The Evolutionary Legacies of the Quaternary Ice Ages

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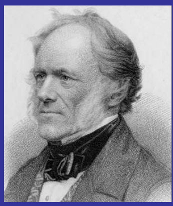
Nordforsk PhD Course, Abisko 2011

- The big question
- Plant biodiversity through time
- The effects of the Quaternary ice-ages on plant diversity
- Tree assemblages in earlier interglacials
- Tree distribution in the last glacial maximum (LGM)
- Allopatric speciation in the Quaternary
- Plant extinctions in the Quaternary
- Biological responses to the repeated Quaternary glacial-interglacial cycles
- Genetic diversification and speciation during the Quaternary
- Stasis – an important but unexpected response
- Molecular data and Q-Time
- Main conclusions

The Big Question

Debate on origin of species began during 19th century. Summarised by the **big question** from Charles Lyell, leading British geologist, posed to Charles Darwin



In his *Principles of Geology* (1830, 1832, 1833), Lyell laid basic foundations for modern geology and argued that the geological record should be interpreted in terms of **modern processes** ("the present is the key to the past") or methodological uniformitarianism.

Lyell's Viewpoint

Lyell's view on species and their origin was that they are created at a single spot, they multiply and **spread**, they **survive** environmental and biotic fluctuations, but are **not** transformed, and eventually they become **extinct**.

Species, Lyell believed, are **stable** units that come into existence at ecologically appropriate points in space and time, survive for a longer or shorter period in a dynamic ecological equilibrium with other organisms and spread to some degree, but are **eventually eliminated** by the pressures of the ever-changing physical and biotic environment.

Lyell not specific about how species came into being. Recognised that Earth was in a state of constant change. Lyell saw that **shifting distributions** were likely to be a more rapid response to environmental change than *in situ* transformation because there would always be species nearby better suited to new conditions than the species on the spot originally.

He pointed out that, following **climate change**, some species would be preserved by shifting their distributions but that the same change would be "fatal to many which can find no place of retreat, when their original habitations became unfit for them" (Lyell 1833, p.170).

"If a tract of salt water becomes fresh by passing through every intermediate degree of brackishness, still the marine molluscs will never be permitted to be gradually metamorphosed into fluviatile species; because long before any such transformation can take place by slow and insensible degrees, other tribes, which delight in brackish or fresh water, will avail themselves of the change in the fluid, and will, each in their turn, monopolise the space." (Lyell 1832, p.174)

Lyell learned of Darwin's ideas about evolution and natural selection before the publication of *On the Origin of Species* (Darwin 1859) and he was not convinced initially.

Lyell had worked extensively on Palaeogene and Neogene (4.0-2.5 million years ago (Tertiary)) molluscs, many of which can be identified to living species. As a geologist, Lyell realised that these species must have **survived changing climates** since the Palaeogene including the Great Ice Age. This appeared to conflict with Darwin's ideas.

The Big Question

Lyell wrote to Darwin on 17 June 1856

"And why do the shells which are the same as European or African species remain quite like the Crag species which returned unchanged to the British seas after being expelled from them by Glacial cold, when 2 million years had elapsed, and after such migration to milder seas? Be so good as to explain all this in your next letter."

Darwin did not reply directly to Lyell's question or comment on it anywhere else.

Lyell was clearly concerned about whether natural selection proposed by Darwin was operative over geological time-scales.

Darwin's Answer

In Chapter 11 of *On the Origin of Species*, Darwin (1859) discusses geographical distributions and includes an extended commentary (18 pages) on the effects of "the great glacial period".

Darwin suggested that plants and animals have spread southwards during times of increasing cold and then spread back northwards during the following climate warming.

"The arctic forms, during their long southern migration and re-migration northward, will have been exposed to nearly the same climate, and, as is especially to be noticed, they will have **kept in a body together**; consequently their mutual relations will not have been much disturbed, and, in accordance with the principles inculcated in this volume, they will not have been liable to much modification." (Darwin 1859, p.368)

Here we have Darwin's view that modification will occur when the environments of species are altered by changes such as those related to continental glaciation. Although Darwin did not directly answer Lyell's question of June 1856, Darwin's passage indicated what his answer would have been like.

