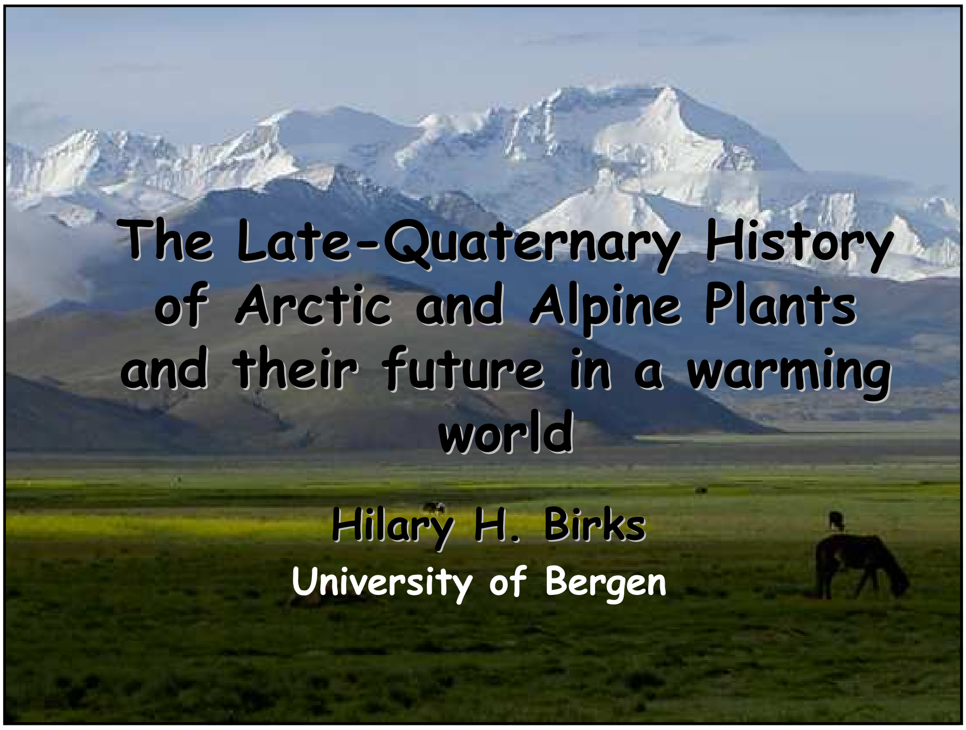
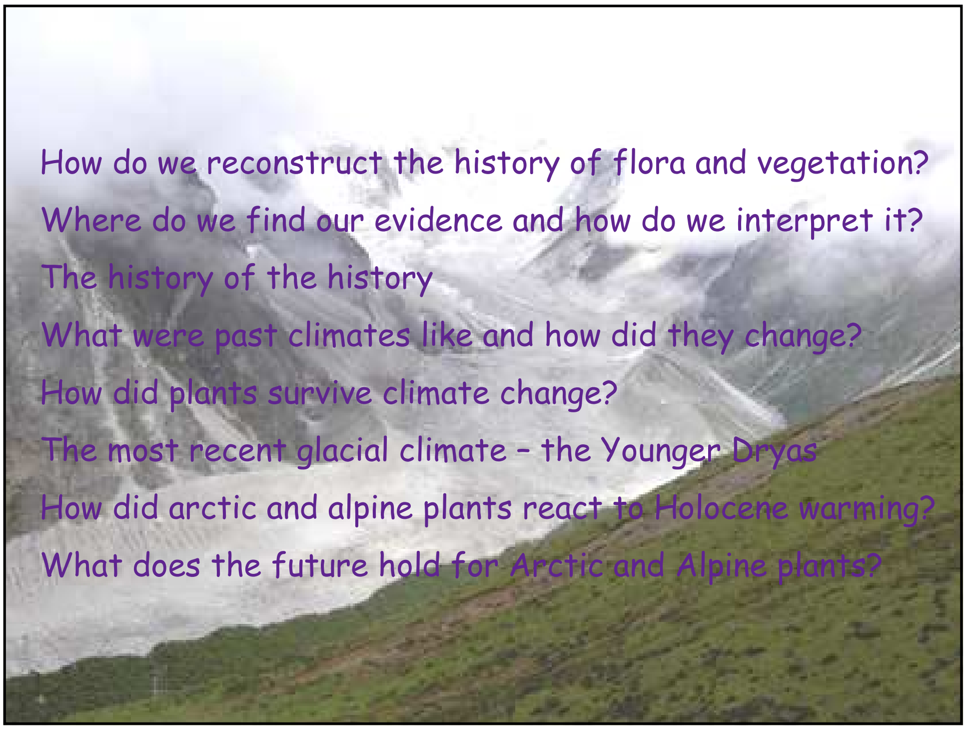

The Late-Quaternary History of Arctic and Alpine Plants and their future in a warming world
Hilary H. Birks
University of Bergen


How do we reconstruct the history of flora and vegetation?
Where do we find our evidence and how do we interpret it?
The history of the history
What were past climates like and how did they change?
How did plants survive climate change?
The most recent glacial climate – the Younger Dryas
How did arctic and alpine plants react to Holocene warming?
What does the future hold for Arctic and Alpine plants?

1. Evidence of past flora and its changes

Fossils

- Pollen - microscopic
- Macrofossils – can be seen with naked eye. Seeds, fruits, leaves, etc.

Molecular DNA analyses of living arctic alpines can complement the fossil record. Find different populations in space today and deduce past migrations

Fossil DNA extraction from sediments or plant remains is becoming increasingly sophisticated

Pollen grains and spores

- Walls are sporopollenin, very resistant to decay
- Preserve well in anaerobic environments, e.g. lake sediments, peats
- Can be extracted from the sediment matrix using chemicals to remove the organic and inorganic sediment components
- Counted under a high-power microscope
- Frequent enough to allow percentage calculations of abundance

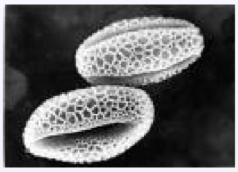
BUT - in glacial and late-glacial environments:

- Wind-dispersed pollen types dominate the assemblages (grasses, sedges, *Artemisia*)
- Arctic and alpine herbs generally produce rather little pollen
- They are frequently insect pollinated
- In landscapes with plants with low pollen productivity, long-distance-dispersed pollen can dominate the assemblage, e.g. tree pollen can be common but there are no trees growing locally (as on Svalbard today)
- Many pollen types are hard to identify to species-level

Some pollen grains

Woody plants

Betula



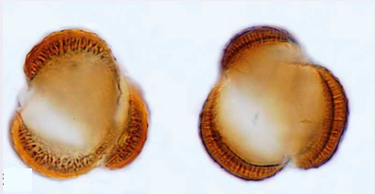
Salix

Ericaceae

Very common glacial pollen types (wind dispersed)

Poaceae (Gramineae)

Cyperaceae

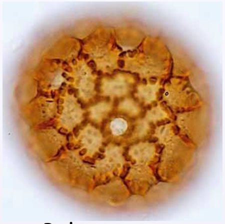


Artemisia

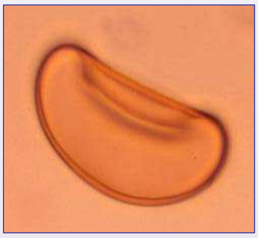
A wide range of herb pollen-types of arctic and alpine environments is found

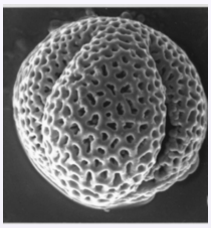

Asteraceae, Tubuliflorae

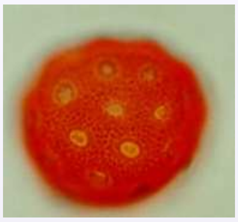

Asteraceae, Liguliflorae


Polygonum persicaria type


Armeria


Fern spore


Brassicaceae


Chenopodiaceae


Caryophyllaceae

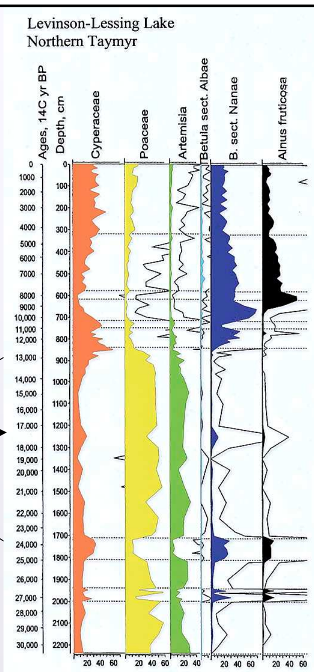

Polemonium

Pollen diagram

30,000 - 0 years

Northern Siberia

Full glacial



J. Hahne and M. Melles, 1999. In: Kassens et al. (eds). Land-Ocean Systems in the Siberian Arctic: Dynamics and History. Springer-Verlag, Berlin, p. 407-423.

Percentages of pollen and spores from intestinal samples mammoth

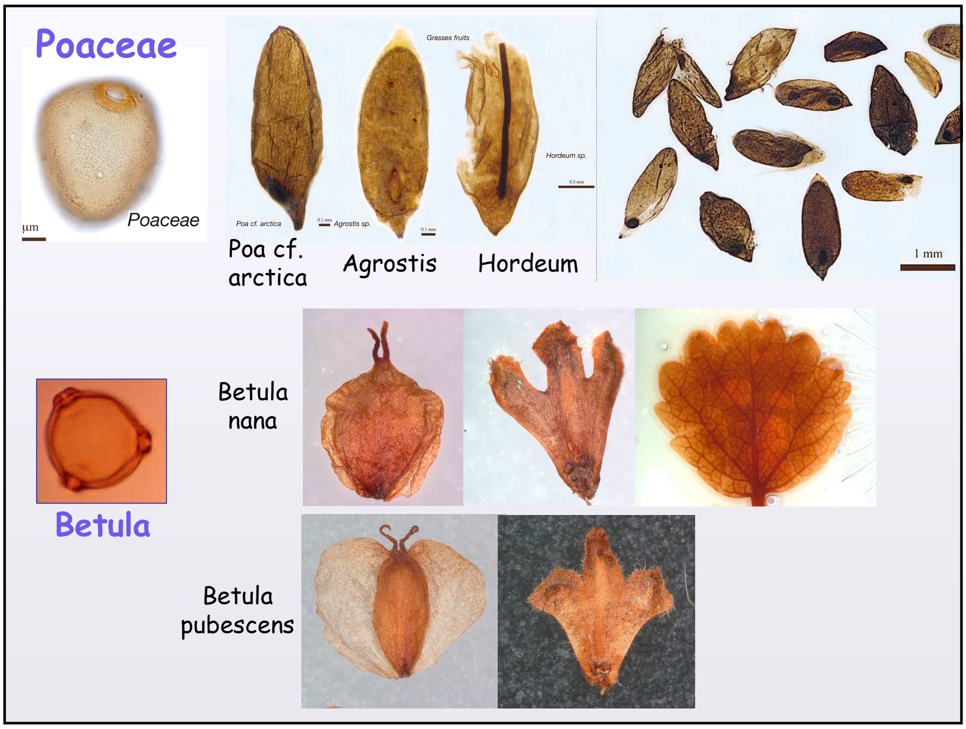
cf. Androsace	0.2
Apiaceae	0.3
Artemisia	16.0 ←
Asteraceae liguliflorae	0.2
Asteraceae tubuliflorae	0.2
Brassicaceae	0.7
Caryophyllaceae	4.7
Chenopodiaceae	0.1
Cyperaceae	0.1
Tricolpate with appendages	1.9
Epipactis	+
Ericales	0.1
Fabaceae	1.4
Liliaceae	+
Lotus	0.2
Papaver	0.1
Periporate with spinules	+
Plantago spec.	0.8
Plumbaginaceae Armeria type	+
Poaceae	70.6 ←
Polemonium	0.2
Polygonum persicaria type	0.3
Potentilla type	0.9
Ranunculaceae	0.7
Rosaceae undiff.	0.2
Rumex acetosa type	0.8
Salix	0.2
Sanguisorba officinalis	0.1
Σ-pollen	1914
Coprophilous fungi:	
Sporormiella type	4.7
Podospora type	+
Sordaria type	0.8
Cercophora type	+
Algae:	
Spirogyra	+
Pediastrum	0.1

