

History, Evolution & Future of Arctic & Alpine Flora

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Abstracts of Talks (in order of presentation)

Monday 25 June

The late-Quaternary history of arctic and alpine plants. (Keynote)

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The climatic importance of fossil arctic plants has been realised since the discovery of “arctic plant beds” in Denmark and Sweden at the turn of the 20th century, very far from where they live today. Arctic and alpine plants characterise treeless habitats above or beyond the altitudinal or latitudinal tree-line where they may be adapted to harsh conditions and intolerant of lowland conditions or confined to these habitats through competition from larger plants. Much more is known of the history of arctic plants than of alpine plants. In glacial periods, arctic plants spread into cold (and often dry) unglaciated areas. They often followed the fluctuating edges of the ice sheets. Deglacial warming allowed many species to flourish briefly on freshly deglaciated terrain. In northwest Europe many were locally exterminated during the warm Allerød-Bølling Interstadial but spread again in the cold Younger Dryas period. Rapid Holocene warming forced species northwards or upwards as trees invaded the landscape. Plants that are tolerant of warm temperatures but intolerant of competition found refugia in open habitats such as sea-shores, cliffs, etc. As global climate warming proceeds today and human impact increases, the area available to arctic and alpine plants will continue to decrease.

Ice-age tundras of Beringia—are they still with us?

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Beringia, encompassing northwest North America, eastern Siberia and the drowned lands between, has been a focus of phytogeographical studies since Hulten highlighted the diversity of its arctic-alpine flora. It is the only extensive northern region to remain largely ice-free during the Quaternary period and is considered a ‘refugium’ in the classic context of a refuge from the ice. Independent lines of evidence suggest that glacial periods were arid and virtually treeless, though not necessarily unproductive, and that xeric plant communities characterized by herbs and graminoids dominated the landscape. In the absence of forest and moist, species-poor shrub tundra the interaction of insolation and topographic complexity created a variety of open habitats. End-member communities of this biome would have been unproductive fellfield and cushion-forb tundra on the one hand and subarctic steppe on the other. Specific physical conditions constrain these communities, and cold-stage and modern species lists are similar. More uncertainty surrounds the zonal vegetation; the modern (elevational) steppe-tundra transition is one possible analogue. The Land Bridge acted as a filter to dispersal: warm-steppe species seldom crossed it, which implies they are immigrants from further south under warm climates, while E-W disjunctions of cool-adapted taxa are more common.

The effect of moisture changes on vegetation in the East Siberian Arctic during the Late Quaternary

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Within the Late Quaternary, the Holocene is unique in terms of sustained modification of arctic ecosystems resulting in the disappearance of tundra-steppe and mammoth fauna. The western part of Beringia, the main refuge of arctic biota throughout the Quaternary, is more than any other region at high latitudes affected by continental climate. Climatic continentality, resulting in a great seasonal temperature gradient and low net precipitation, has always been characteristic of this region, but was more extreme during Pleistocene Sea level low stands, when the shallow Laptev and the East Siberian Shelves became exposed and the Eurasian land mass expanded several hundred km northwards.

Connected with the Holocene marine transgression and the resulting rise of oceanic influence, increasing moisture in the East Siberian Arctic resulted in a decreasing seasonal temperature gradient including summer cooling and lower habitat and species diversity. Plants that are typical of low or fluctuating moisture or locally warm summer conditions were displaced inland. This modification of large-scale vegetation patterns culminated about 5000 to 6000 years BP, when the East Siberian Shelf Seas reached their current position and global cooling took place. According to existing data, such a diversity decrease did not happen during the Eemian interglacial. During my presentation, I shall compare the Eemian and Early Holocene palaeovegetation reconstructed by frozen plant macrofossils with the Late Holocene tundra in the East Siberian Arctic.

Alpines, trees, and refugia

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During the Quaternary there have been major climate shifts resulting in a series of glacial – interglacial cycles. Because of the very different environmental conditions in the glacial and the interglacial stages, refugia have been critically important for species survival. The classical view of glacial-stage refugia is that alpine and arctic plants were widespread in the lowlands of central Europe and around the margins of the continental ice-sheets, whereas trees were restricted to localised refugial areas in southern Europe. New palaeobotanical evidence suggests that this classical view is not complete and that trees were growing during periods of the last glacial maximum considerably further north than previously thought in so-called ‘cryptic’ or northern refugia. The concept of cryptic refugia also applies to arctic and alpine plants in interglacial stages where small localised populations may grow in open habitats that are not beyond or above the tree-line. I review the new palaeobotanical evidence for trees growing in northern refugia because such evidence is very important in our understanding of glacial-stage floras, vegetation, landscapes, and environments.