The most significant part of Darwin's passage is that major climate changes such as those associated with glaciations will have **not** caused 'modification' because, as species shifted their distributions, they will have remained in the same communities ("**kept in a body together**").

Much Quaternary palaeoecological evidence to suggest that this did **not** occur. Species responded individualistically and created assemblages in the past with no modern analogues today (and will create assemblages in the future with no current analogues today).

Modern analogs in Quaternary paleoecology – here today, gone yesterday, gone tomorrow? Jackson & Williams (2004) Ann Rev Earth Planet Sci 32: 495-537.

Major theme in Darwin's *On the Origin of Species* is how to link **processes observable today** to patterns in the **fossil record** to produce a coherent theory of evolution by natural selection.

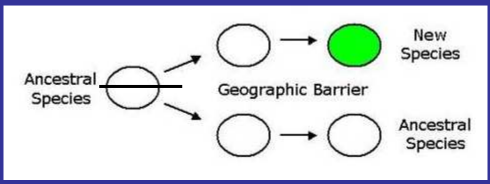
Link was challenged by Niles Eldredge and Stephen J Gould with their view that fossil record shows **long periods of little change** in lineages interspaced with **brief periods of relatively rapid change** ('punctuated equilibria') as speciation takes place through geographical isolation (**allopatric and peripatric speciation**).

Gould (1985) proposed an evolutionary theory that includes processes of **three separable tiers of time**.

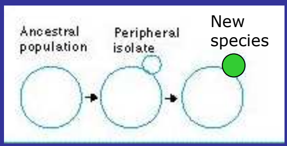
1. Ecological moments – natural selection
2. Geological time (Ma) – speciation through geographical isolation
3. Mass extinctions

Allopatric speciation – differentiation of geographically isolated populations into species

Commonest form



Peripatric speciation – speciation by evolution of isolating mechanisms in populations located at the periphery of a species range. Special case of allopatric speciation. Marginal, isolated populations often differ markedly from main-range populations.

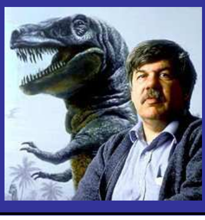


Fossil record clearly shows that once diversification began on a major scale (Cambrian to present day), it was not continuous.

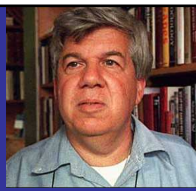
Periods of dramatic increase, interspersed by some times of major setbacks or periods of relative **stasis** (or at least no marked directional trend in diversity).

History of biodiversity is thus one of **radiations** (allopatric speciation) and **stabilisations**, punctuated by **mass extinctions**.

Punctuated equilibrium –
S.J. Gould and Niles Eldredge



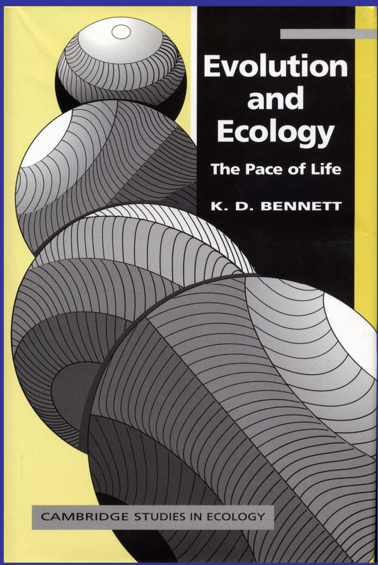
Three levels of processes controlling evolutionary patterns as seen in the geological record – Gould (1985)



Level	Period	Cause	Evolutionary processes
First	-	-	Microevolutionary change through natural selection in more-or-less stable assemblages
Second	-	Geographic isolation (continental drift, creation of islands, etc)	Macroevolutionary change through speciation in conditions of geographical isolation (allopatric speciation)
Third	Ca. 26 Myr	Mass extinctions	Loss of species and higher taxa

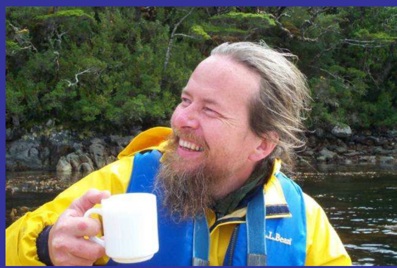
Is this a complete picture?