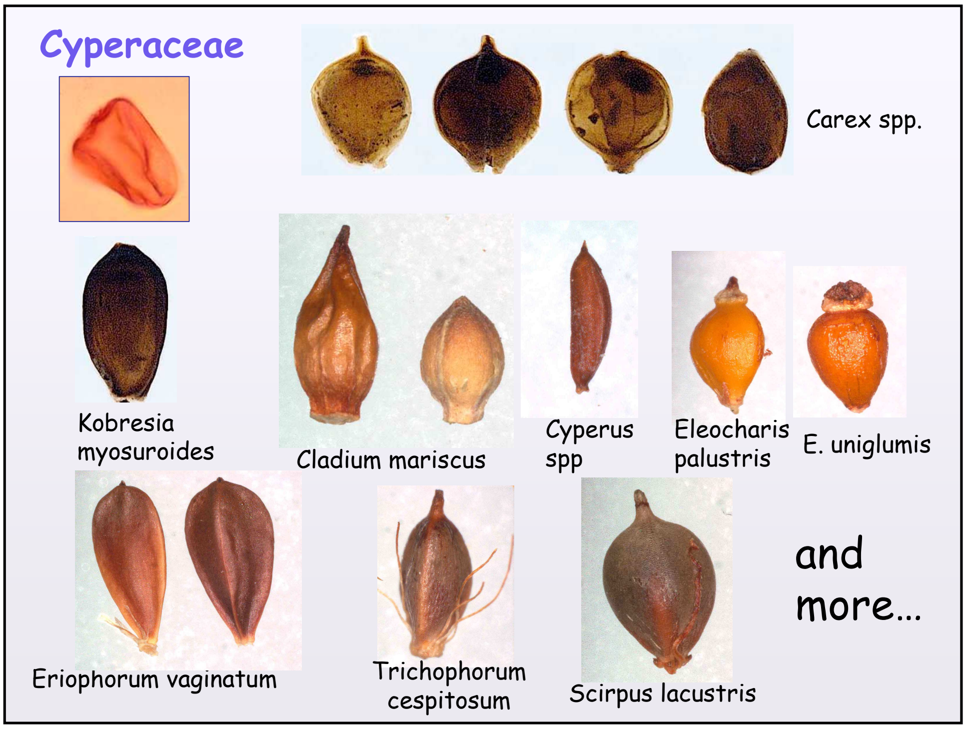
Macrofossils

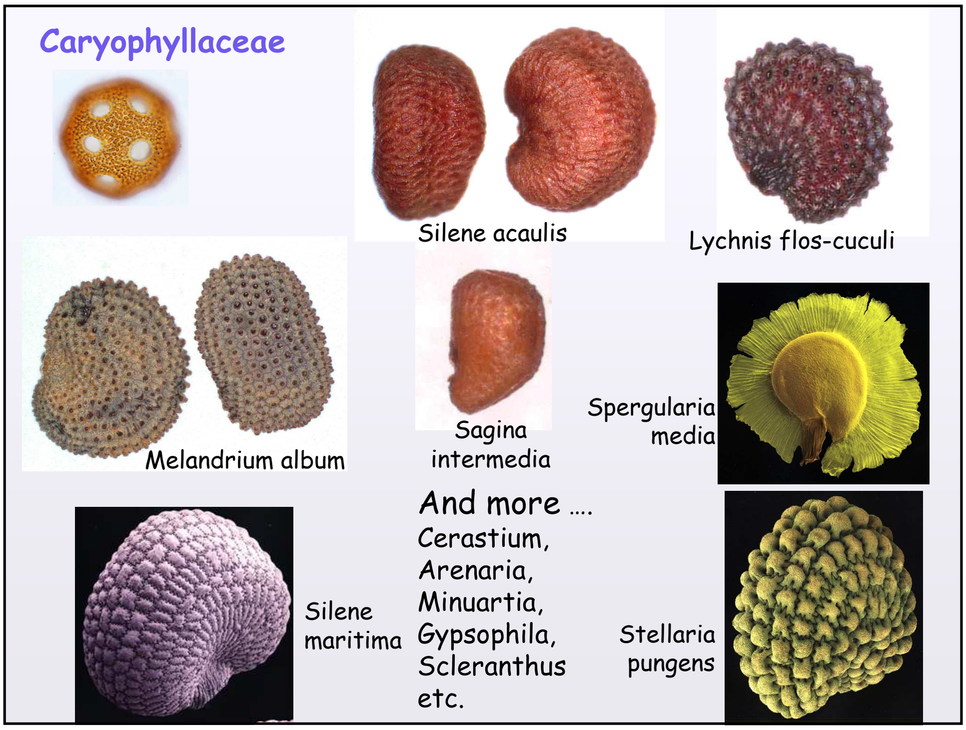
- Seeds, fruits, leaves, twigs, buds, megaspores, mosses etc.
- Macrofossils can often be identified to a lower taxonomic level than pollen (e.g. to species or genus)
- They are often well preserved in anoxic environments and also in glacial environments such as glacial river deposits and permafrost
- Being relatively heavy, macrofossils are usually not transported far from their place of origin
- Therefore they give a good idea of plants that were growing locally

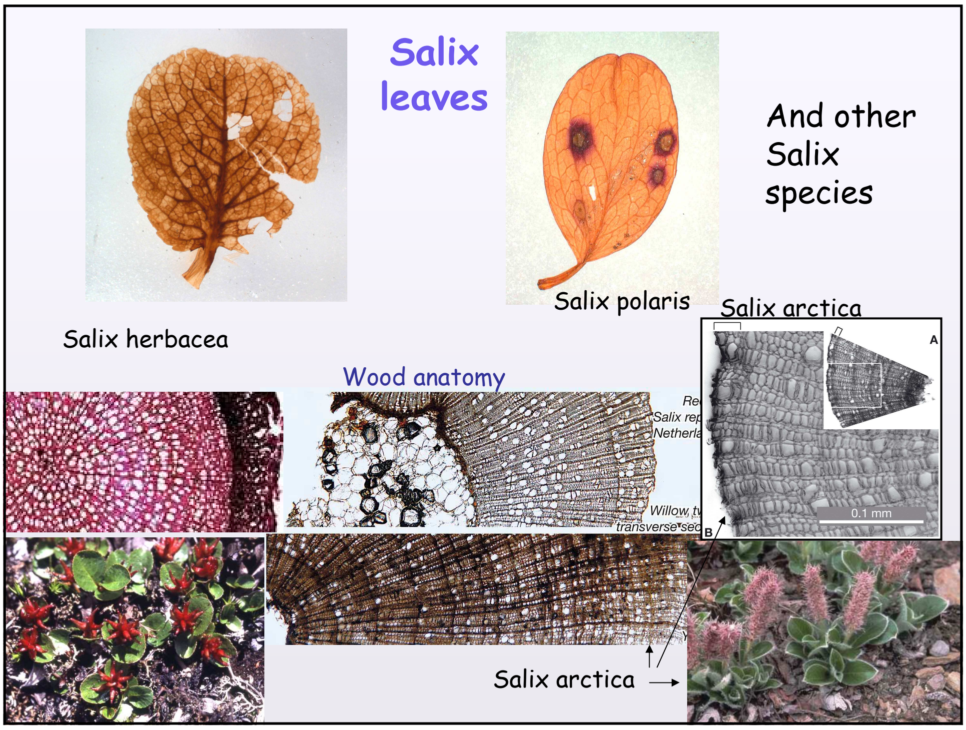
BUT

- Macrofossils are usually found in smaller quantities than pollen, so larger amounts of sediment need to be collected and analysed
- The representation among species is very variable, so they are expressed as concentrations in a volume or mass of sediment, rather than percentages
- Many potential macrofossils do not reach sites of deposition and the reconstruction of the vegetation follows an analogue approach based on modern ecological knowledge and indicator species




Cyperaceae
Carex spp.
Kobresia myosuroides
Cladium mariscus
Cyperus spp
Eleocharis palustris
E. uniglumis
Eriophorum vaginatum
Trichophorum cespitosum
Scirpus lacustris
and more…


Caryophyllaceae
Silene acaulis
Lychnis flos-cuculi
Melandrium album
Sagina intermedia
Spergularia media
And more ….
Cerastium,
Arenaria,
Minuartia,
Gypsophila,
Scleranthus
etc.
Silene maritima
Stellaria pungens



Pollen　　Herbs　　Macrofossils

Asteraceae Tubuliflorae: e.g. Cirsium, Carduus, Senecio, Petasites, Gnaphalium, Aster, Artemisia, Eupatorium

Asteraceae Liguliflorae: e.g. Taraxacum, Leontodon, Crepis, Cicerbita, Sonchus, Hieraceum, Saussurea

Brassicaceae: e.g. Draba, Cochlearia, Rorippa, Arabis, Subularia, Cardaminopsis, Cardamine, Braya

Ranunculaceae: Ranunculus spp., also Batrachium, Caltha, Thalictrum, Trollius, Pulsatilla, Clematis, Anemone, Aquilegia

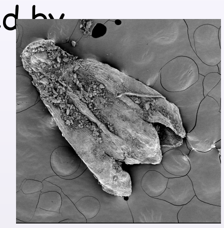
Rosaceae: Potentilla spp., Dryas, Filipendula, Rubus, Alchemilla

Saxifragaceae: Saxifraga most species, Parnassia, Chrysosplenium

Some pollen types can give genus or species information, e.g. Armeria, Thalictrum, Dryas, Filipendula, Trollius, Plantago spp.

Some pollen types are poorly represented by macrofossils: **Artemisia**

Macrofossils have been found in Yukon and Siberia during full-glacial period



Pollen and macrofossil analyses complement each other

Birks and Birks 2000, J. Biogeography

2.Where do we find fossil evidence?

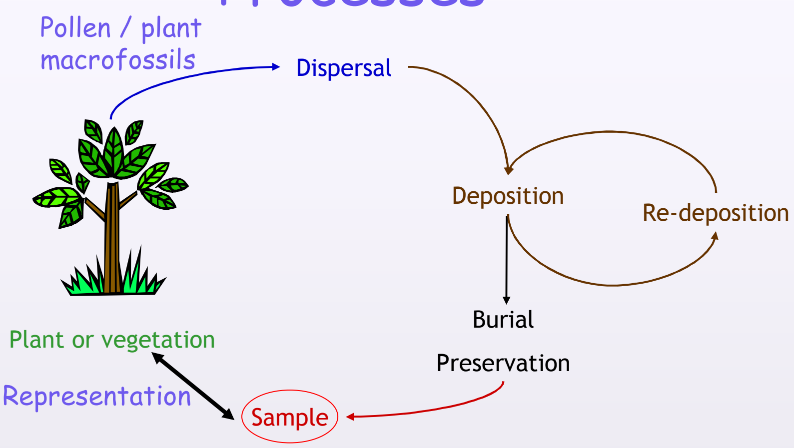
Anaerobic environments:

- 1. Lake sediments
- 2. Glacio-fluvial sediments
- 3. Peat sediments / permafrost soils
- 4. Dung / stomach contents

Dry environments

- 5. Rodent middens or nests in permafrost

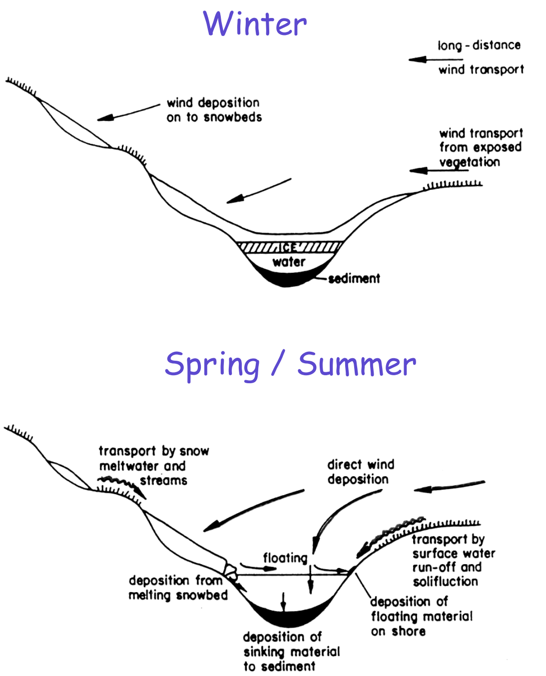
Processes



The sample will always be an imperfect representation of the occurrence of species and their abundance in the vegetation. Therefore we interpret past vegetation by use of indicator species and modern analogues. But this does not provide evidence of the occurrence of species not present in the fossil assemblage

How do plant remains reach lake sediments in the arctic or alpine regions?

Diagrammatic representation of processes leading to deposition of plant parts in the sediments of a small lake in the arctic or above the tree line.



Birks (1991) Holocene 1

Snowbed leaf assemblage in Alaska – Dryas leaves

Salix herbacea leaf assemblage in Norway

Fanaråken, Norway

2. Glacio-fluvial Environments

Pleistocene gravels

Beetley gravel pit, S. England

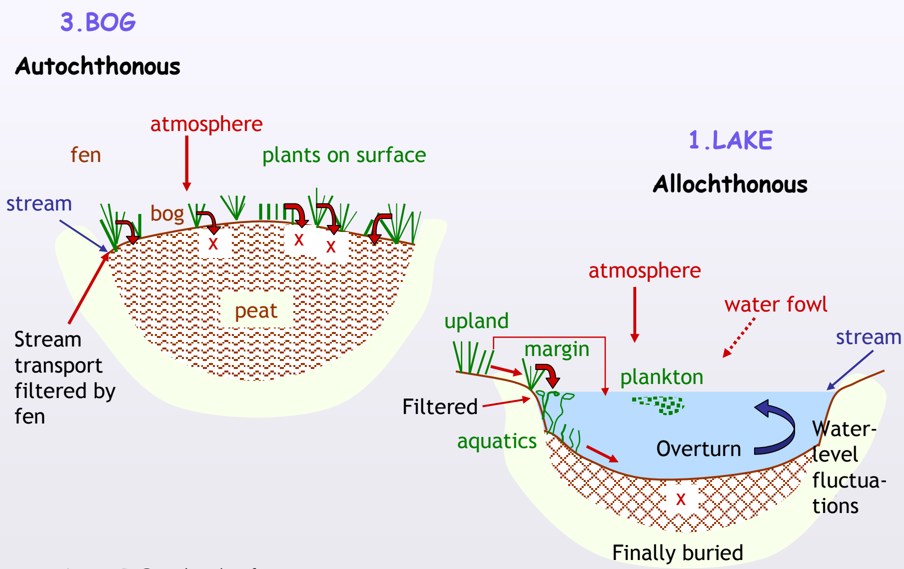
Last Glacial Maximum

Modern analogues

Tanana River – modern braided river in Alaska

Spitsbergen, Longyearbyen

Taphonomy is important for interpretation of pollen and macrofossils



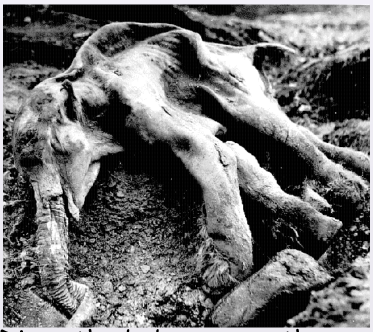
H.H. Birks, 2007, Encyclopedia of Quaternary Science.

