Welten & Sutter 1982).

The aim of the first project by Stehlik, Schneller & Bachmann is to test explicit phylogeographic hypotheses on alpine species from the middle part of the Alps. Three species will be investigated for which clear biogeographic hypotheses of glacial survival were given in the literature, and an appropriate sampling strategy seems to be feasible: (1) immigration from western refugia, *Erinus alpinus*, (2) survival on high-alpine nunataks, *Eritrichium nanum*, and (3) immigration from eastern refugia or eastern nunataks, *Rumex nivialis*. AFLPs (Vos *et al.* 1995) and PCR-RFLPs of cpDNA (Demesure *et al.* 1996) will be used for molecular genetic analysis.

The second project by Holderegger & Abbott takes a different approach. It asks: is it possible to deduce upon the biogeographic history of a widespread, common alpine species by using molecular markers. Because common, widespread alpine species often exhibit no particular geographic characteristics, it is not possible to state any specific hypothesis on the biogeographic history based on their distribution patterns. The holarctic *Saxifraga oppositifolia* was chosen as a model species, since its breeding system in alpine populations (Gugerli *et al.* 1999; von Flüe *et al.* 1999) and its phylogeography in Northern Europe (Abbott *et al.* 1995; Gabrielsen *et al.* 1997) are well investigated. A whole set of molecular genetic tools is necessary to analyse different types and parts of the genome, which could contain different biogeographic information: classic RFLPs and PCR-RFLPs of cpDNA, RAPDs and oligonucleotide-fingerprinting using microsatellite probes (Weising *et al.* 1995). RAPDs were chosen to make the results comparable with those of Gabrielsen *et al.* (1997) and Gugerli *et al.* (1999).

### Species investigated, hypotheses tested and sampling strategies

Many published phylogeographic investigations on plants using molecular techniques have taken relatively few samples over large geographic distances (for references see Soltis *et al.* 1997). This does not permit an accurate evaluation of migration routes or exact location of ancient refugia. Therefore, Soltis *et al.* (1997, p. 370) concluded that "... future studies should seek to construct a regional phylogeography". The strong demand for sampling strategies that really fit the questions asked has also been emphasised by Smouse (1998). One particularly important point is that the biogeographically relevant parts of the distribution of the species investigated should be sufficiently covered. For instance, testing the *tabula rasa* hypothesis requires increased sampling along postulated migration

routes out of a peripheral refugium. Additionally, populations from alternative source regions should be analysed as well, in order to allow the falsification of the main hypothesis.

#### *ERINUS ALPINUS*: RE-IMMIGRATION FROM SOUTH-WESTERN REFUGIA

*Erinus alpinus* L. has a central and south-west European distribution (Fig. 1) and occurs on calcareous rock and rubble. It is perennial and grows in sparse mats of integrated rosettes. Brockmann-Jerosch & Brockmann-Jerosch (1926) hypothesised that *E. alpinus* survived glaciation in south-west peripheral refugia, i.e. the Grajic-Cottic Alps, since its present-day distribution does not show any disjunction in a west-eastern direction, and the species' main distribution is at subalpine elevations, which makes an *in-situ* survival of the ice-ages unlikely. Thus, *E. alpinus* had to