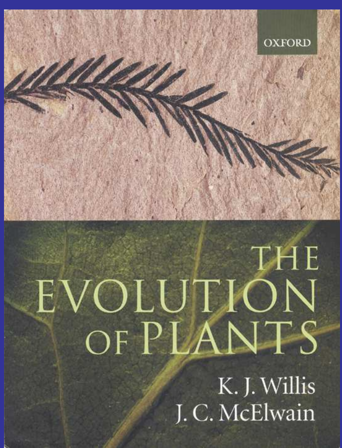
What can Quaternary palaeoecological data tell us about speciation, extinction, and biodiversity in Q-Time and also ecological and evolutionary time?



1997

Keith Bennett has provided the missing 'tier of time' in Gould's evolutionary theory





Kathy Willis and Jenny McElwain have revolutionised our ideas on the causes of changing plant biodiversity patterns through Deep-Time and Quaternary-Time


Kathy Willis


Jenny McElwain

Four main questions in plant diversity changes in Deep- and Q-Times

1. What effects did mass extinction events have on plants? (Deep-Time)
2. What may have caused the radiation and diversification of angiosperms in the Cretaceous? (Deep-Time)
3. What may have influenced the tempo and mode of plant diversity and speciation in the last 50 million years? (Deep-Time)
4. What effects did the Quaternary ice ages of multiple glaciations and intervening interglacials have on plant diversity? (Q-Time)

Can only consider **question 4** in this course

(Answers to 1 led to major changes in abundance but no primary role in plant evolution

Answer to 2: declining CO_2 concentrations in Cretaceous may have triggered expansion of angiosperms

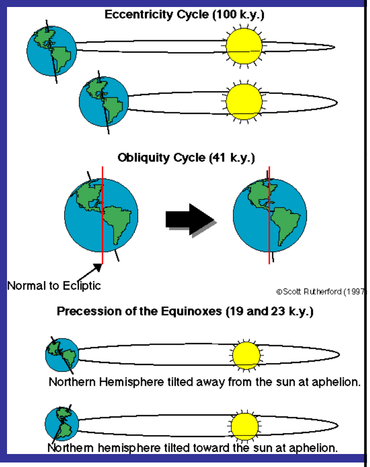
Answer to 3: changes in thermal energy and in variability in energy flux, also in UV-B flux)

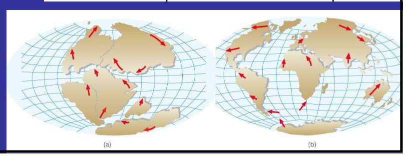
How has thermal energy changed through geological time?

Relevant to questions 3 and 4

Well known that incoming energy has varied through time associated with the position of the Earth in relation to its orbit around the Sun (**Milankovitch oscillations**), vertical mountain uplift, and horizontal movement of continental plates.

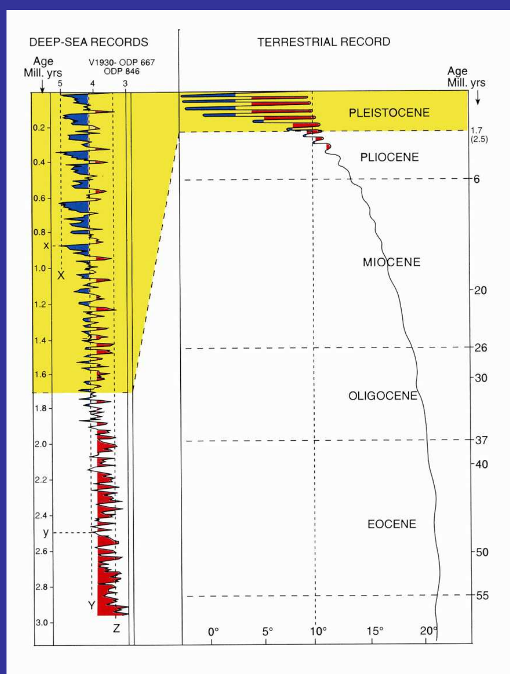
Milankovitch oscillations have occurred throughout Earth's history and are known to have resulted in significant variations in incoming solar radiation with periodicities of about 400, 100, 40, and 21-19 thousand years. 'Pacemaker of Ice Ages'.