4. Permafrost-preserved bodies and dung

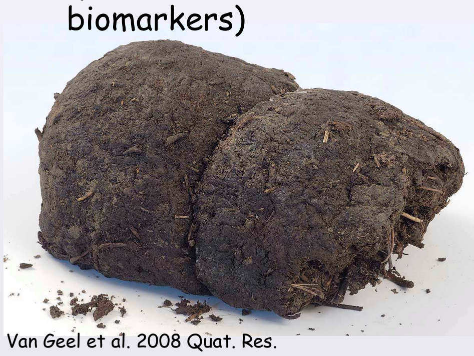
Yukagir Mammoth

Many mammoths have been discovered preserved in permafrost in Siberia. You may have seen the story of the Jarkov mammoth on 'Discovery Channel'

Dung – diet and flora (pollen, macros, DNA, biomarkers)



Dima, the baby mammoth



Van Geel et al. 2008 Quat. Res.

The Iceman Ötzi

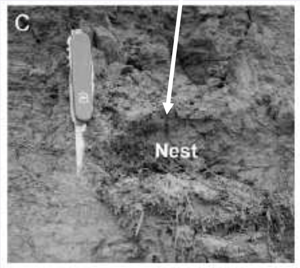
The Iceman returned to Italy in 1998. He is housed in the museum in Bolzano. Kept at -6ºC in 100% humid atmosphere

Macrofossils provided evidence of his clothing, equipment, and diet. Pollen provided evidence of his home

5. Rodent nest and vegetation overlain by 28,000 year old tephra and preserved in permafrost, Yukon

Many grasses, sedges, and *Kobresia myosuroides*

Diversity of herbs and bryophytes of xeric steppe-tundra and mesic riparian meadow



Zazula et al. 2006 Palaeo3, 242

Obtaining Samples

1. Open section -

Whitrig Bog Late Glacial (Scotland)

2. Coring from open water


raft

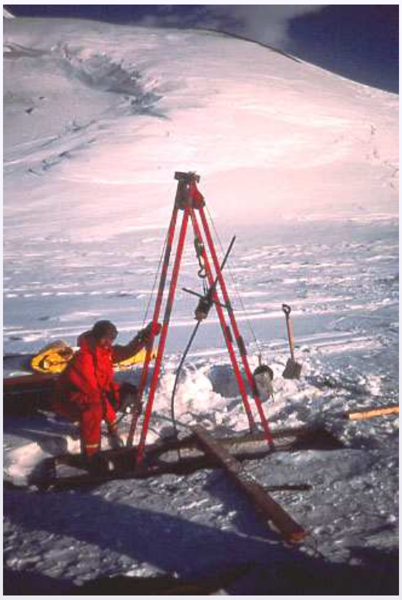

piston corer


extruding the core

Wide diameter (11 cm) 6m long cores for multi-proxy analyses

3. Coring from ice

6 m long, 11 cm diameter
'Nesje corer'



Looking for vegetation history
on Svalbard

4. Coring from a marsh or bog

Deep
sediments

11 cm diameter, 2 m long, piston
corer and heavy frame; Kråkenes

Shallow
sediments

Sediment Cores

'Russian' core

Piston core

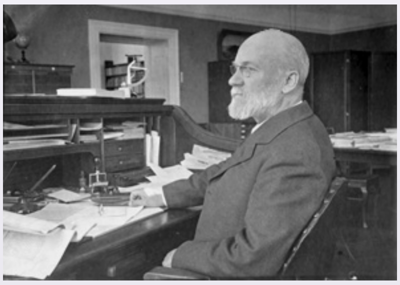
3.

Interlude

History of Late-glacial investigations; the discovery of past climate change

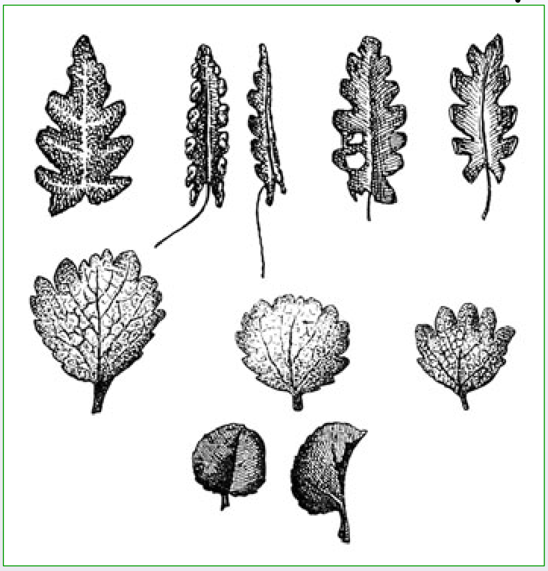
- 1870: Alfred Gabriel **Nathorst** (Swedish) found the remains of arctic plants (leaves and fruits) in a clay layer under a peat bog in southern Sweden (Dryas clays)
- 1871: **Nathorst** and Japetus **Steenstrup** found similar arctic layers in Denmark (Dryas octopetala, Betula nana, Saxifraga oppositifolia). 'Dryas time'.

Steenstrup



Nathorst

Leaves of the 'Dryas' Flora



Dryas octopetala

Betula nana

Salix herbacea

J. Iversen 1973. Danm Geol Unders V Række 7-C

1887-1900: **N. Hartz** and **V. Milthers** (1901) found a gyttja layer within the clay layer at **Allerød** brickpit (teglverksgrav) in Denmark. It contained a flora with tree-birch, whereas the clay contained an arctic flora. They had found the late-glacial oscillation

1935: **Knud Jessen** described the stratigraphy in three zones: Older Dryas, **Allerød**, and Younger Dryas. They could be distinguished by pollen analysis as well as by plant macrofossils

He later (1949) investigated the vegetation history (including the late-glacial) in Ireland

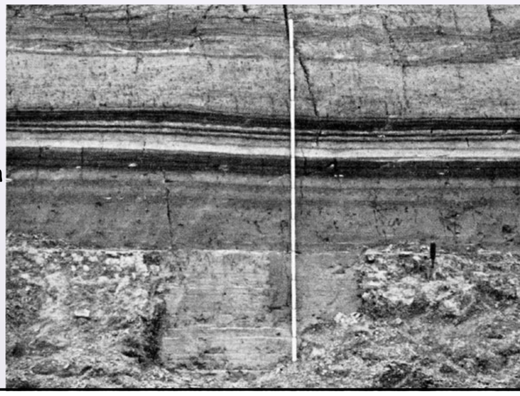
Knud Jessen

Late-glacial stratigraphy

Section of Ruds Vedby Brickwork's clay pit (Denmark). The Allerød layers appear as two dark layers (gyttja) separated by a light one (marl).

Part of the section from which the samples for ^{14}C-dating and pollen analysis were taken.

Rule = 2m.



Holocene
post glacial

Younger Dryas

Allerød

Oldest Dryas

1942: **Johs Iversen** described a second gyttja layer below the first at **Bølling**. It contained a tree-birch pollen flora

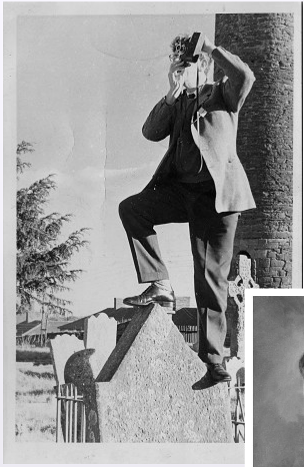
Johannes Iversen

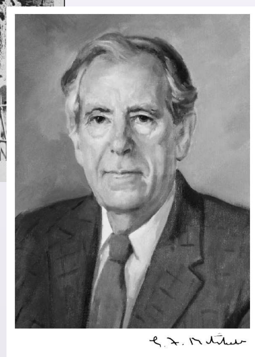
Late-glacial stratigraphy

^{14}C ages BP		Calibrated ages BP
	Holocene	
10,000		11,550
	Younger Dryas	
11,000		12,700
	Allerød	
12,000		14,000
	Older Dryas	
12,200		14,200
	Bølling	
13,000		~15,000
	Oldest Dryas	

Frank Mitchell in 1954 recorded the occurrence of 120 plant taxa in the late-glacial of Ireland. Salix herbacea was particularly common – 'Salix herbacea clays' – Jessen (1949)

63 species were recorded from both the Irish late-glacial and in Lapland today on dry, south-facing slopes with open vegetation – a modern analogue





Phytogeographical element (according to Hultén 1950 – Atlas)	Modern Lapland slopes	Late-glacial Ireland
Arctic circumpolar	1	0
Arctic-montane, including mountains of Europe	49	15
Arctic-montane, excluding mountains of Europe	5	1
Boreal circumpolar	13	31
Boreal montane	12	10
Eurasiatic	5	24
Other	6	22
Total	91	103

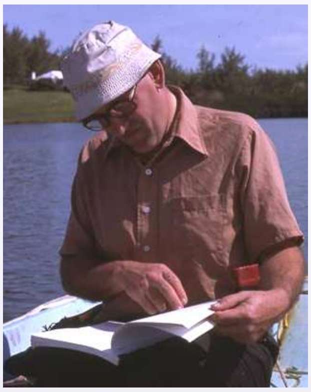
Mitchell (1954) Danmarks Geologiske Undersøkelse II Række, 80: 73-86

Modern analogue for full- and late-glacial vegetation

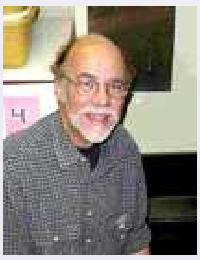
Artemisia frigida

Moose Creek
Bluff, Alaska

Investigations were continued by **Bill Watts** in Ireland. (W.A. Watts (1977) Phil Trans R Soc B 280:273). He also did the first detailed macrofossil analyses from the late Wisconsin in USA (Watts and Winter (1966) Bull Geol Soc Am 77).



His student **Dick Baker** continued macrofossil analyses of late-glacial sediments in mid-west USA. **Norton Miller** also did important work in eastern USA, including identification of fossil mosses.

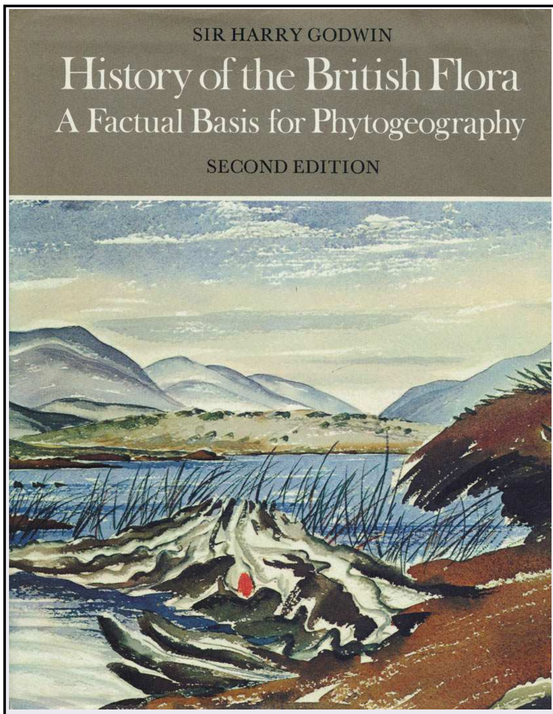


Meanwhile in Central Europe early work on historical phytogeography was done by **Oswald Heer, Adolf Engler, Carl Albert Weber, Wladyslaw Szafer, Werner Lüdi, Helmut Gams, Franz Firbas,** and **Max Welten**.
(see **G. Lang**, 1994, Quatäre Vegetationasgeschichte Europas)

Some syntheses of the fossil history of arctic and alpine plants in Europe have been made by **Hans Tralau** (1963) and **Gerhard Lang** (1994)

In Britain, the pioneers were **James Geike** and **F.J. Lewis,** followed by the study of the Lea Valley arctic plant beds by **C. & E. Reid** and other glacial deposits by **M.E.J. Chaloner**

Harry Godwin then played a central role in synthesising all fossil records from Britain as 'The History of the British Flora' (1956, 1975)



This was the first data-base* of Quaternary floristic records. Godwin's synthesis showed how fossil evidence provided the factual basis for phytogeography

*Paleo-eco-informatics!