The IntraBioDiv project: comparison between species diversity and genetic diversity in alpine plants. (Keynote)

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Species richness is the most widely used measure for biodiversity assessment. However it is intraspecific diversity (genetic polymorphism) that represents the evolutionary and adaptive potential of each species in changing environments. In this project, we asked the following questions, using plants of the Alps and the Carpathians as model systems: (i) is there congruence between intra-/interspecific biodiversity? (ii) do areas of high endemism, often coinciding with glacial refugia, harbour a great degree of intraspecific diversity? (iii) is habitat variation, characterised by environmental parameters, a good surrogate for intra- and interspecific diversity? In order to accomplish our aims, we mapped the intraspecific diversity by using molecular markers in 27 model species in the Alps and 25 in the Carpathians, we mapped the species richness on the same area using mainly existing data on plant distributions, we compiled environmental data for a map of habitat diversity, and we compared these maps to find possible correlations among these variables. Our results clearly demonstrate that species richness and genetic diversity do not covary in Alpine plants. As a consequence, conservation strategies must take into account not only species biodiversity, but also genetic polymorphism. Despite an extensive analysis of both biological and environmental parameters, we did not find reliable surrogates for intraspecific diversity.

Unearthing the evolutionary history of tundra flora through comparative coalescent analyses

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Eric Hultén proposed that Beringia, a vast region of the Arctic spanning northeastern Siberia and northwestern North America, was ice-free throughout the climate cycles of the Quaternary. Geological, phytogeographic, palynological, and molecular evidence support Hultén's hypothesis and suggest that Beringia was central to the preservation of tundra flora. But to date, the role that Beringia played in the evolution and diversification of Arctic plants remains unclear. This is largely due to the difficulties inherent in inferring the history of a region. For instance, the evolutionary histories of only a limited number of species have been examined and those taxa likely responded differently to the paleoclimatic cycles. Furthermore, stochastic variation inherent in the evolutionary process, such as that associated with gene tree topologies and divergence times, exacerbates the uncertainty in historical inferences. By simulating genealogical histories for diverse taxa, a comparative coalescent approach can explicitly account for species-specific differences as well as the uncertainty in estimates of gene trees. This comparative approach was used to specifically test *a priori* hypotheses and evaluate the evolutionary history of the region. The results from these coalescent analyses demonstrate the importance of Beringia as a region integral to the evolution of tundra flora.

Comparative plant phylogeography in the circumpolar Arctic

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When species with similar distributions and climatic requirements are subjected to the same physical forces over time, one intuitively expects a high degree of congruence amongst their phylogeographies. However, several studies have shown that species tend to show individual patterns. Large-scale comparative phylogeographies published so far are typically based on compilations from the literature, thus involving different sampling strategies and genetic marker systems. In this study, 17 widespread arctic-alpine and north boreal plant species were sampled following the same protocol throughout their distribution range and about 8000 individuals from 882 local populations were analysed for Amplified Fragment Length Polymorphisms (AFLPs). The main genetic patterns were determined using PCO and clustering methods (Structure, BAPS). We found some clear large-scale congruence; e.g. all species had a group with a European center, and all circumpolar species had at least one group with a Siberian center and another with an American and/or Beringian center. Many plants also had a group centered in East Canada/Greenland. To search for an explanation of the observed genetic patterns, we are currently integrating various geographical data, such as topography and glacial extension at various time intervals, using Geographical Information Systems (GISs) software. It seems, for example, that topographical barriers such as the Ural Mountains have affected the genetic pattern in several species, but to different degrees and at different time levels.

