

that post-glacial recolonization of high altitude habitats has probably been achieved separately by each ecotype.

Tests of Pleistocene speciation among alpine and montane species of *Globularia* (Globulariaceae) from the European high mountains Hans Peter Comes and Joachim W. Kadereit

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There has been a resurgence of debate among zoologists on whether the Pleistocene glaciations inhibited speciation. Here we test the hypothesis of Pleistocene speciation by focusing on the phylogenetic relationships and divergence times of various alpine and montane plant species of the genus *Globularia* L. from the European high mountains.

Parsimony analyses of nrDNA (ITS) sequences for the entire genus suggest a near simultaneous origin of altogether three alpine/montane clades, and two Mediterranean clades, all of which form a basal polytomy in the strict consensus tree. Such a branching pattern would be expected if these clades arose from the fragmentation of a widespread – most likely Mediterranean – ancestor. Under this hypothesis the three European alpine/montane lineages identified [(i) *G. nudicaulis*, *G. gracilis*; (ii) *G. neapolitana*, *G. stygia*, *G. cordifolia*, *G. repens*; and (iii) *G. punctata*, *G. trichosanthes*] arose independently, most likely in the western, central, and eastern parts of the Mediterranean region, respectively.

All these European high mountain species appear to have originated within the Pleistocene. In general, sequence divergence among species *within* lineages is less than 1.9%, corresponding to divergence times less than 2.4 million years ago (assuming a conservative divergence rate of 0.79% per Myr). However, comparisons of sequence divergence across lineages or sister taxa suggest that speciation events were associated with different glacial-interglacial cycles.

The three European alpine/montane lineages identified (i–iii) are rather ancient and differ in their ecological requirements, growth form and/or chromosome number. In accordance with one of the major criteria for adaptive radiation, they «pass the test of sympatry» in areas of range overlap. Contrastingly, sister species *within* lineages, with their recent Pleistocene origins, are ecologically and morphologically very similar, differing primarily in leaf shape and minute floral characteristics, or – rarely – ploidy level (only *G. cordifolia* / *G. repens*). In view of the pronounced vicariant pattern of distribution within lineages, it is posited that morphological character differences simply accumulated as a consequence of geographic isolation and allopatric divergence among sister species maintaining similar ecological niches.

Despite periodic glacial cycles, associated distributional shifts of taxon ranges, and possibly ample opportunities for population mixing, the dynamic history of the Pleistocene apparently did not preclude speciation within *Globularia*. Rather, by fostering geographic isolation, these climatic fluctuations may have increased the initiation of species. This is in accordance with our recent molecular-systematic studies on other European high mountain taxa (e.g., *Gentiana* sect. *Ciminalis*, *Soldanella*, *Primula* sect. *Auricula*).

Genetic diversity, biogeography, and evolution of apomixis in North American *Arabis holboellii* Hornem. and *Arabis drummondii* Gray (Brassicaceae). Experimental approach. Christoph Dobeš and Marcus Koch

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Taxa of North American *Arabis*, treated as genus *Boechea*, are of a Pleistocene origin. They are not related to Eurasian *Arabis* or taxa such as *A. glabra*, *A. pauciflora* or *A. turrita*. The genus *Boechea* consists of more than 70 species. Polyploidy and even aneuploidy is widespread, and apomixis is thought to represent one major force which is driving the evolution of the species complex.

Arabis holboellii in several respects is a remarkable species. (1) The species is highly polymorphic, consisting of a number of varieties or microspecies with various chromosome numbers. (2) It has a disrupted range, being an American-

Greenlandic species with its main distribution in West America. It is absent from arctic Northeast America, but is found on the Gulf of St. Lawrence, which might indicate periglacial survival. (3) Apomixis is wide-spread. In contrast, *A. drummondii* is clearly defined morphologically. Its distribution area matches those of *A. holboellii*, and, throughout the sympatric range of both species the putative hybrid *A. ×divaricarpa* occurs more frequently.

The hybrid status of some *A. ×divaricarpa* accessions have been demonstrated by ITS sequence analysis. Chloroplast DNA sequences (*trnL* intron and *trnL-F* spacer) should provide information about the distribution and spatial transmission of maternal inherited genetic variation within *A. holboellii*, within *A. drummondii*, within *A. ×divaricarpa* and between these taxa. Sequencing of the ITS region will provide additional information about multiple hybridisation and reticulation.

The analysis of ITS sequences is biased by a mechanism called concerted evolution. In order to analyse an independent, biparentally inherited marker, microsatellites will be analysed. The information of the total *Arabidopsis* genome sequence has been successfully used to identify numerous *Arabidopsis* microsatellite loci with defined genomic positions (in *Arabidopsis*). Using a synteny approach microsatellites will be selected covering the total genome. This procedure should provide additional information about «genom-wide» genetic differentiation. The initial study is based on approximately 800 specimens covering the total distribution area and morphological variation. To get further information about the ploidy levels of the specimen, pollen size measurements have been tested as indicator.



Abb. 6: *Arabis ×divaricarpa*

Do refugial populations exhibit greater genetic diversity? René Fächter, Alex Widmer and Matthias Baltisberger

The genetic consequences of the survival of plant populations in glacial refugia are contradictory. Many authors suggest that putative refugial populations harbour higher levels of genetic diversity relative to their likely descendant populations. Others assume a massive loss of allelic variability in refugial populations through inbreeding, founder events and population bottlenecks, at least if refugial areas and population sizes are small.

Considering the glacial refugia of tree species the situation appears to be clear: a decline in the number of haplotypes with increasing distance from a refugium is consistent with theoretical models of postglacial migration in species undergoing leptocurtic dispersal. However, much less is known about alpine plants where the situation may be different (e.g. generally smaller refugial areas and a fragmented distribution even during interglacial stages).

In order to formulate hypotheses concerning the distribution of genetic diversity in refugial versus non-refugial populations, the mode of preglacial retreat and postglacial re-dispersal needs to be considered. Many authors imply that plant populations contract into small refugial areas, which suggests an active retreat from the forward pushing glaciers. In this case, refugial populations might harbour great genetic diversity. Alternatively, one may assume that only plants which were already growing in a later refugial area were able to survive the ice age in situ, which implies a loss of most of the diversity at the beginning of the ice age. In this case, the initial genetic diversity of the refugial population is restricted. Depending on the mode of postglacial colonisation, non-refugial populations may show higher diversity today if recolonisation from several refugia has occurred.

With regard to postglacial expansion, it is crucial to consider the widely differing abilities of taxa for dispersal and gene flow, factors which depend on traits such as the mode of seed dispersal and the pollination system. These are likely to have an impact on the genetic diversity of the descendent populations and therefore influence our ability to detect differences between refugial and non-refugial populations.

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