Data bases

Godwin's data-base and his synthesis in his book have proved invaluable for phytogeographers – The Factual Basis

Much of the older literature is inaccessible or in the authors' native language.

Modern, computerised, interactive data-bases are now being made for fossil data

Active public pollen data-bases exist for North America (Neotoma), Europe, (Africa)

There is an active public macrofossil data-base in N. America, (Neotoma) [http://www.neotomadb.org] and one is being prepared for Europe and N. Asia

For the study of the phytogeography and evolution of alpine and arctic plants, data-bases for all parts of the world are an invaluable tool

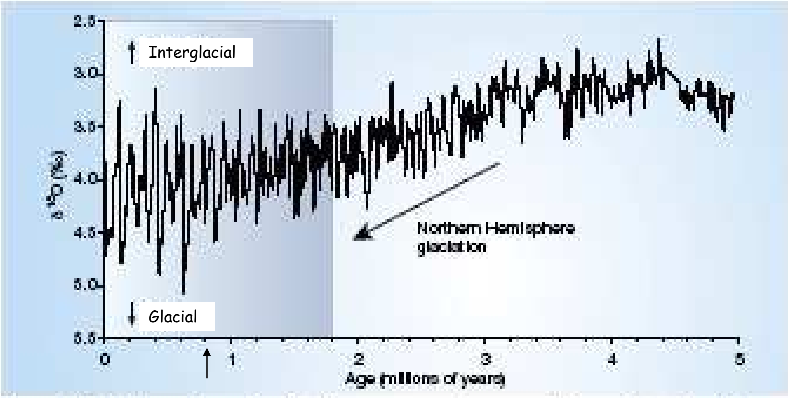
4.

Past Climate Change

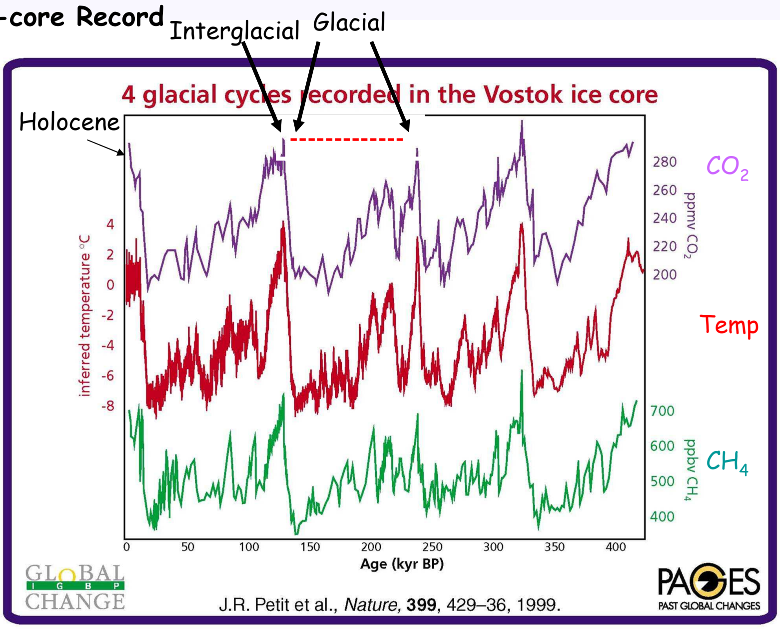
What did plants have to put up with?

- The **Quaternary** period is the past 2.7 million years (Myr) of Earth's history. A time of very marked **climatic** and environmental **changes**
- Large terrestrial ice-caps started to form in the Northern Hemisphere about 2.7 Myr, resulting in multiple **glacial-interglacial cycles** driven by variations in orbital insolation on Milankovitch time-scales of 400, 100, 41, and 19-23 thousand year (kyr) intervals
- **Glacial conditions** account for up to **80%** of the Quaternary
- **Remaining 20%** consist of shorter **interglacial** periods during which conditions were similar to, or warmer than, present day

Global Climate Change 5 million years to present
(Oxygen isotope record in marine foraminifera; higher values indicate more ice)



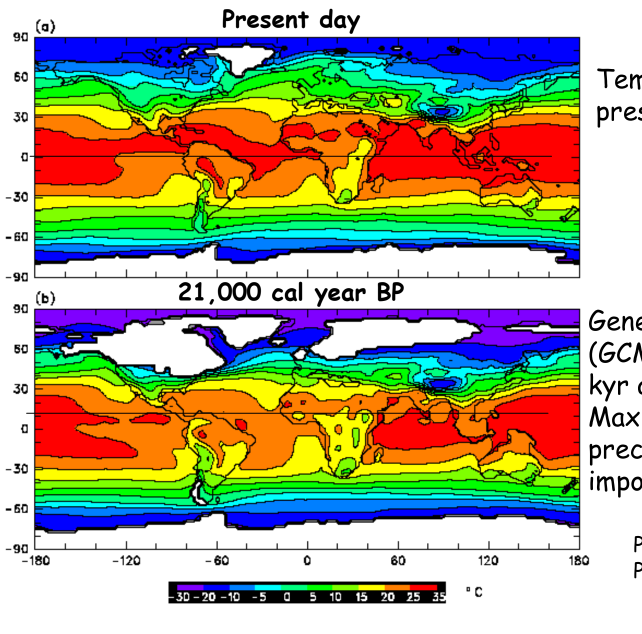
Ice-core Record



Sudden rapid warming. Gradual oscillating cooling
100,000 years of glacial, 25,000 years of interglacial

Glacial conditions:

1. Large terrestrial ice-sheets
2. Widespread permafrost
3. Temperatures 10-25°C lower than present at high-mid latitudes
4. High aridity and temperatures 2-5°C lower than present at low latitudes
5. Global atmospheric CO_2 concentrations as low as 180 ppmv rising to pre-industrial levels of ca. 280 ppmv in intervening interglacials
6. Steep climatic gradient across Europe and Asia during the Last Glacial Maximum (LGM)



Temperatures of present day

General circulation model (GCM) simulations of 21 kyr ago - Last Glacial Maximum. Changes in precipitation are also important

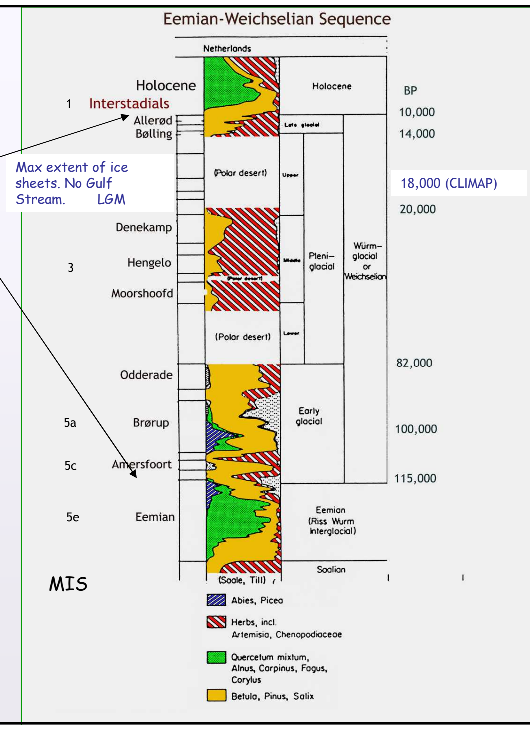
Pollard & Thompson, 1997; Peltier, 1994

Last Glaciation in North-west Europe
(Weichselian)

115,000 – 11,550 yrs ago

Discontinuous sequence on land

Detailed continuous sequences from Greenland ice cores and marine sediments



In each cold stage, arctic-alpine plants spread southwards in Europe and out from the C. European mountains

Britain – records of cold-stage plants

Beestonian (Cromerian complex): Betula nana, S. herbacea, Saxifraga spp., Oxyria digyna, Thalictrum alpinum, T. minus, Ranunculus hyperboreus, Salix polaris

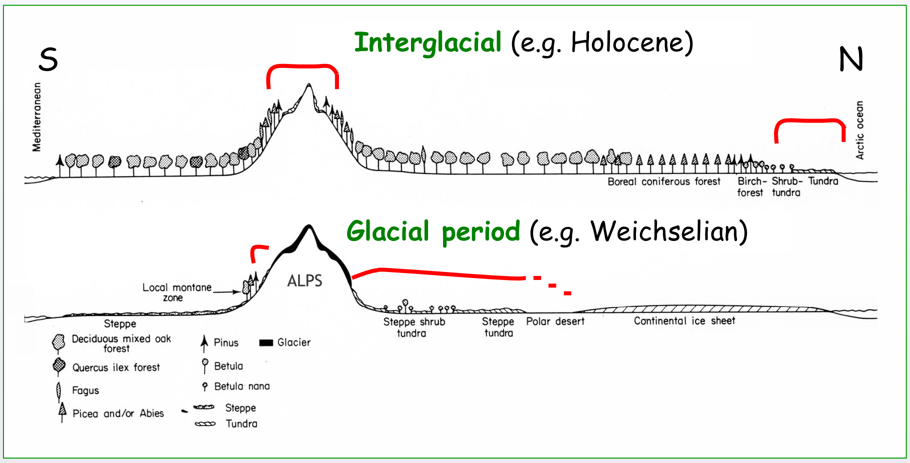
Early Weichselian: Arenaria ciliata, Draba incana, Thalictrum alpinum, Armeria maritima

Middle Weichselian – arctic plant beds in S. England (LGM): Salix herbacea, S. phylicifolia, S. viminalis, Juniperus, Empetrum, Oxyria digyna, Saxifraga hypnoides, Potentilla fruticosa, Minuartia stricta, M. verna, Primula cf. farinosa, Thalictrum alpinum, Draba incana, Arenaria spp., Silene furcata, Stellaria crassifolia, Papaver sect. Scapiflora, Ranunculus hyperboreus, R. aconitifolius, Carex capitata, Pedicularis hirsuta, P. lanata, Salix polaris.

(Extinct in British Isles)

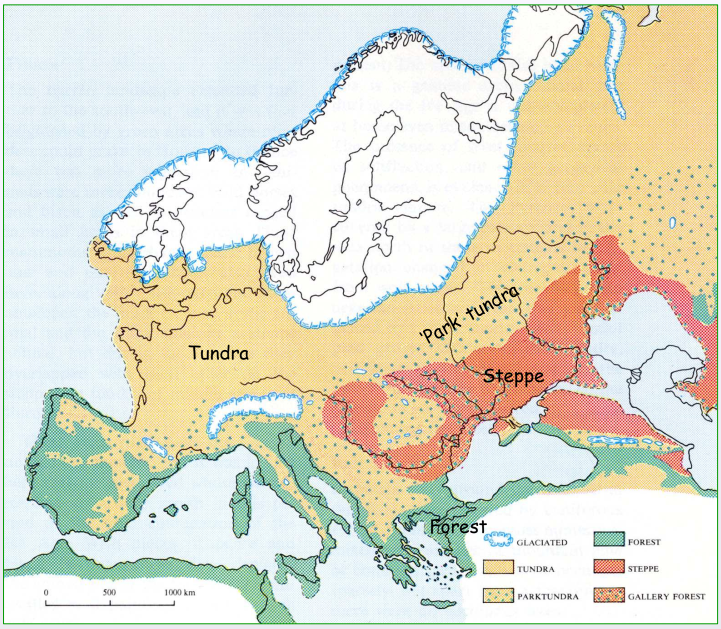
From Godwin 1975

Where were the arctic alpines?



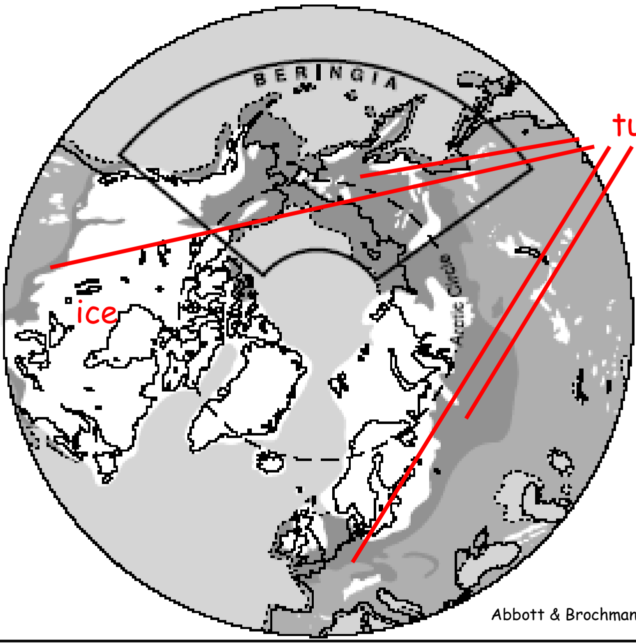
Schematic representation of the vegetation during an interglacial and during a glacial, in a south-north section through Europe.

Europe 20,000 years ago (Last Glacial Maximum or LGM)



Iversen (1973)

Ice sheets and tundra at the LGM (20,000 yr ago)



Large areas in Beringia and Siberia, moderate areas in Europe, small areas in N. America

Abbott & Brochmann 2003; Molecular Ecology 12.