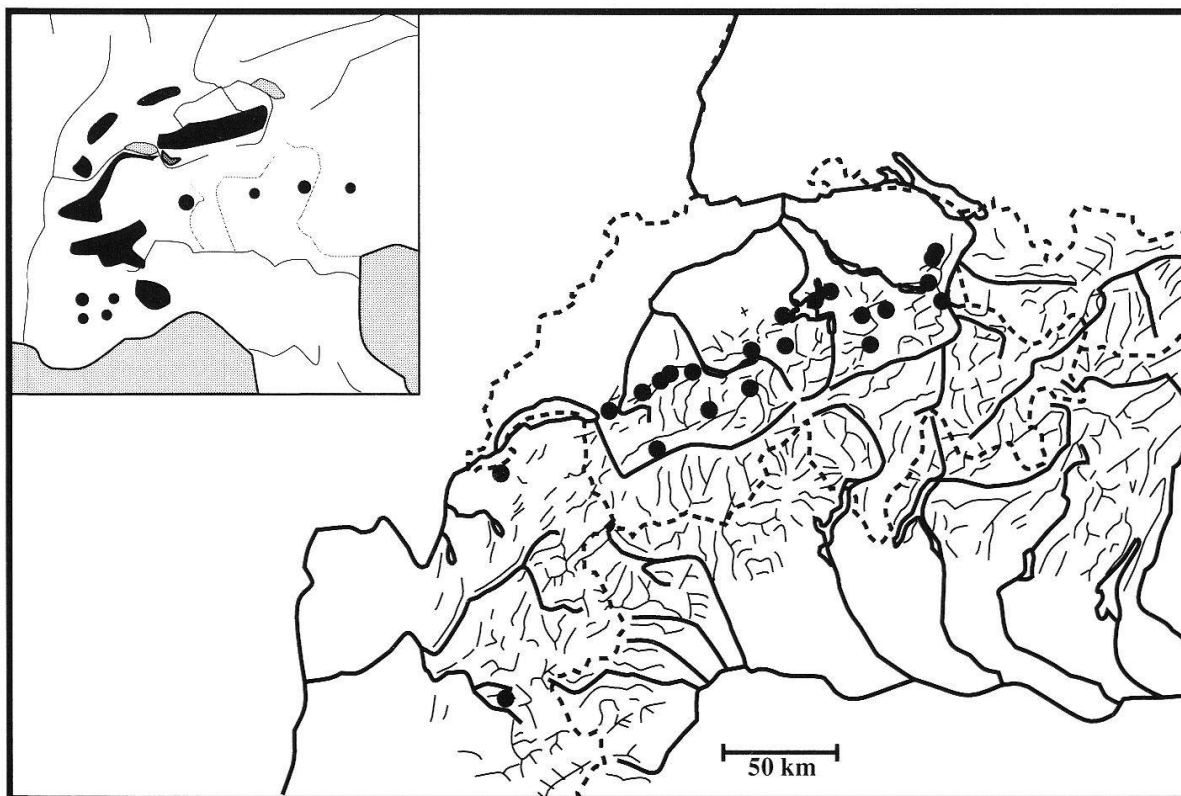


Fig. 1. Distribution map of *Erinus alpinus*: 22 populations sampled in the middle part of the Alps (dots); Central European distribution (inset).





Fig. 2. A cushion of *Eritrichium nanum* on the proposed high alpine nunatak of Piz Nair (3050 m a.s.l.) in the Upper Engadine, Switzerland.

re-colonise the Alps on a broad migration front. Nevertheless, the present distribution of the species in the northern Prealps also covers areas known as northern alpine refugia (Briquet 1906). Thus, there is, although quite improbable, the possibility that *E. alpinus* could have survived the ice-ages *in-situ*.

The arrangement of the 22 populations sampled with twelve individuals each in *E. alpinus* is linear along the proposed migration route from the southwestern Alps with ten of the populations also located in areas known as possible north-alpine peripheral refugia. One population is located in the Cottic Alps in France, a possible source region, and another represents the eastern distribution limit of the species at the Swiss-Austrian border. If the re-immigration hypothesis is true, then the latter population should have been founded lately, eventually showing less genetic variation because of a genetic thinning effect.

#### *ERITRICHIMUM NANUM*: *IN-SITU* GLACIAL SURVIVAL ON NUNATAKS

*Eritrichium nanum* (L.) Gaudin is a high-alpine, long-lived perennial cushion plant (Fig. 2). It is strictly alpine, mainly growing on siliceous rocks. In the middle part of the Alps the distribution of *E. nanum* covers areas with many postulated high-alpine nunataks (Fig. 3; Brockmann-Jerosch & Brockmann-Jerosch 1926). The species is mainly outcrossing, although it is partly self-compatible (H. Zoller, pers. comm.).