Phylogeography of arctic and boreal lichens: Difficulties in reconstructing ancestral areas and postglacial dispersal

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Lichens – symbioses between a fungus and a cyanobacterium and/or a green algae - form an important part of the biodiversity in arctic and boreal terrestrial ecosystems. Most lichens occupy large distributional areas with frequent intercontinental disjunctions. So far, few studies have dealt with the population genetics and phylogeography of lichen species and only a single arctic (bipolar) species complex has been studied in detail. The wide distribution of arctic and boreal species is often matched by a comparably wide distribution of single haplotypes. Phylogeographic reconstructions based on DNA-sequence data are consequently difficult. The few available examples show that arctic populations of the bipolar species *Usnea sphacelata* may have originated from refugia in the High Andes and that Western North America may have served as an important glacial refugium for some but not all circumboreal species and species complexes. More phylogeographic studies based on multilocus datasets are necessary to render a more coherent picture of the postglacial history of lichen populations.

Demographic inferences in Norway spruce based on nuclear DNA sequences

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The phylogeography of arctic flora has to a large extent been dominated by the analysis of chloroplast and mitochondrial DNA. While the analysis of those cytoplasmic markers certainly led to very interesting reconstructions it also has obvious restrictions: the timescale of inferences is intrinsically more limited than for nuclear DNA due to lower “effective population sizes” and inferences are necessarily based on a single realization of the genealogical process because of the lack of recombination. The analysis of multilocus nuclear DNA sequences should therefore lead to new insights on the history of arctic flora. In the present study DNA polymorphism at 22 loci was studied in an average of 47 Norway spruce (*Picea abies* (L.) Karst.) haplotypes sampled in 7 populations representative of the natural range. All populations, with the exception of the Romanian population, could be divided into two main domains, a Baltico-Nordic and an Alpine one. Mean Tajima’s D and Fay and Wu’s H across loci were both negative, indicating the presence of an excess of both rare and high-frequency-derived variants compared to the expected frequency spectrum in a standard neutral model. Multilocus neutrality tests based on D and H led to the rejection of the standard neutral model and exponential growth in the whole population as well as in the two main domains. On the other hand, in all three cases the data are compatible with a severe bottleneck occurring some hundreds of thousand years ago, i.e. long before the last glacial maximum. The implications and generality of this result will be discussed.

Causes of the genetic architecture of southwest European high mountain disjuncts

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Climatic warming and the successive retreat of cold-demanding species into higher elevations after the Last Glacial Maximum, starting in southwest Europe (i.e. the Sierra Nevada) and proceeding to the north (i.e. the Pyrenees and the Alps), should have resulted in a pattern of successive vicariance. Alternatively, long-distance dispersal might explain extant distribution patterns. Here, AFLP variation was used to investigate six alpine plant species (963 individuals, 52 populations) co-occurring in the Sierra Nevada, the Pyrenees, and the southwestern Alps/Massif Central. Our aim was to distinguish between vicariance and long-distance dispersal as alternative explanations for the geographical distribution observed. We also investigated the question whether datable disjunctions can be used to establish an AFLP-clock. We found that successive vicariance best explains the disjunct distribution of all six species. The only exception to this general pattern was one long-distance dispersal event from the Sierra Nevada to the Pyrenees in *Papaver alpinum*. Degree of AFLP divergence between populations from the different mountain systems and time of isolation of these populations show a linear correlation. In all species except *Saxifraga oppositifolia* this correlation was significantly positive implying constant but species-specific AFLP divergences rates. Although comparison of rates among

species revealed no universal clock-like behaviour, AFLP divergence rates are of comparable magnitude in *Gentiana alpina*, *Kernera saxatilis*, *Papaver alpinum*, and *Silene rupestris*. Such AFLP divergence rates may serve to absolutely date geologically young evolutionary events which can not be dated with DNA sequence data because of lack of sequence variation.