LGM climates

Greenland and eastern N. America – much colder (10-20°C lower mean annual temperature)

Central Europe - cold but with milder areas in the south, e.g. river valleys, south-facing slopes. Habitats for steppe animals and people.

Siberia and Beringia – cold winters, relatively warm summers - continental. 'Tundra' was 'Mammoth Steppe'.

Most areas were relatively **arid**, especially Beringia and Siberia – high insolation, low cloud cover. Western Norway received much precipitation at the western side of the Fennoscandian ice sheet.

What was the European LGM landscape like?

In the lowlands **north of the Alps**, a mosaic of:

1. **open-ground habitats** on well-drained soils (permafrost) and exposed sites supporting a mixture of alpines, steppe, and 'weed' taxa
2. **snow beds; willow scrub** on damper soils
3. **tree populations** on sheltered localities along river banks, in valleys, and in depressions where there was moisture and some shelter, especially in the south (scattered refugia)

In the mountains **south of the Alps**, a mosaic of:

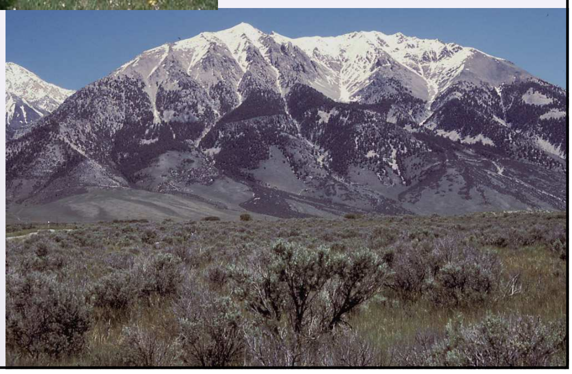
1. low-altitude **steppe** or **shrub steppe**
2. **belt of trees** at mid-altitudes where there was adequate moisture and temperatures were not too cold (tree refugia)
3. high-altitude **open habitats** with alpines and cold-tolerant steppe plants

North of the Alps

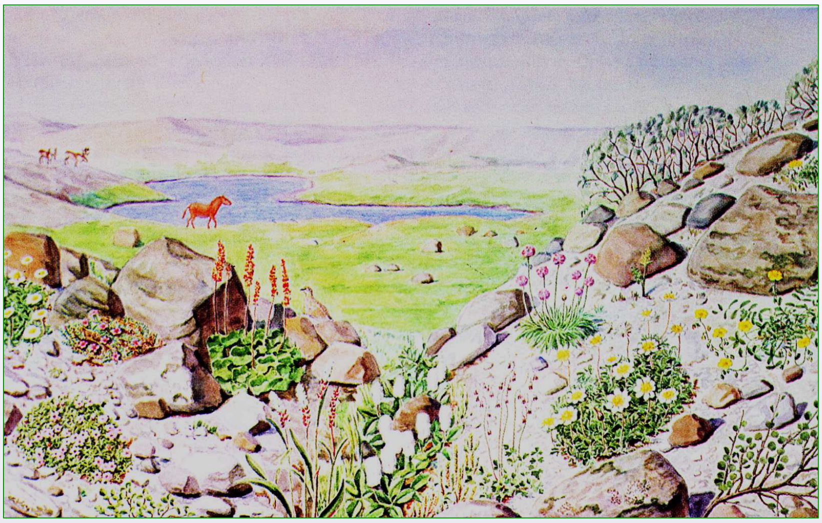
(Sichuan, China)

South of the Alps

(Borah Peak, Idaho)



Summer in the 'Older Dryas' period (LGM) in Denmark Iversen (1973)



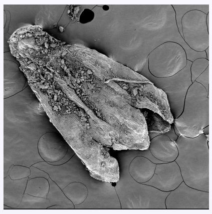
Treeless steppe and tundra; permafrost, soil disturbance; wind, loess deposition; mineral soils, no humus (calcareous 'white earth'); arctic-alpine and steppe plants; steppe animals, horses, bison, mammoths, woolly rhinos, sabre-toothed cats, humans etc.

Possible analogue LGM landscapes in central Europe

Open steppe with abundant *Artemisia* and Chenopodiaceae, and extensive loess deposition

The pollen assemblages are dominated by grasses (Poaceae) and *Artemisia* plus other steppe taxa

LGM Yukon macrofossils



Xeric steppe species:

Artemisia frigida (leaves, flowers)

Bunch grasses (e.g. *Poa, Elymus, Festuca, Kobresia)*

Xeric herbs – open habitats:

Potentilla, Chenopodium, Draba, Papaver Sect. *Scapiflora, Androsace septentrionalis, Cerastium, Silene uralensis, Minuartia rubella, Draba* spp., *Achillea, Saxifraga oppositifolia.*
Plus pollen of *Phlox, Plantago, Selaginella sibirica, Saxifraga tricuspidata, etc.*

Meadow plants:

Deschampsia, Carex aquatilis, C. maritima, Juncus/Luzula, Polygonum alaskanum, Oxyria, Ranunculus, Taraxacum ceratophorum

Shrubs; *Salix, Dryas*

Mosses; *Drepanocladus vernicosus, Scorpidium scorpioides, Calliergon* spp.

Zazula et al. 2006 Quat International 142

Full-glacial species on a buried soil on Seward Peninsula, Alaska

- A mosaic of graminoids and herbs in an acrocarpous moss matrix, and Salix snow-beds. Continuous Ca-rich loess supply
- The most abundant, ubiquitous plant was <u>Kobresia myosuroides</u>
- Common plants, found in many samples

Draba (abundant)	Polygonum viviparum
Carex nardina-type	Potentilla hookeriana
Minuartia obtusiloba	Potentilla hyparctica-type
Papaver sect. Scapiflora	

Goetcheus & Birks
QSR 2001

Rare plants – indicator species

Salix arctica	*Carex bigelowii*-type
Bupleurum triradiatum	*Campanula uniflora*
Cerastium beeringianum	*cf Artemisia* (seed)
Melandrium affine	*Melandrium apetalum*
Minuartia arctica	*Oxyria digyna*
Potentilla nivea-type	Primulaceae
Ranunculus sp.	*Saxifraga oppositifolia*
Taraxacum	*Valeriana*

Mosses of dry, open habitats

Nearly all are calciphiles

Abietinella abietina *Aloina* cf. *brevirostris*

Bryoerythrophyllum recurvirostrum

Desmatodon leucostoma

Didymodon rigidulus var. *icmadophila*

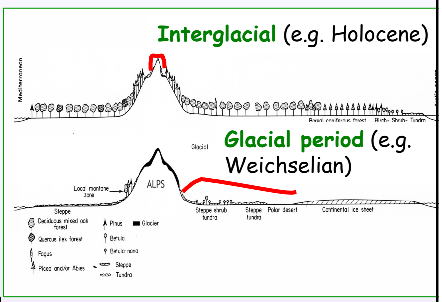
Distichium capillaceum	*Ditrichum flexicaule*
Encalypta alpina	*Eurhynchium pulchellum*
Fissidens arcticus	*Grimmia* spp.
Hypnum vaucheri	*Myurella julacea*
Stegonia pilifera	*Timmia austriaca*
Timmia norvegica var. *excurrens*	*Tortula norvegica*

Mosses of damp habitats

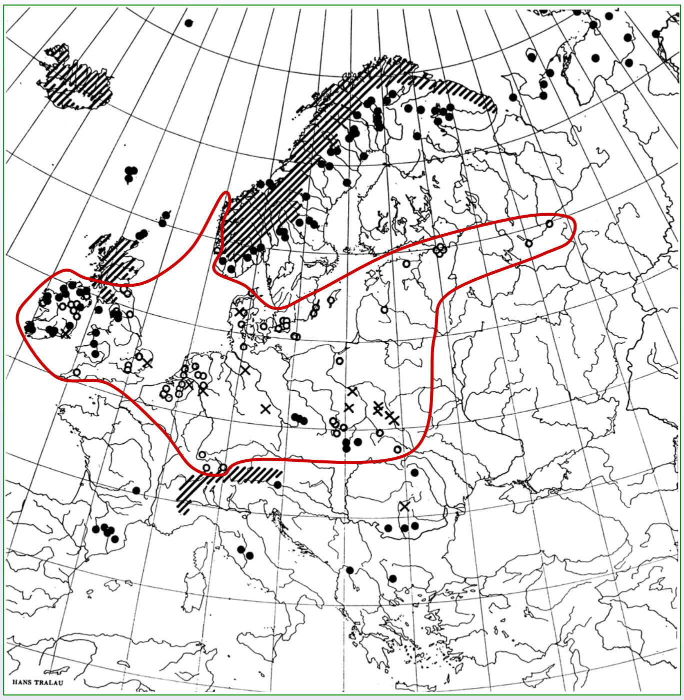
Amblystegium spp.
Brachythecium cf. *nelsonii*
Bryum neodamense
Campylium stellatum
Dicranum bonjeanii
Hypnum bambergeri
Plagiomnium ellipticum
Scorpidium turgescens
Tomenthypnum nitens
Brachythecium groenlandicum
Bryum cf. *pseudotriquetrum*
Campylium hispidulum
Dichodontium pelludicum
Drepanocladus brevifolius
Orthothecium strictum
Pohlia cf. *wahlenbergii*
cf. *Sanionia uncinata*

5. How did plants survive climate changes?

1. Cooling and cold glacials



- Pushed south by ice-sheets
- The area available became larger south of the ice and in unglaciated Siberia and Beringia
- Plenty of evidence that species were widespread south of the ice in Europe
- Nunataks? Definitely were unglaciated areas within the ice sheet, e.g. east Greenland, none in Norway. Very hardy species could perhaps have survived there; spread subsequently. No fossil evidence from nunataks
- In N. America, forest was close to the ice. Not much known about ice-age distributions of arctic alpines



Distribution of Salix herbacea in Europe

Present (/// ●), Weichselian (O), pre-Weichselian (X)

Tralau (1963) Kungl. Svenska Vetenskapsakademien

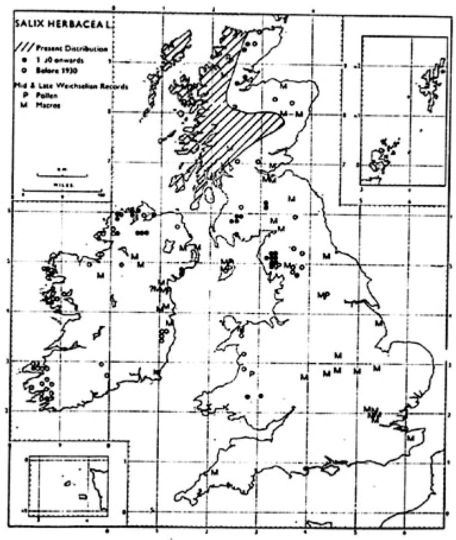
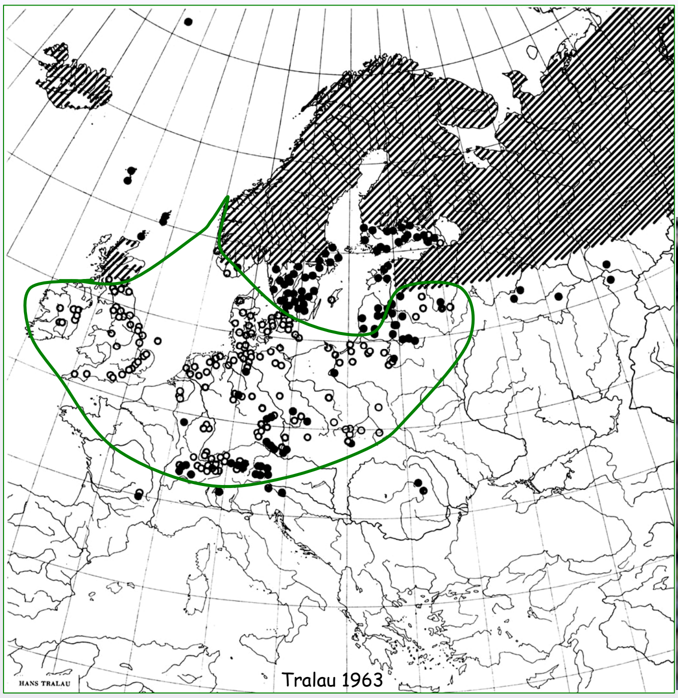


Fig. 98. Present and Weichselian distribution of *Salix herbacea* L. in the British Isles.