Oxygen isotope fluctuations. Observations made from several deep sea cores (Modified from Shackleton *et al.* 1993 and Shackleton & Opdyke 1976)

Climate and glacier fluctuations observed in deposits on the continent in Europe. Red: warm phases, blue: cold phases.



Andersen (2000)

What Effects did the Quaternary Ice Ages have on Plant Diversity?

The **Quaternary** period is the past 2.7 million years (Myr) of Earth's history. A time of very marked **climatic** and environmental **changes**

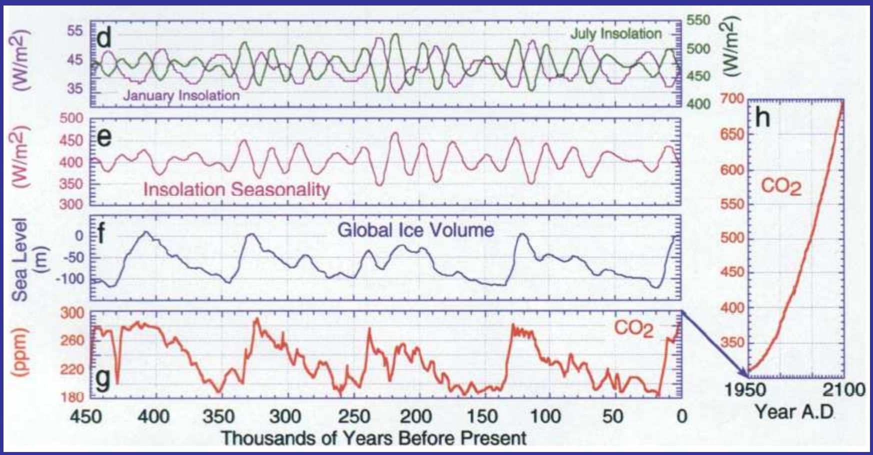
Large terrestrial ice-caps started to form in the Northern Hemisphere about 2.75 Myr, resulting in multiple **glacial-interglacial cycles** driven by variations in orbital insolation on Milankovitch time-scales of 400, 100, 41, and 19-23 thousand year (kyr) intervals

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

Main features of Quaternary climate change

1. At least **17 glacial phases**, and 9 in last 700,000 years. Can see last 3 in Antarctic ice cores.
2. Quaternary is not 1 million, but **2.7 million years** long.
3. About 125,000 years for each **glacial-interglacial cycle**.
4. Interglacials ~10,000-30,000 years. Glacials ~70,000-100,000 years.
5. **Asymmetry**. Coldest at end of glaciations.
6. ^{18}O : ^{16}O in planktonic foraminifera (marine) show 90% of last 450,000 years had **more ice** than today.
7. The present post-glacial (Holocene) is simply the **latest interglacial**. 11,500 years long.
8. Glacial environment is the **norm**. Interglacials are unstable interruptions.
9. Unlike Tertiary, only a relatively **short time** (~10,000 years) for vegetation and soil development.
10. Cause of glaciations? **Milankovitch cycles**; mountain building in Tertiary (Alps, Himalaya, Rockies); plate tectonics.



Major climate forcing for the last 450 kyr calculated at 60°N. Global ice volume (f) plotted as sea-level, so low values reflect high ice volumes.

Jackson & Overpeck (2000)

Causes of glacial-interglacial changes

Earth is subject to **perpetual cyclic changes** over a wide range of frequencies because of its position and movement relative to other bodies in the solar system (e.g. diurnal, annual, tidal, lunar cycles).