Glacial survival and phylogeography within a narrow spatial scenario in the Central Pyrenees: the endemic dwarf yams (*Borderea*, Dioscoreaceae)

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Three molecular data sets (allozymes, RAPD and SSR) were used to delimit the genetic boundaries and divergence of the two relictual endemic Pyrenean taxa *Borderea chouardii* and *B. pyrenaica* (Dioscoreaceae), and to infer the different life histories followed by each species. A single evolutionary scenario was recovered for the split of the two dioecious, strictly sexually reproducing, long-living geophyte *Borderea* taxa from a common Tertiary ancestor in the Prepyrenees. Microsatellite markers revealed the tetraploid nature ($2n=24$; $x=6$) of *Borderea*. A Bayes factor test for patterns of inheritance of SSR alleles favored an allotetraploid origin for the two *Borderea* taxa and the analysis of the data indicated a common ancestry for at least one parental genome donor. Surprisingly, *B. chouardii* was nearly rendered extinct during the glacial periods and failed to colonize new habitats at postglacial times whereas *B. pyrenaica* evolved into a postglacial subalpine species that successfully colonized the central Prepyrenees and Pyrenees. SSR markers detected that the single Prepyrenean population of *B. chouardii* was subdivided into two groups of individuals genetically isolated and vertically separated by 150 m. On the other hand, the SSR data favored a stepping-stone south-to-north migratory cline followed by *B. pyrenaica* from the Prepyrenees toward the southern Pyrenees and then the northern Pyrenees after sheet ice retreat. The *B. pyrenaica* lineages followed two migratory pathways in their northwards colonization, suggesting several founder events for the populations that eventually reached the northernmost territory of the northern Pyrenees.

The evolution and origin of European alpine plants. (Keynote)

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Our work in four different plant taxa will be used to illustrate various aspects of the evolution and origin of European alpine plants. For *Primula* sect. *Auricula* (Primulaceae), it will be shown that the Quaternary was a period of active speciation in the European Alps. The possibility of speciation in geographically isolated glacial refugia will be investigated in two pairs of sister species from the central and southwest Alps. *Epimedium* (Berberidaceae) will serve to investigate the biogeographical relationships between the European Alps and Asia where the highest diversity of *Epimedium* (and of many other alpine plant taxa) can be found. I will show that connection through southern mountain ranges (Hindukush, Elburz, Caucasus/Taurus) appears to have been of no importance but instead existed through more northern lowlands. Finally, *Gentianella* and *Halenia* (Gentianaceae) will be used to illustrate how almost rather short period of time, and how centres of diversity are far removed from likely centres of origin. In these two (and probably many other) genera mountain ranges appear to have been major highways of rapid dispersal even between hemispheres.

Tuesday 26 June

The importance of refugia for the evolution of alpine and arctic-alpine plants

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During severe climatic changes only populations of those organisms survive that are able to migrate to suitable habitats, to adapt to the new environment quickly or that live in environmentally stable regions. An area where living conditions are suitable and stable throughout climatic fluctuations is often termed a *refugium*. Stability is usually a factor in areas less affected by natural climatic changes, like in mountainous areas, where altitudinal migrations of populations are easily possible. Several studies were published that deal with the relevance of refugia in Europe for explaining distribution and phylogeographic patterns and the paradigm that refugia were mainly situated in the main Mediterranean peninsulas was created. Recently this view has been changed, although strong support for *Northern refugia* far beyond these areas is still limited. In my presentation I would like to show the relevance of the European mountains and some areas in the Arctic as refugia by discussing published and my own phylogeographic data on several alpine and arctic-alpine plants. Moreover I will explain that *potential refugia*, where organisms were potentially able to survive climatic changes should be discriminated from *realized refugia* that are supported by biological data. Knowing the location of such realized refugia holds a key to our understanding of many (intraspecific) phylogeographic patterns found, but does not explain the evolutionary significance wholly. The questions, as to whether phylogeographic patterns are stable simply because of genetic drift and limitations of gene-flow or whether phylogroups diverged by adaptation to different habitats associated with refugial patterns as a first step towards speciation remain open and will be important for future research.

Evolution and phylogeography of *Androsace* sect. *Aretia* (Primulaceae)

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Due to historical climatic factors, and the scattered distribution of mountain ranges, alpine plants in Europe often have distributions which are on some scale disjunct, either between mountain ranges, or within a larger mountain range. Simple geographical arguments have often been used to suggest that current patterns of disjunction match the former locations of refugia during the ice ages. While this may hold true for narrow endemic taxa, found only in one small area, it need not be so for more widely distributed taxa. We studied intraspecific genetic variation in *Androsace* section *Aretia* to probe the causes of patchy distributions in alpine plants. This European-centred group contains species with disjunctions at all ranges from a few tens of kilometres to several hundred, but which are otherwise similar in floral syndrome and apparent dispersal abilities. Our results show that, even if the current disjunct distributions coincide with potential glacial refugia, more recent dispersal between areas is a better explanation in many cases, and that other biological factors such as hybridisation, extinction and cryptic speciation can further disrupt our ability to draw conclusions simply from cartographical data.