Salix herbacea

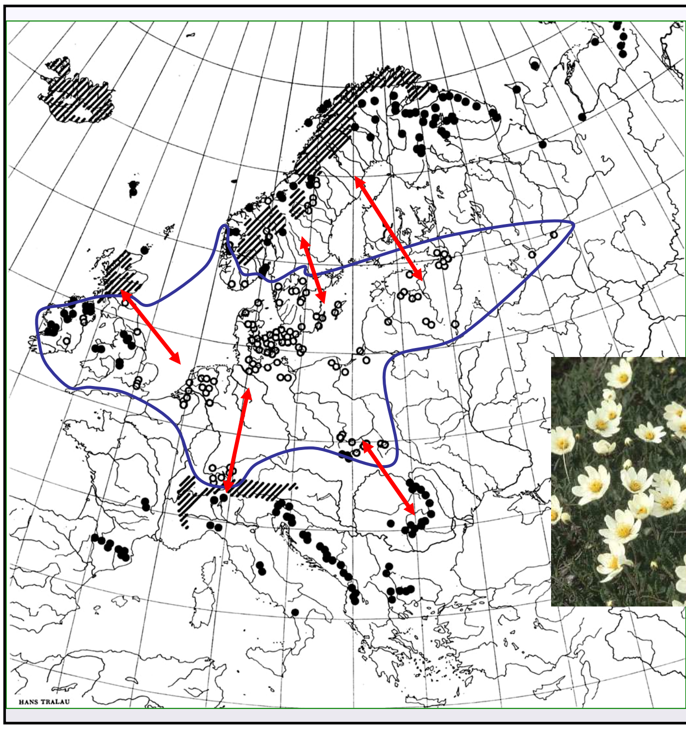
Salix herbacea in Britain

Godwin (1975) History of the British Flora



Distribution of *Betula nana* in Europe

Present (/// ●)
Weichselian (○)



Distribution of *Dryas octopetala* in Europe

Present (/// ●)
Weichselian (○)

Tralau 1963

Having been separated during warm periods, floras mixed again during glacial periods. Renewed gene mixing. Generally kept species stable. Some differentiation occurred through polypoidy etc.

Plants may have mixed across the N. Atlantic on moraine-covered ice-bergs (Fickert et al. (2007) Arctic, Antarctic, and Alpine Research 39, 245)

Glacial floras consisted of many elements all mixed together: Alpine, Arctic-alpine, Arctic-sub-arctic, Northern montane, Continental widespread, Continental southern, Continental northern, and, in W.Europe, various Atlantic elements

No modern analogues for these assemblages

How did plants survive climate changes?

2. Warming – transition to interglacial

- Pushed upwards or northwards by a) intolerable warmth or b) forest development and competition
- Spread from the deglaciated margins and possibly from nunataks as pioneers on deglaciated soils. Rapid spreading ability is documented
- Confined to circum-arctic areas or above the tree-line
- Relict populations in suitable places in the forest zone
- Holocene was wetter and cloudier. Permafrost with a shallow active layer developed in Siberia and Beringia. Impermeable soil became waterlogged and tussock tundra (*Eriophorum*) developed widely. Alpines confined to suitable refugia, e.g. steep south-facing slopes

How did plants survive climate changes? 3. Transition to Holocene; Younger Dryas

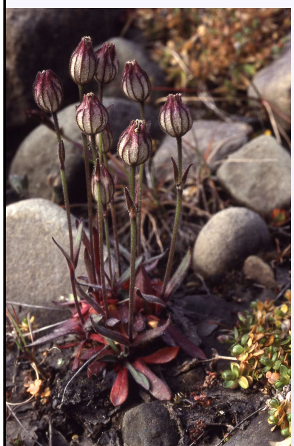
Younger Dryas – return to glacial climate for 1200 years after the initial warming (Bølling-Allerød Interstadial)

Strongly marked in NW Europe

Arctic alpines spread again as warmth-demanding vegetation was restricted once more

However some species had already been extirpated from some areas, e.g. Pedicularis hirsuta, Papaver radicatum agg., Silene uralensis, Salix polaris, from Britain; Koenigia islandica, Ranunculus hyperboreus, from central Europe

Some northern plants found as fossils in central Europe in LGM but not afterwards

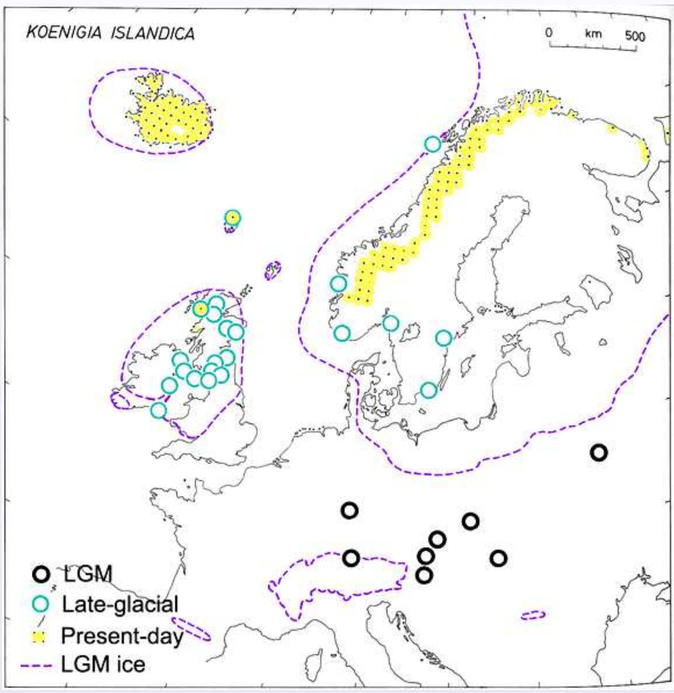


Silene uralensis

Salix polaris

Ranunculus hyperboreus

Pedicularis hirsuta

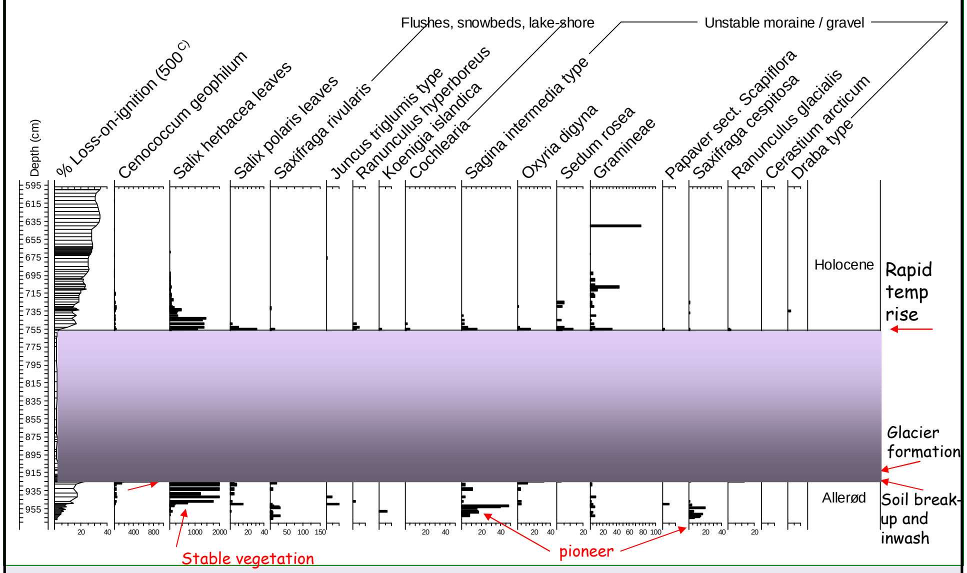


Koenigia islandica

Did not return to central Europe in the YD

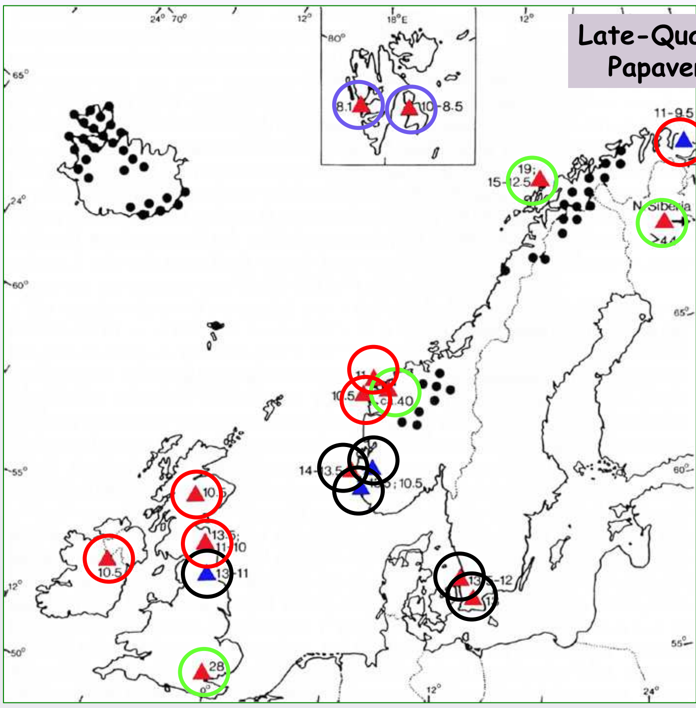
Arctic alpines spread in the YD in western Norway

Kråkenes macrofossils, Allerød and Younger Dryas



Papaver radicatum agg.
Absent from Britain today,
localised in Norway

Late-Quaternary history of Papaver radicatum agg.



● Modern distribution of *Papaver radicatum agg. (P. dahlianum* in Svalbard).

▲ Macrofossil (seed) localities for *Papaver* sect. *Scapiflora* with approximate ages (k yr BP).

▲ Localities of *Papaver* pollen with approximate ages (k yr BP).

Birks (1994) Diss. Bot. 234, 129

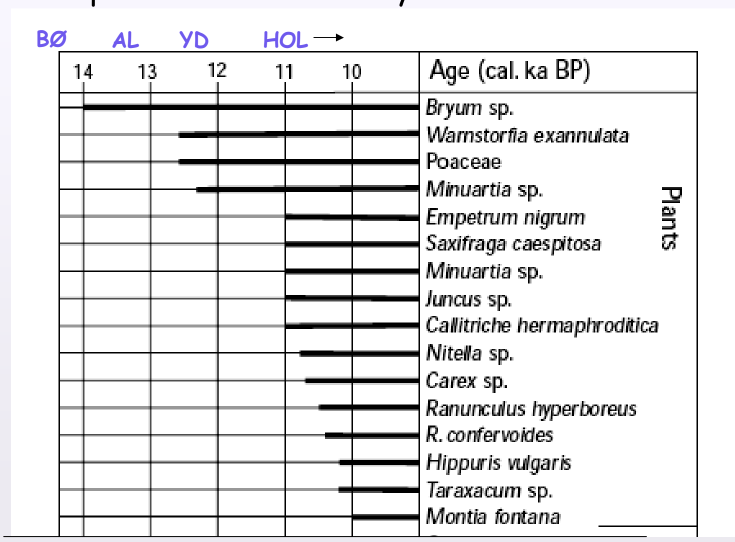
How did plants survive climate changes?

4. Transition from Younger Dryas to Holocene – rapid warming

- Temperature rose very fast ca. 11,600 yr ago; 6°C in 500 yr
- Organisms reacted equally fast; immigration, establishment, expansion / emigration, local extinction
- Open vegetation became closed after ca. 50 years
- Soils stabilised and developed. Humus accumulated

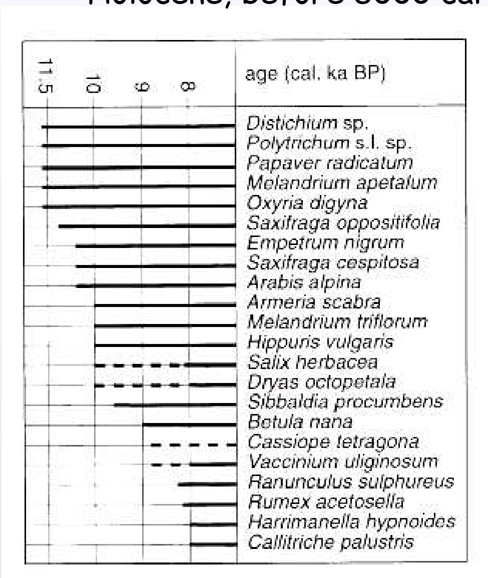
Arctic alpines were rapidly restricted to beyond tree-line or to refugia within the forest zone; e.g. refugia for alpines on glacier snouts at low altitudes in the Alps. Within the circumpolar tundra and alpine zones, plants had to cope with rapid climate change, e.g. increased precipitation, temperature, and they may have diverged genetically (evolved in isolated refugia)

Arctic alpines in south Greenland. Most species colonised early in the Holocene



Bennike & Björck (GEUS 2000)

Arctic alpines in northeast Greenland. Most species colonised early in the Holocene, before 8000 cal yr BP



Bennike (1999) J. Biogeography 26: 667

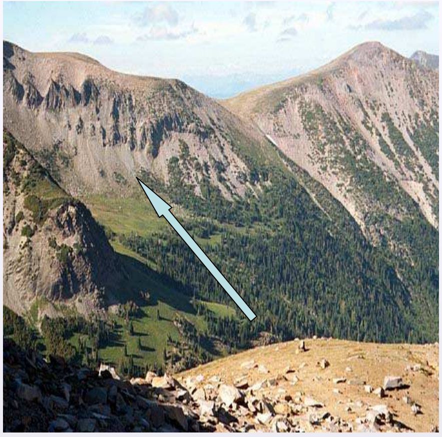
HOLOCENE survival - **Tough times for arctic-alpines**

Found refugia above or beyond the tree-line (alpine or arctic zones).

Temperatures increased steadily over the first few thousand years of the Holocene. The period of highest temperatures is called the Holocene thermal maximum. In NW Europe it was between about 6-8 kyr with summers about 2-2.5°C and winters 1-1.5°C warmer than today.
There is good evidence that the tree-line was higher than today and that forest- and scrub-zones reached their **highest levels** at this time.