The species' distribution in high alpine elevations of the Central Alps suggests an *in-situ* survival of the ice ages. Thus, a test of the nunatak hypothesis is appropriate and intensive sampling in nunatak areas and their adjacent regions is necessary. Three main sampling regions were selected (Valais, Ticino, Graubünden), each with six populations. This permits a statistical hierarchical evaluation of the genetic variation found. Of the above mentioned 18 populations, eight populations are located in the centre of postulated nunatak areas (Zermatt, Simplon, Bernina). Additionally, one population in Northern Italy (Passo Tonale) and one in the Cottic Alps in France (Ecrins) were selected as possible sources for the alternative hypothesis of re-immigration of *E. nanum* after the ice-ages. In total, 20 populations with twelve individuals each will be investigated.

#### *RUMEX NIVALIS*: HOW DID THE RE-COLONISATION OF THIS SNOW-BED PLANT HAPPEN?

The dioecious *Rumex nivalis* Hegetschw. is a strictly alpine species and is found on calcareous rubble and in snow beds. It is a perennial rosette plant with small flowering stalks and inconspicuous flowers (Wagenitz 1981).

Two aspects of the distribution of *R. nivalis* are interesting (Fig. 4). (1) There is a clear

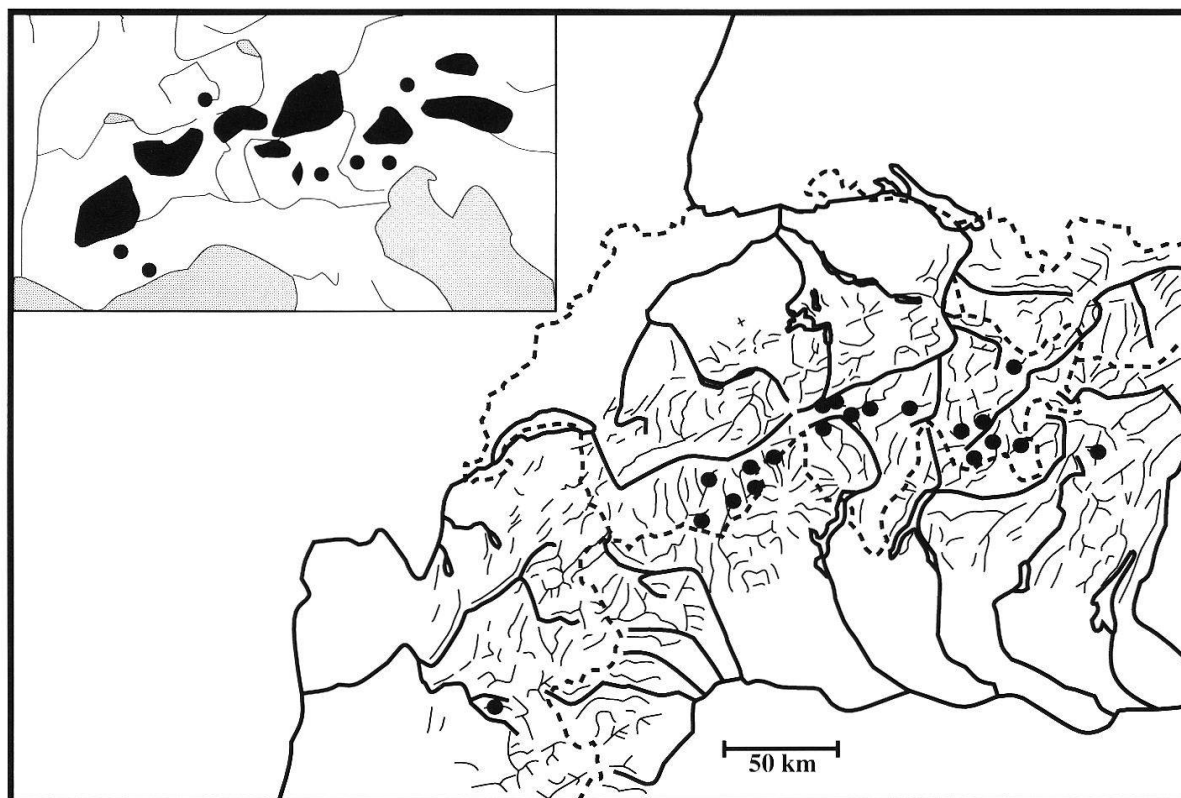


Fig. 3. Distribution map of *Eritrichium nanum*: 20 populations sampled in the middle part of the Alps (dots); total distribution (inset).

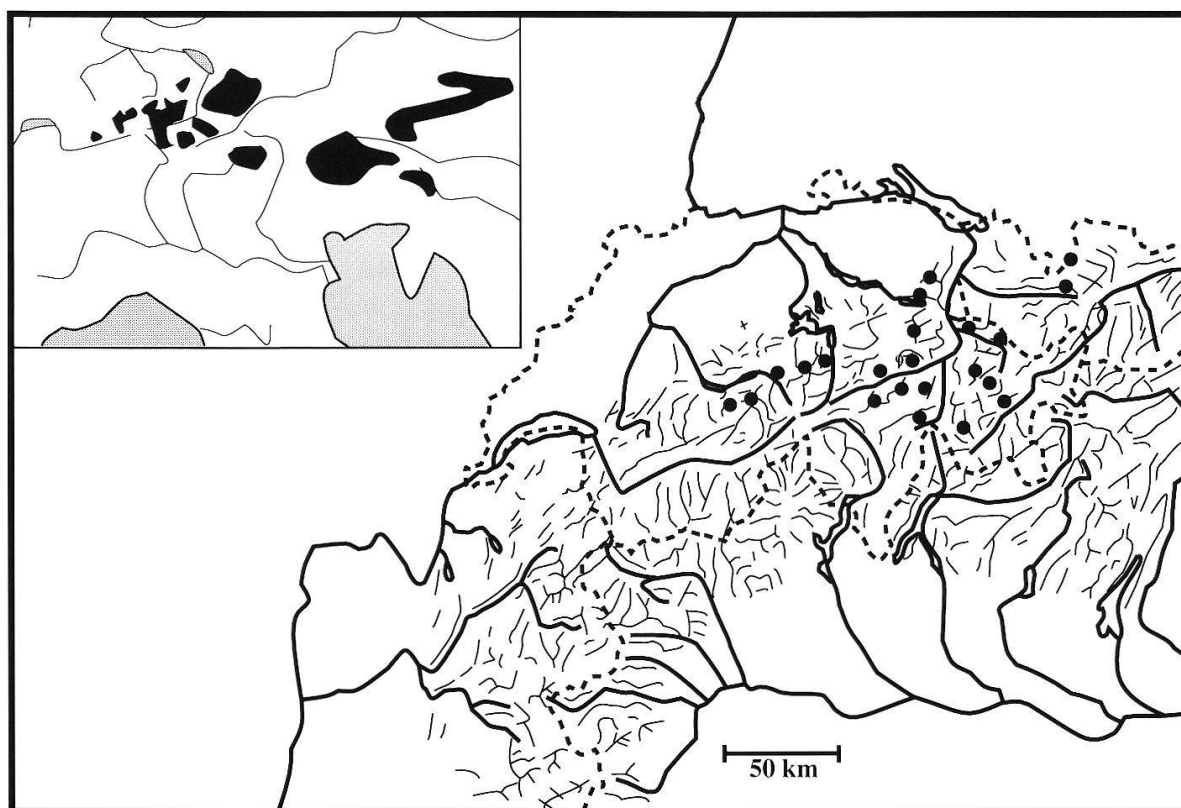


Fig. 4. Distribution map of *Rumex nivalis*: 22 populations sampled in the middle part of the Alps (dots); total alpine distribution (inset).