Beyond neutral markers: Adaptive genetic variation of alpine plants in a landscape context

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Molecular studies of alpine plants have mainly relied on neutral genetic markers. For instance, phylogeographic research has led to the detection of glacial refugia or pathways and suture zones of re-immigration. However, the question remains as to whether different phylogeographic lineages are of any evolutionary significance with respect to adaptation or whether they simply reflect historical events without adaptive consequences? In this conceptual talk, we first show why neutral markers cannot be used to infer adaptive genetic variation or differentiation (H_e vs h^2 ; F_{ST} vs Q_{ST}). We then sketch a next step, which is to investigate the variation in adaptively favourable traits and how it is spread over landscapes. However, the study of adaptation in a landscape is a formidable task due to technical (adaptive markers are difficult to find) and logistic problems (work load). Therefore, we briefly introduce current concepts to study adaptive variation in a landscape context (ecological genomics) and discuss their benefits and limits. Third, we then demonstrate one particular approach that we argue to be of special relevance and feasibility (environmental association analysis). We will illustrate this approach with results from our own, on-going research on an alpine plant (*Arabis alpina*).

The Arctic – an evolutionary freezer? (Keynote)

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The traditional view of the Arctic as an ‘evolutionary freezer’ with low evolutionary rates caused by extreme environmental constraints (e.g., low temperature, short growing season, drought) has been repeatedly challenged in recent years. New data for birds and mammals suggest that although species diversity decreases towards high latitudes, recent rates of speciation as well as extinction are highest at high latitudes (Weir & Schluter 2007, *Science* 315: 1574-1576). In plants, recent development of sterility barriers resulting in high biological species diversity within single taxonomic species has been demonstrated in arctic diploid *Draba* (Grundt et al. 2006, *PNAS* 103: 972-975; cf Skrede’s talk at this symposium). In arctic species complexes of polyploid *Cerastium*, data from low-copy nuclear genes and a new network-building algorithm have been used to untangle a recent, dynamic evolutionary history (Brysting et al. in press, *Systematic Biology*; cf Brysting’s talk at this symposium). High levels of intraspecific (genetic) diversity have also been demonstrated in many arctic plants, for example where lineages expanding from different ice age refugia meet (cf Eidesen’s and Tribsch’ talks at this symposium). Recent data also suggest that the arctic flora is highly mobile, with long-distance colonization occurring at much higher rates than previously envisioned (Alsos et al. in press, *Science*; cf Alsos’ talk at this symposium). Taken together, these lines of evidence suggest that the turbulent climatic history at high latitudes, with frequent re-formation of ‘unsaturated’ habitats, may have induced elevated recent rates of divergence, dispersal, hybridization, and speciation.

Sibling speciation in arctic diploid *Draba* (Brassicaceae)

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Incomplete to fully developed postzygotic sterility barriers within species were recently demonstrated in three circumpolar species of the genus *Draba*, suggesting numerous sibling species (Grundt *et al.*, 2006; PNAS, 103, 972-975). Because the three species are selfers and of recent, Pleistocene origin, Grundt *et al.* argued that hybrid sterility evolved quickly and possibly by genetic drift. The present study employs a combination of quantitative trait locus (QTL) and meiotic analyses to determine whether the sterility has a chromosomal or genic basis and, if the latter, whether the sterility is caused by interactions among alleles at a single locus or by interactions among alleles at different loci. We have generated an F₂ population of 383 individuals by crossing two *Draba nivalis* plants, one from Alaska and one from Norway (F₁ hybrids were ~30 % fertile). All F₂ plants have been tested for pollen viability, seed set, and growth rate, and were on average 54% fertile. A microsatellite-enriched library has been made for *Draba*, and 50 loci have been genotyped for all individuals in the F₂ population. These markers have been linked, and QTLs have been found for most traits, including two QTLs underlying hybrid sterility. Alleles at the QTLs exhibited additive rather than underdominant inheritance patterns, an observation more consistent with gene incompatibilities than chromosomal rearrangements.