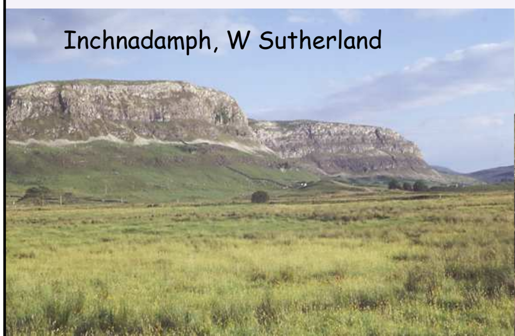
Lower limits for many alpines are controlled directly or indirectly by summer warmth or its close correlates, and competition from more vigorous, larger lowland species

Close correlation in Scandinavia between lower altitudinal limits of many alpines and maximum summer temperature (Dahl 1951)



As many alpines can be successfully grown in lowland gardens, their lower limits are more likely to be controlled by **competition** rather than by **temperature directly** (e.g. *Sedum rosea, Dryas*)

The species that are not killed by high temperatures can survive today in small, isolated 'cryptic' refugia within the potential forest zone. They include sea-cliffs, other coastal habitats, inland cliffs and screes, open river-gravels, rocky gorges, and shallow soils on steep limestone slopes (Pigott & Walters 1954) and low altitude moraine-covered glacier tongues



Some refugia in UK

Holocene thermal maximum may have **eliminated** altogether some of the most **warmth-sensitive** or cold-demanding species of the LGM and late-glacial flora (e.g. *Cassiope hypnoides, Papaver radicatum* agg. from UK)

Others may have only survived in scattered localities in the mountains (e.g. *Diapensia lapponica, Sagina intermedia, Saxifraga cernua, Gnaphalium norvegicum*). Competition-sensitive **and** warmth-sensitive

Warmth-tolerant species may have remained widespread over a greater altitudinal range (e.g. *Dryas octopetala*). Competition-sensitive **only**

Between these extremes, there are all degrees of 'relictness'

Almost **nothing is known** from the fossil record about Holocene history of alpines

Species that became extinct or extremely rare (relict) in Britain and Ireland after the last glacial period – Holocene casualties

Papaver sect. Scapiflora, Silene uralensis (Melandrium apetalum), Cassiope hypnoides, Salix polaris, Ranunculus hyperboreus, R. aconitifolius, Pedicularis hirsuta, P. lanata, Stellaria crassifolia, Corispermum pallasii

Koenigia islandica, Polemonium caeruleum, Linnaea borealis, Arenaria ciliata, A. gothica, Artemisia norvegica, Lychnis alpina, Saxifraga cespitosa, Astragalus alpinus, Minuartia stricta, M. rubella

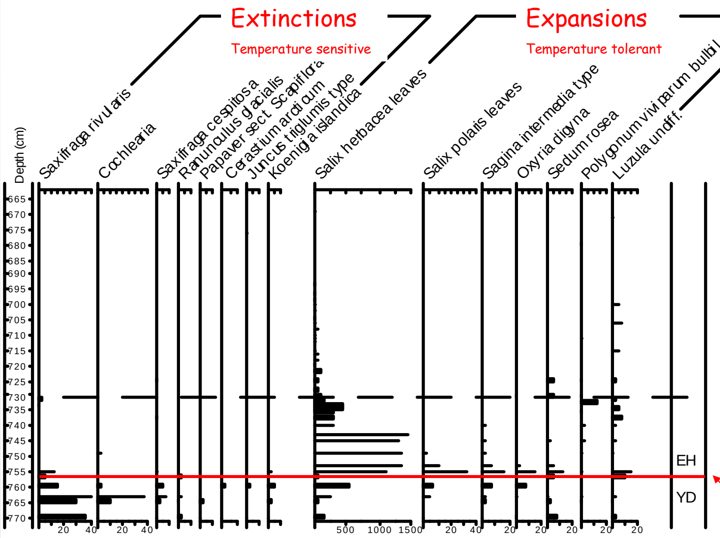
Mosses: e.g. Aulacomnium turgidum, Polytrichum sexangulare

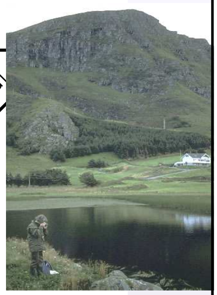
Extinct in Britain

Relict

(All are common in the Norwegian mountains)

Species dynamics driven by the Holocene temperature rise at Kråkenes, Western Norway





How fast?

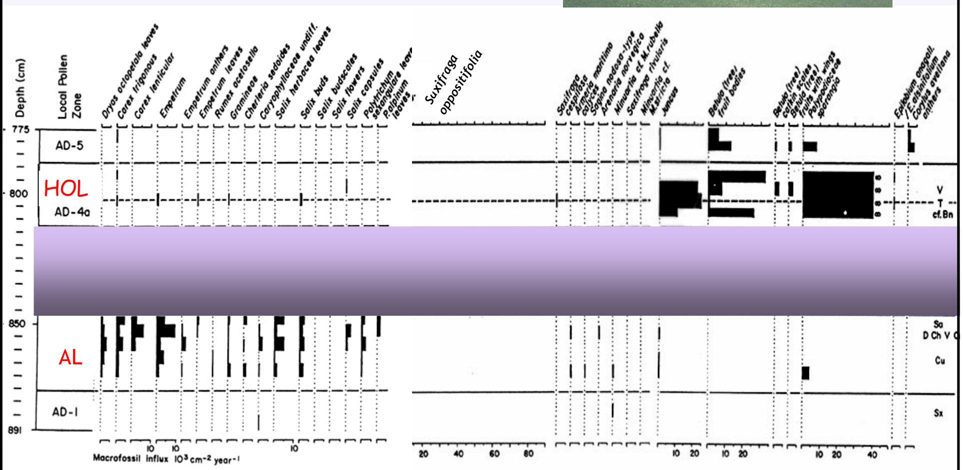
350 years competition

50 years temperature

Holocene boundary

An Druim, Eriboll, NW Scotland, late-glacial

macrofossils



Birks (1984) Lake Sediments and Environmental History, ed. Haworth and Lund

How did plants survive climate changes?
5. Holocene in the Arctic

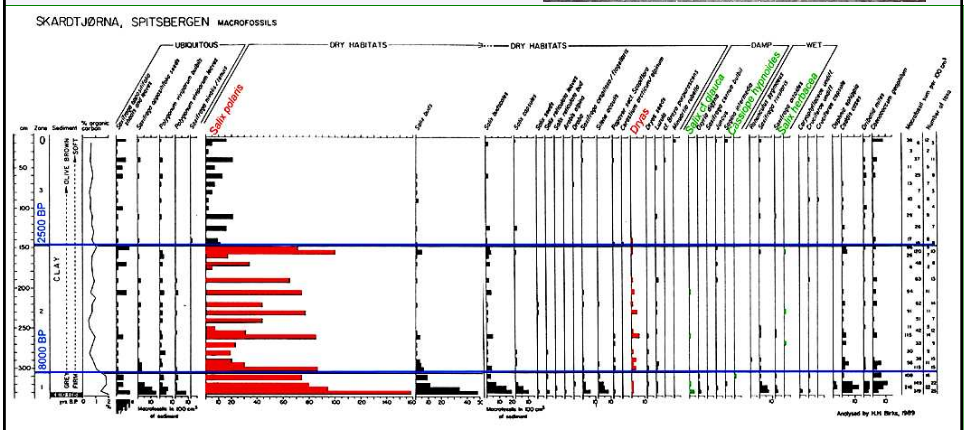
Holocene climate changes are marked in the arctic, e.g. on Svalbard

Svalbard was ice-covered during the glacial period

It was colonised very rapidly by arctic and alpine plants following Holocene warming

Summer temperature was about 2°C higher than today until about 8000 years ago. Cooling occurred, increased ca. 2500 years ago, and culminated in the Little Ice Age glacial readvance, ca. 1600-1900 AD

Skardtjørna, outer west coast of Spitsbergen



Birks (1991) The Holocene 1

6. How will plants survive climate changes? The future

The Arctic and the Andes are warming more strongly than temperate regions. Glaciers are retreating world-wide

Will arctic plants be pinched between advancing shrub-tundra and forest and the ever-rising sea-level?

Will alpine plants be pushed off the top of mountains?

Can plants adapt to local habitat changes, e.g. caused by increased dryness or wetness? Many may be able to do so because they are highly polyploid and can exploit a large genetic pool of variability (ecotypes)

At a Global scale

Alpine vascular plant flora 10,000-15,000 species, 2,000 genera, 100 ± 10 families. About 6% of world's flora (3% of land is alpine; high diversity)

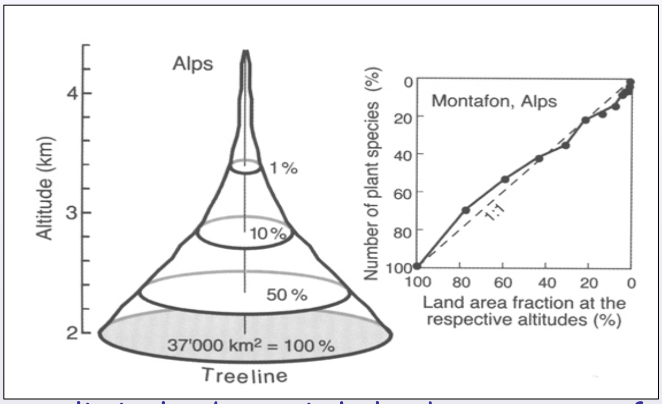
Arctic flora 1,000-1,500 species, less than 1% world's flora (5% land is arctic; low diversity)

General rule: arctic flora 1/10 alpine flora

Will these abundances change in the future? The Arctic is hard to model, but we can assess mountains more easily

Area and elevation with altitude

Area changes with elevation. Species number decreases as available area decreases with increasing altitude. Habitat diversity also decreases with decreasing area.



Above tree-limit, land area is halved, on average, for every 167 m increase in altitude (150 m in Alps, 178 m in Andes)

C. Körner (2002)

Results of increased elevation

ISOLATION. Missing or restricted corridors reduce the functional space and hence the species pool that alpines can exploit. May result in genetic divergence. May result in local extinctions

SHORTER GROWING SEASON. A decrease in growing season length (drought, low temperature) restricts the period during which evolutionary processes for adaptation can occur. Vascular plants compensate by fast and efficient reproduction and thus maintain one reproductive event per year.

Factors at high elevations may respond to isolation and reduced growing season through:

1. Greater available habitat diversity
2. Genetic diversification related to habitat fragmentation (endemism/micro-endemism)
3. Many arctic-alpine plants are highly polyploid and thus contain a large genetic potential for adaptation to habitat and climate change
4. efficient breeding systems; flower buds are formed in the previous summer.
5. There are many pollination and seed-ripening adaptations

Rheum nobile

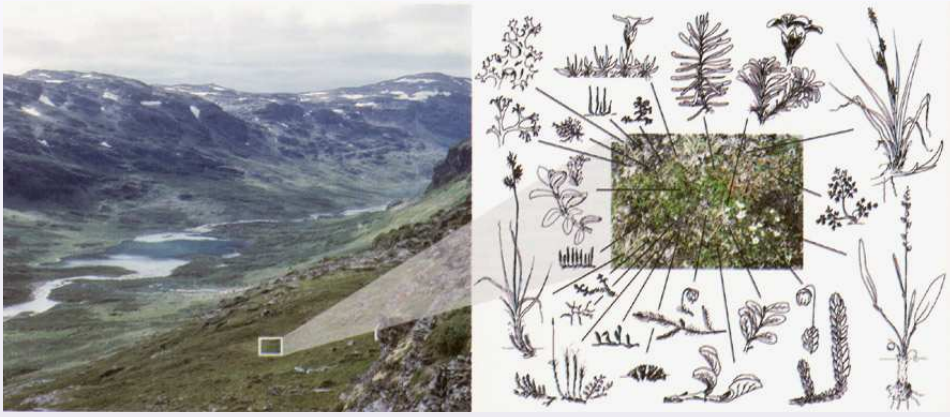
1. Micro scale habitat diversity in the alpine zone

At a global scale, alpine diversity is about average

At a regional scale, alpine diversity is high compared to other temperate areas

At a micro scale ($1m^2$), the highest diversity and variability of anywhere – can get 50-60 species in $1m^2$, whereas in forest or heath there may be only 5 species in $1m^2$

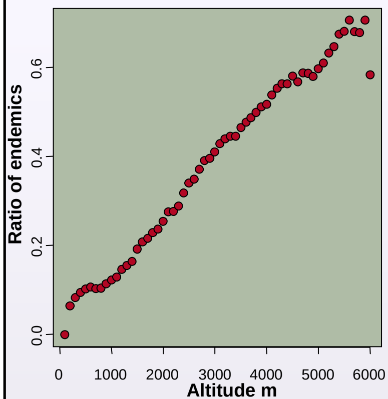
Small plants can utilise the high micro-habitat differentiation (ridges, hollows, late-snow, cliffs, rock outcrops, moving screes, hydrology, geology, etc.)



34 species in an alpine area 25 x 35 cm,
northern Sweden

C. Körner (2004)

2. Micro-evolution; endemism caused by isolation



Himalaya

Ratio of Himalayan endemics to total species richness steadily increases with altitude.

Isolation effect is more and more important at high altitudes above 5000 m.