thinning in population density within the north-western calcareous Alps in an east-western direction. This distribution pattern points to an immigration from a north-eastern peripheral refugium (*tabula rasa* hypothesis). Suitable habitats of *R. nivalis* were probably abundant just after the retreat of the glaciers. Therefore, the species could possibly have immigrated on a broad front of which the outline is still visible. As environmental conditions changed, population density of *R. nivalis* decreased again, which would explain its present scattered distribution. (2) Its disjunct, high alpine distribution and affinity to extreme habitats could also point to glacial *in-situ* survival on nunataks. Possibly, *R. nivalis* has immigrated from the North-East before the last glaciation. As the glaciers advanced, a more continuous, ancient distribution got fragmented, and *R.*

*nivalis* survived, like *Eritrichium nanum*, on several island-like nunataks.

Both scenarios suggest long-time isolation of populations, though the time spans of isolation would be quite different. According to the nunatak hypothesis, the continuous distribution of *R. nivalis* already became fragmented during the ice ages, while in the *tabula rasa* hypothesis, they were fragmented after re-immigration. Therefore, genetic differentiation among populations should be higher in the case of *in-situ* survival on high alpine nunataks due to longer isolation and drift.

A similar approach will be taken for *R. nivalis* as is described above for *Erinus alpinus* with intense sampling along possible immigration routes (22 populations in total with 12 individuals each). One population will represent the western distribution limit of *R. nivalis* (Mürren), and two eastern populations will