Statistical testing of evolutionary trends in multiple lineages of arctic *Artemisia*

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The aim of our study on *Artemisia* was to examine whether long-standing hypotheses of plant origin and evolution in the Arctic (such as precedence for allopolyploidy or strong connections to alpine temperate habitats) are also true for multiple closely related lineages which may have colonized arctic habitats repeatedly and can be subjected to statistical tests. *Artemisia* with 33 of its about 450 species occurring in arctic habitats is among the most diverse genera of the Arctic. We collected data on morphology, karyology, distribution range and ecological preferences from the literature and produced a molecular phylogeny of 133 taxa based on nuclear 3'-ETS and ITS sequences including almost all arctic species. We compared arctic lineages with their respective sistergroups and applied statistical tests to assure that the observed patterns were not due to chance. We found: 1) *Artemisia* has independently adapted to arctic habitats multiple times. 2) Ecological pre-adaptations that might determine the colonization success were not apparent in our data set. 3) There were proportionally no more polyploids in arctic lineages than in other habitats or in their respective sistergroups. 4) We found strong evidence that small plants with unusual large flowering heads have evolved repeatedly probably for better pollinator attraction and this seems to be a precondition for the flourishing of lineages in the Arctic. We suggest that this strategy replaces the evolutionary effects of allopolyploidy typical for other arctic taxa.

Wednesday 27 June

Evolution of breeding systems and ploidy levels in *Primula* sect. *Aleuritia*, a paradigm of the secondary contact model

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According to the secondary contact model, glacial advancement during the Pleistocene caused the fragmentation of diploid, allogamous populations that later came into contact again as glaciers retreated, giving origin to polyploid, autogamous taxa. The model thus provides a reasonable scenario for the higher proportion of polyploid species at higher latitudes and has been proposed to explain the observed association between polyploidy, homostyly, and distribution at higher latitudes in *Primula* sect. *Aleuritia* (*Aleuritia*). We investigated the plausibility of the secondary contact model for *Aleuritia* and the hypothesized parental origins of its polyploids by using evidence from direct sequences of the chloroplast and nuclear genomes, in combination with extensive cloning of the nuclear ribosomal DNA marker. Phylogenetic, consensus network, principal component, and diagnostic sites analyses allowed the identification of three, geographically discrete polyploid lineages in North America, South America, and Eurasia, each originating from ancestors related to contemporary diploid species occurring in the same region. The results also support the hybrid origin of the intersectional tetraploid *P. egaliksensis* from a *P. mistassinica*-like (sect. *Aleuritia*) maternal ancestor and a *P. nutans*-like (sect. *Armerina*) paternal ancestor and the polyphyletic origin of the ampho-atlantic, 14-ploid *P. stricta* from two, distinct progenitor pairs. Overall, the study highlights the importance of using multiple analytical approaches to disentangle complex patterns of reticulation.

The complex causality of geographic parthenogenesis: insights from studies on apomictic buttercups (*Ranunculus* spp., *Ranunculaceae*)

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The phenomenon that apomictic complexes and their sexual relatives have different distributions has long been recognized, but is still not well understood. Higher plants reproducing by gametophytic apomixis have larger distributional ranges, tend to occur at higher latitudes and altitudes, and have a higher presence in previously glaciated areas than their sexual relatives. The main hypotheses to explain these patterns are (1) indirect advantages because of polyploid and/or hybrid origin, (2) intrinsic advantages of uniparental reproduction, (3) introgression of apomixis into sexuals, (4) advantages of general-purpose genotypes, (5) better niche exploration because of clonal diversity (the Frozen Niche Variation model), and (6) less selective pressure of pathogens and predators on genetic diversity in colder climates because of less biotic interactions (the Red Queen model). A review of the literature on agamic complexes provides no unequivocal support for any single hypothesis. Investigations on reproductive biology and genetic diversity of sexual and apomictic cytodes in the widespread *Ranunculus auricomus* complex and the alpine species *R. kuepferi* give insights into the causality of the phenomenon. Reproductive assurance via breakdown of self-incompatibility and maintenance of heterozygosity after uniparental reproduction are probably the most important intrinsic advantages of apomicts. Nevertheless, although reproductive features suggest a potential maintenance of single genotypes and advantages for colonization after long distance dispersal, population genetic studies do not confirm the existence of widespread clones, but rather that

genetic diversity is distributed among populations. Apomictic populations may use the available habitat spectrum more effectively than sexual populations, which may be in accordance with the Frozen Niche Variation model. Predispositions to apomixis in certain taxa and geographical preferences of sexual progenitors may be important aspects of the phenomenon. Altogether, results support a pluralistic model for the causality of geographical parthenogenesis, whereby many aspects are still unexplored.