A recently discovered endemic in Tibet and Bhutan

3. Adaptation potential

Saxifraga oppositifolia ecotypes

Wet habitat form

Dry habitat form

Alpines' response to Global Warming over the last 70 years in Norway

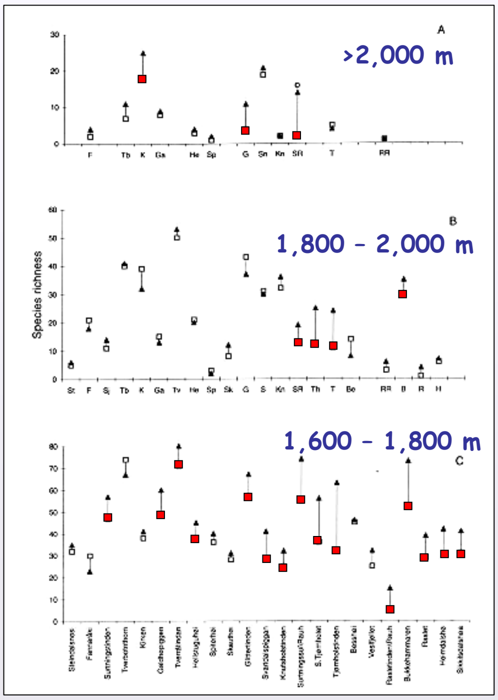
Jotunheimen mountains surveyed in 1930 and 1996

Galdhoppigen, Norway's highest peak
2469m

Little change

Some increase

Big increase



Changes in species numbers

❑ 1930-31

▲ 1998

Klanderud & Birks (2000)
The Holocene 13: 1-6

Some plants have **extended** their altitudinal limits in last 70 years, by 200-300 m

1. Dwarf-shrubs –

   Phyllodoce caerulea *Vaccinium myrtillus*

   Empetrum nigrum *Vaccinium vitis-idaea*

   Salix lapponum

2. Grasses –

   Festuca vivipara *Deschampsia flexuosa*


Vaccinium myrtillus
Norway
Phyllodoce caerulea Norway
Vaccinium vitis-idaea
Swedish Lapland


Empetrum nigrum
Norway
Salix lapponum
Scotland

Some summit plants have **declined** in frequency in the last 70 years (e.g. *Saxifraga cespitosa, Cerastium alpinum, Erigeron uniflorus, Ranunculus glacialis*)

Decline is because of **direct warming** in temperature-sensitive species, or more commonly by **increased competition** from faster-growing species expanding from lower altitudes

Cerastium alpinum

Erigeron uniflorus

Saxifraga cespitosa

A temperature-sensitive species, *Ranunculus glacialis*

Ranunculus glacialis needs cold roots

Root-zone temperatures at 10 cm depth at 3184 m altitude in the Austrian Alps exceed 0°C for 3 months only

2.8°C July
0.7°C August
0.6°C September

For the rest of the year, the soil is frozen with temperatures down to -12.5°C

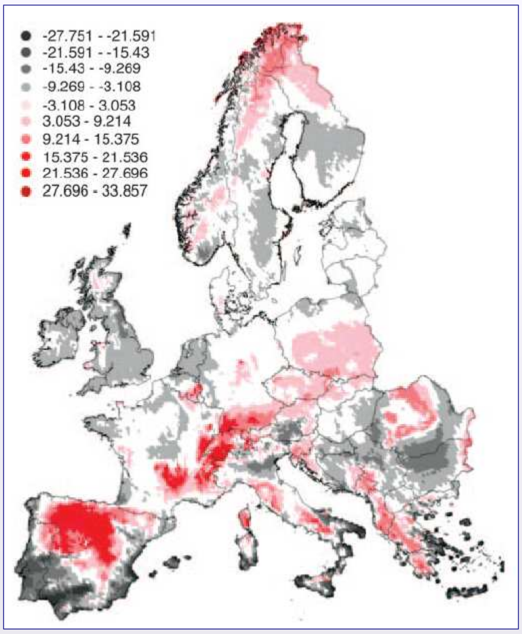
When plants start growth in late June, the mean soil temperature is about 0.7°C

Specialised plants like this are impossible to grow in the lowlands (e.g. gardens)

Similar floristic altitudinal changes are reported from the Swiss and Austrian Alps, the Swedish mountains, north-east Greenland, and Glacier National Park, Montana

The long-term future for high alpines is not good if they continue to decline, even on the highest mountains in the Alps or Scandinavia

Modelling the future



Thuiller *et al.* (2005)

Attempt to assess species status by 2080 under various future climate scenarios. Main drivers are temperature and moisture changes

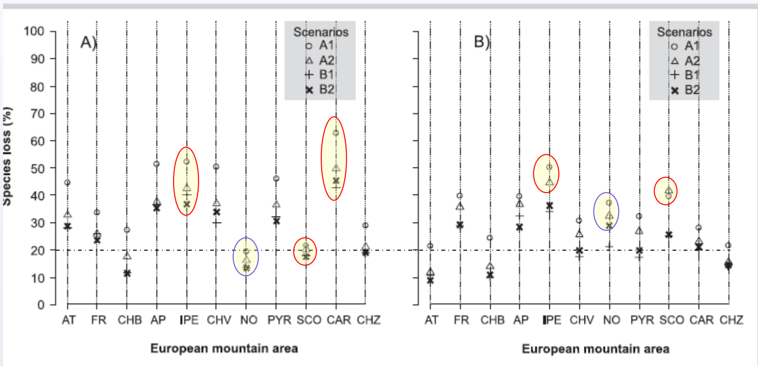
Greatest species loss (red) is predicted in the Alps, Pyrenees, central Spain, Balkans, north Scandinavia, Carpathians, and Corsica.

For the European Alpine flora ≈60% loss is predicted

Modelling with four different climate scenarios

European scale extinction

Local scale extinction



AT=Austrian Alps, FR=French Alps, CHB=Swiss Central Alps[1], AP=Apennines, IPE=Pyrenees[1], CHV=Swiss Western Alps, NO=Norway, P=Pyrenees[2], SCO=Scotland, CAR=Carpathians, CHZ=Swiss Central Alps[2]

MRI (2007)

Extinction rates generally >20%. Highest European extinction rate in mountains with high endemism, e.g. Carpathians, Pyrenees. Highest local extinction rates are predicted to be in the Pyrenees and Scotland

The long-term future for high alpines looks gloomy

If global change and global warming continue to the extent predicted by climatologists, the Arctic and Alpine Worlds will be very different places in 2100 compared to 2000

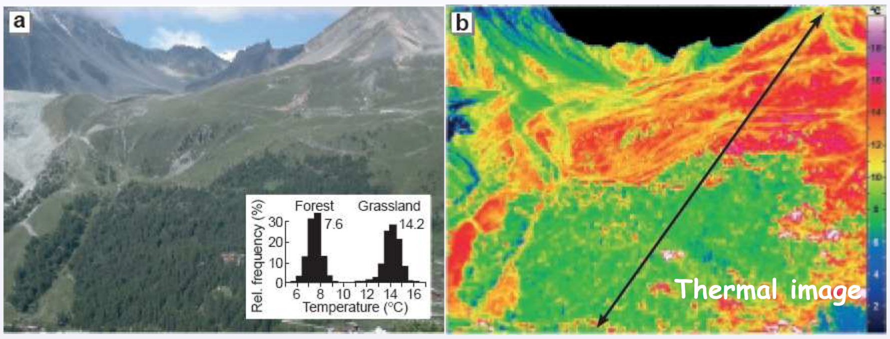
Models are predicting that many species may go extinct or be committed to extinction because of climate warming, loss of specialised habitats (e.g. snow-beds), the absence of anywhere higher or cooler to spread to, and competition from larger, faster growing dwarf-shrubs, grasses, and trees that are rapidly moving upwards and northwards in response to climate warming

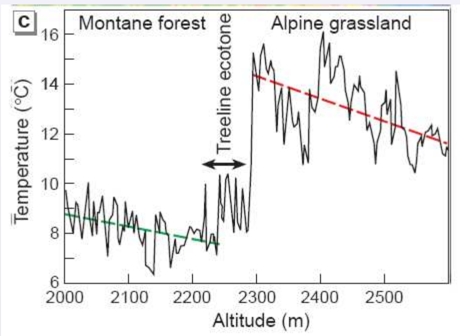
Maybe there is some hope?

- Large habitat diversity in alpine zone. Many potential refugia, even for warmth-sensitive species

- Forest soils are colder than those above tree-line. Therefore forest advance may be delayed as forest development causes a negative feedback.

- Small arctic-alpine plants create their own microclimate; cushions trap heat and are warmer than ambient air temperatures. This may facilitate colonisation and persistence by other species





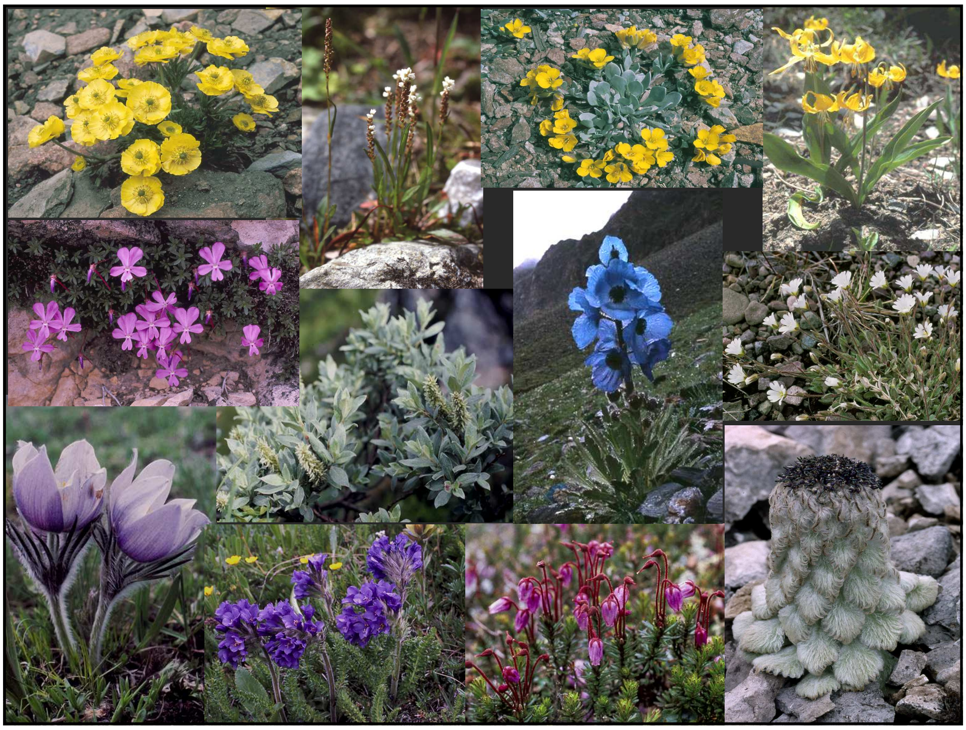
Land-surface temperature across an elevational transect in Central Swiss Alps shown by modern thermal imagery. Forest has a mean of 7.6°C whereas the alpine grassland has a mean of 14.2°C. There is a sharp warming from forest into alpine grassland

C. Körner 2007

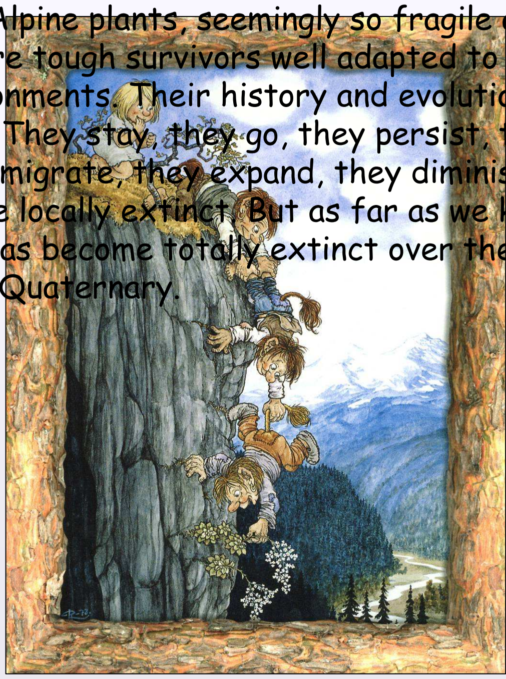
Arctic and alpine plants have survived periods of warm temperatures in the past, e.g. in the Holocene thermal maximum and in previous interglacials, such as the Eemian, when summer temperatures were about 2°C higher than today and sea-levels were higher.

We can hope that the inherent adaptations of Arctic and Alpine plants, their capability of adapting to changing conditions through polyploidy, and the existence of both high-altitude and lowland refugia will ensure their survival until the next ice-age

Let's celebrate them while they are still with us!



Arctic and Alpine plants, seemingly so fragile and beautiful, are tough survivors well adapted to their tough environments. Their history and evolution are fascinating. They stay, they go, they persist, they adapt, they migrate, they expand, they diminish, they become locally extinct. But as far as we know, no species has become totally extinct over the time-span of the Quaternary.



Birks H.H. (2008) The late-Quaternary history of arctic and alpine plants. Plant Evolution & Diversity 1 (2), 135-146.