Earth's orbit around the sun is influenced by gravitational attractions of the moon and other planets, producing long period fluctuations or Milankovitch cycles with frequencies of

23 k yr (precession of the equinoxes)

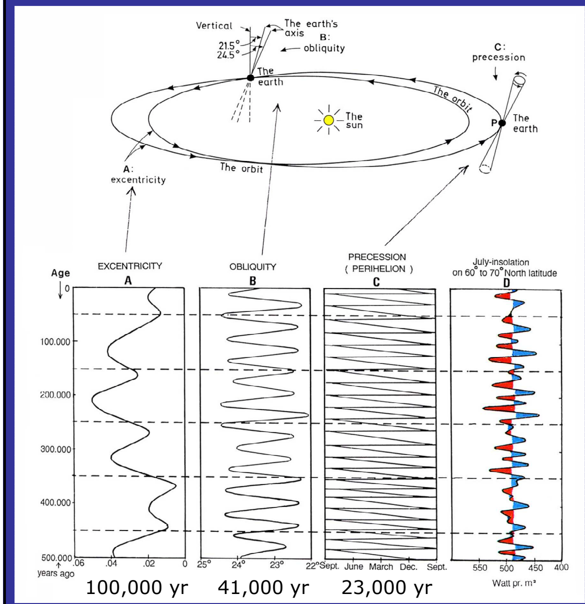
41 k yr (oscillation of Earth's axial tilt) = obliquity

100 k yr (eccentricity of orbit)

Amplitude of variations in **orbital eccentricity** set by the initial orbit of the Earth in the early history of the solar system. **Mean tilt** or obliquity probably varied little. Periodicity of **precession** is increasing as the moon moves away from the Earth.

Other causes of long-term global climate change include plate tectonics and mountain building.

'Milankovitch' Orbital Factors affecting insolation of the Earth



A: The eccentricity of Earth's orbit varies in 100,000 year cycles.
B: The obliquity; the tilt of Earth's axis relative to the orbital plane fluctuates in 41,000 year cycles.
C: The precession fluctuates in 23,000/19,000 year cycles, resulting from the wobbling of Earth's axis. P = perihelion, the point of the earth's orbit closest to the sun.

Calculated fluctuations of the Milankovitch factors during the last 500,000 years, and the resulting fluctuation of insolation to the earth on the 60-70ºN latitudes. A: Eccentricity. B: Obliquity. C: Precession (at perihelion). D: Fluctuation of insolation to Earth at 60-70ºN as a result of the fluctuation of all Milankovitch factors combined. Red = warm; blue = cold periods. (Modified from C. Covey, 1984.)

Andersen & Borns. Ice Age World (1994)

Milankovitch cycles control the pace of Quaternary ice ages with 100 k yr eccentricity cycle dominant in the late Quaternary and the 41 k yr tilt cycle dominant in the early Quaternary.

Milankovitch cycles produce variations in amount of **solar radiation** and latitudinal and seasonal distribution of this radiation.

Last glacial maximum about 18-25,000 yr ago; 4.0 – 2.5°C cooler than today depending on location, some tropical oceans as warm or slightly warmer than today, great differences in precipitation, especially the strength and location of subtropical monsoons.

Milankovitch cycles are a consequence of gravitational attractions between celestial bodies. They are therefore a **perpetual feature** of Earth's history.

Quaternary ice sheets may have developed because of the late Cenozoic configuration of the continents and/or mountain building.

Other glaciations known in Earth's history (e.g. Permian, Carboniferous, Devonian, Silurian, Ordovician, Cambrian, Pre-Cambrian).

Balance of glacial and interglacial conditions has not been constant through the Quaternary

kyr	
0	Late Pleistocene
	Eccentricity-dominated 100 kyr cycles ‘100 kyr world’
	Glacial:interglacial 85:15 of 100 kyr
64-99	Middle Pleistocene transition
	Top of Jaramillo subchron at MIS 25
99-260	Early Pleistocene
	Obliquity-dominated 41 kyr cycles ’41 kyr world’
	Glacial:interglacial 10:30 of 41 kyr
260	Gauss-Matuyama
	Precession-dominated world

Quaternary long **assumed** to be an important time for genetic diversification and speciation.

Based on premise that Quaternary climatic conditions favoured the **isolation** of populations and, in some instances, **allopatric speciation**.

Basic idea of Quaternary ice-age speciation model has **two major assumptions**.