Untangling complex histories of genome merging in arctic-alpine *Cerastium*

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Today, the Arctic is one of the Earth's most polyploid-rich areas, in particular of high-level and recently evolved polyploids. Polyploidization has probably occurred repeatedly throughout the entire Quaternary, resulting in high-polyploid species complexes in many plant groups, as exemplified here by the morphologically polymorphic *Cerastium alpinum* group. In allopolyploids, genome duplication is associated with hybridization between two or more divergent genomes. Successive hybridization and polyploidization events can build up species complexes of allopolyploids with complicated network-like histories. Recently there has been growing interest in reconstruction of reticulate evolution in plants and calls for development of markers and methods for inferring reticulation events and network construction. The history of complex genome mergings within a high-polyploid species complex is here untangled by the use of a network algorithm and non-coding sequences of low-copy number genes. The resulting network illustrates how hybridization and polyploidization have acted as key evolutionary processes in creating a plant group where high-level allopolyploids clearly outnumber extant parental genomes.

Global migration and speciation patterns in the genus *Draba*: The integration of genetic diversity, phylogeny, and biodiversity.

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Draba, the largest genus in Brassicaceae, with 363 accepted taxa (Warwick et al., 2006) is widely distributed in arctic-alpine habitats across the globe and is estimated to be about 5 million years old (Koch et al., 2002). It is an exceptional model for studying continent wide macroevolution processes like adaptation, speciation and rates of evolution. This model is also exceptionally fit to study phylogeography in general. Genetic and species diversity, number of lineages through time, and mutation rate data will be correlated in this study. The combination of this data will allow us to investigate the migration of *Draba* across the globe over the past 5 million years. Its migration is most likely a combination of ancestral, late-tertiary diversification events and more recently due to Quaternary glaciation and deglaciation cycles.

This study will continue the investigation of the glacial survival theory, glacial refuge areas, and geographical barriers such as water/glaciers and mountain ranges. Currently we are accessing the biodiversity (species diversity) of *Draba* and are comparing the distribution with the genetic diversity of almost 70% of the genus on a worldwide scale. The numbers of species of *Draba* in a region are being obtained from published Floras, herbaria, and checklists. Sequence information from *Draba* was obtained for the plastidic trnLF and nuclear ITS regions.

One main question we seek to explore is whether the origin of species is also the area of highest biodiversity. The data are being projected onto maps with ESRI ArcView 8.2 allowing for superior visualization not otherwise available. In conjunction with diversity analysis, by observing the lineages occurring over time we can determine radiation events in the evolution of the species. In our preliminary results of lineage through time plots, we have concluded there have been two major radiation events. The first occurred between the origin of *Draba* and about 4 million years ago. The second was possibly sometime during the Pleistocene cyclic glaciation period. We are currently working on calibrating the time scale for these events using various rate smoothing tests. This calibration of time will be done by investigating mutation rate variability over time in the different lineages currently in our study. Recent phylogenetic analysis of the genus will also be presented.

Morphological stasis and molecular divergence? A common pattern of differentiation in alpine *Veronica*?

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Detailed phylogeographic studies in a number of *Veronica* species allows some generalizations. AFLP-analyses of *V. alpina* (Europe), *V. bellidioides* (Alps, Pyrenees, Balkan), *V. nutans* (western North America) and *V. saturejoides* (Balkan) all demonstrate the existence of genetically divergent groups, which are not or barely discernible either by morphological analyses or plastid DNA sequence variation. In *V. alpina*, this differentiation even seems to be among sympatric groups. Reasons for morphological and cpDNA stasis will be discussed. Low cpDNA variation is not found in the Japanese alpine species, *V. schmidtiana*, which exhibits higher genetic variation than its sister group, the 10+ lowland species of *V. subgen. Pseudolysimachium* that range from Japan to Britain, combined.