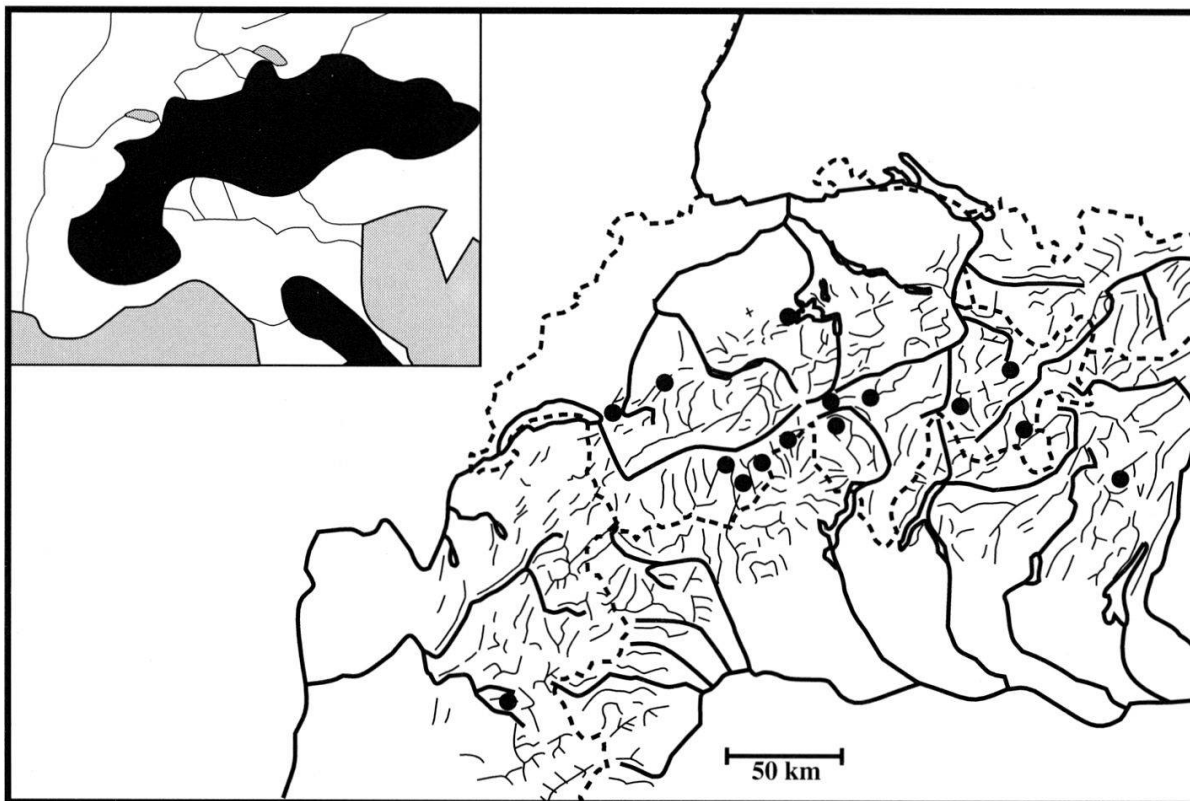


Fig. 5. Distribution map of *Saxifraga oppositifolia*: 15 populations sampled in the middle part of the Alps (dots); distribution in the Alps and Northern Appennines (inset).

serve as possible source populations for re-colonisation (Oberstdorf in Germany, St. Anton a.A. in Austria, respectively). Only four populations are directly located in nunatak regions.

#### *SAXIFRAGA OPPOSITIFOLIA*: POPULATION HISTORY OF A COMMON ALPINE SPECIES

*Saxifraga oppositifolia* L. is common and widespread throughout the Alps (Fig. 5), growing at subalpine to nival elevations (Kaplan 1995). The species is mainly outbreeding and populations are genetically very variable (Gugerli *et al.* 1999; von Flüe *et al.* 1999).

It is still debated how *S. oppositifolia* survived the ice-ages in Northern Europe. Abbott *et al.* (1995) supposed arctic glacial refugia, while Gabrielsen *et al.* (1997) concluded that the species was totally eradicated in Scandinavia and re-immigrated from more southerly periglacial refugia after the ice-ages. Based on its wide alpine distribution (Welten & Sutter 1982), no specific hypothesis on the biogeographic history of *S. oppositifolia* in the Alps can be formulated. Both, the *tabula rasa* and the nunatak hypotheses might have been involved, although there are late-glacial fossil records of the *S. oppositifolia* pollen type from the Swiss lowlands and Alps (Burga & Perret 1998). Therefore, a sampling strategy was adopted, that considered populations from nunatak regions in the middle part of the Alps, especially those proposed by Brockmann-Jerosch & Brockmann-Jerosch (1926; e.g. Simplon, valleys of Visp, Bernina), populations from north-alpine peripheral refugia (e.g. Vanil Noir, Pilatus) and one population each from the Cottic and the Judicarie Alps in France and Northern Italy, respectively (15 populations in total with ten individuals each). Explicit sampling in proposed refugia but on a broad geographic scale should allow statistical tests of the two main

hypotheses of *in-situ* survival and re-immigration. The comparison of the results of *S. oppositifolia* with those of the three species investigated in the first project (see above) enables an evaluation of the resolution power that biogeographic molecular studies can achieve in a common, widespread species.

#### Relevance of the projects

The proposed projects will be among the first to investigate general biogeographic patterns of alpine plant species using molecular methods. Compared with the few studies published so far, their strength is in the formulation of explicit hypotheses and in the application of adequate sampling strategies.

Similar studies on plant phylogeography of the Alps are currently carried out at the Universities of Mainz and Vienna. The research group in Mainz has an additional focus in looking for congruencies of Quaternary history between several unrelated taxa, while the Vienna group is concentrating on the Eastern Alps. All these projects as well as those presented here will provide population genetic data on large geographic scales and for many populations from large parts of the Alps.

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