Evolutionary outcomes of hybridization in *Rhododendron*

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Rhododendron is a genus that occurs across a wide range of altitudes. Subgenus *Hymenanthes* includes species that occur well above and well below the treeline. Remarkably, populations of fertile hybrids between such species can serve as a barrier to gene flow between them, apparently due to habitat-mediated selection effects. Hybrid speciation may have had a key role in allowing subgenus *Hymenanthes* to occupy a wide range of niches in the Himalayas, as cpDNA data now indicate an ancient hybridisation event in the history of this group.

Cold climate plants in a warmer world. (Keynote)

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The European Alps and the Arctic are warming at a rate that is approximately three times that of the mean global rate. Will such a rate of change threaten the biodiversity of these marginal areas? It might be supposed that the adaptations that have enabled plants to survive in the world's coldest habitats will prove maladaptive in a warmer world. There is however an alternative hypothesis. As climatic fluctuations are frequent in marginal areas, the vegetation of these regions may be pre-adapted to climatic change. The habitat-tenacity of the arctic and alpine floras are examined in terms of their capacity to adapt physiologically, phenologically, and genetically to a warmer world.

Frequent long-distance plant colonization in the changing Arctic

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The ability of species to track their ecological niche following climate change is a major source of uncertainty in predicting their future distribution. Based on DNA fingerprinting (AFLP) of nine species we show that long-distance colonization of a remote arctic archipelago, Svalbard, has occurred repeatedly and from several source regions. Propagules are likely carried by wind and drifting sea ice. The intensity of the founder effect was strongly correlated with the temperature requirements of the species, indicating that establishment limits distribution more than dispersal. Thus, assuming unlimited dispersal may be appropriate when predicting long-term range shifts in the Arctic.

Experimental approaches to predicting the future of tundra plant communities

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Predicting the future of tundra plant communities is a major intellectual and practical challenge and it can only be successful if underpinned by an understanding of the evolutionary history and genetics of tundra plant species, their ecophysiology, and their responsiveness (both individually and as component parts of communities) to multiple environmental change drivers. Although we can use the past as a key to understanding the future distribution and composition of tundra plant communities we cannot consider it the key; this is because on-going and predicted environmental change may have no direct analogues in the past. Furthermore, botanists are dependent upon atmospheric scientists, climatologists, economists and others for the prognoses of change upon which predictions of biological responses must be based. The purpose of this presentation is to consider the types of experimental approaches that have been used to

understand and to predict the future of tundra plant communities and the ecosystems of which they are part. In particular the use of ‘environmental manipulation’ experiments in the field is described, and the merits and limitations of this type of approach are considered. The presentation aims to be candid and critical; the author welcomes a constructive debate, both during and subsequent to the symposium.

Conservation of sub-arctic willow scrub in Scotland

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Sub-arctic willow scrub is one of the most endangered habitat types in the UK. The constituent willow species that make up this community are themselves of conservation concern, and one species in particular has attracted high conservation attention (*Salix lanata*). To provide information to support ongoing conservation initiatives for sub-arctic willows, a collaborative research project has looked at various aspects of their biology. A combination of morphological and AFLP approaches has been used to examine species limits and the extent of hybridisation to assess whether conservation programmes are being carried out on the units they were intended for. SSRs have been used to estimate population genetic variation to provide an approximation of which populations might be susceptible to the negative consequences of genetic diversity loss, to assist in donor choice for restoration programmes, and also to examine the relative importance of clonal versus sexual reproduction. DNA sequencing approaches have been used to investigate the diversity of fungi associated with willows. Finally a series of manipulative experiments have been undertaken to investigate some of the factors likely to limit willow regeneration. The results of these studies will be discussed in the context of conservation programmes for sub-arctic willow scrub.

Can we protect the Scottish Arctic Alpine higher plant flora?

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Using data obtained from monitoring carried out for Scottish Natural Heritage (SNH), I describe the species composition and size of the Scottish Arctic Alpine flora and how it is distributed including in relation to altitude and aspect. I will indicate the history of the conservation of these plants and discuss whether we can continue to protect these species in future.