1. Biotic responses to climate change during the Quaternary were significantly **different** from those of other periods in Earth’s history
2. Mechanisms of isolation during the Quaternary were **sufficient** in time and space for genetic diversification to result in speciation

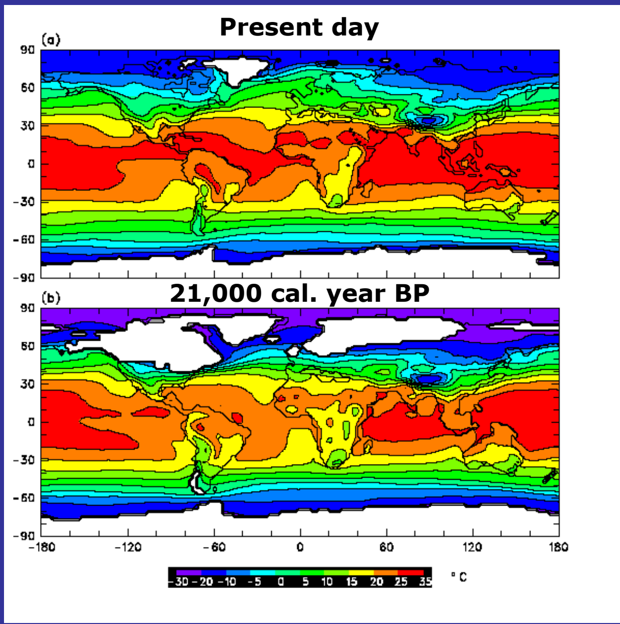
Need to know

1. Where did plants grow in the **glacial ice-age stages**?
2. How **long** were the glacial stages?
3. Is there any evidence for **speciation** in the Quaternary?
4. Is there any evidence for **extinction** (local, regional, global) in the Quaternary?

Q-Time palaeoecology can provide answers to these questions

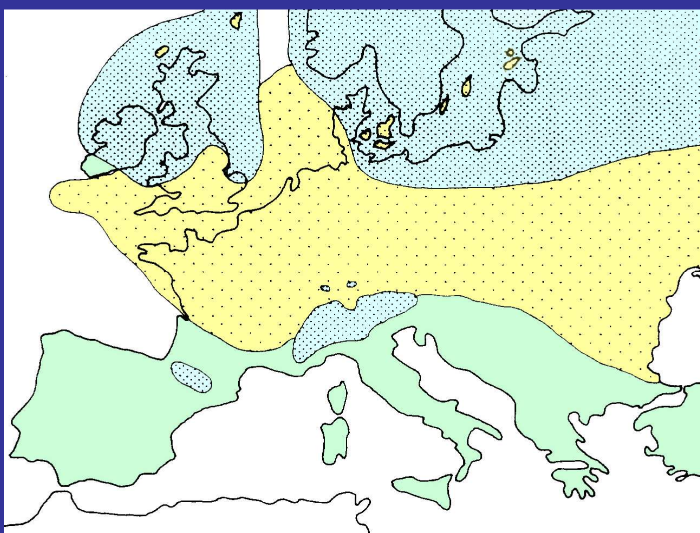
Glacial conditions:

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 280 ppmv in intervening interglacials
6. Steep climatic gradient across Europe and Asia during the Last Glacial Maximum (LGM)



General circulation model (GCM) simulations of 21 kyr Last Glacial Maximum (LGM)

Pollard & Thompson (1997); Peltier (1994)



Ice-sheets

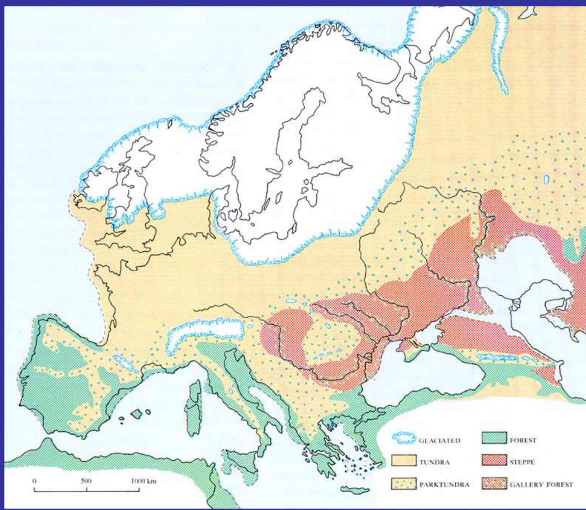
Permafrost

Relict soils

Approximate extent of ice and continuous permafrost in Europe during LGM – what was the vegetation like?

Willis (1996)

Last Glacial Maximum (LGM)

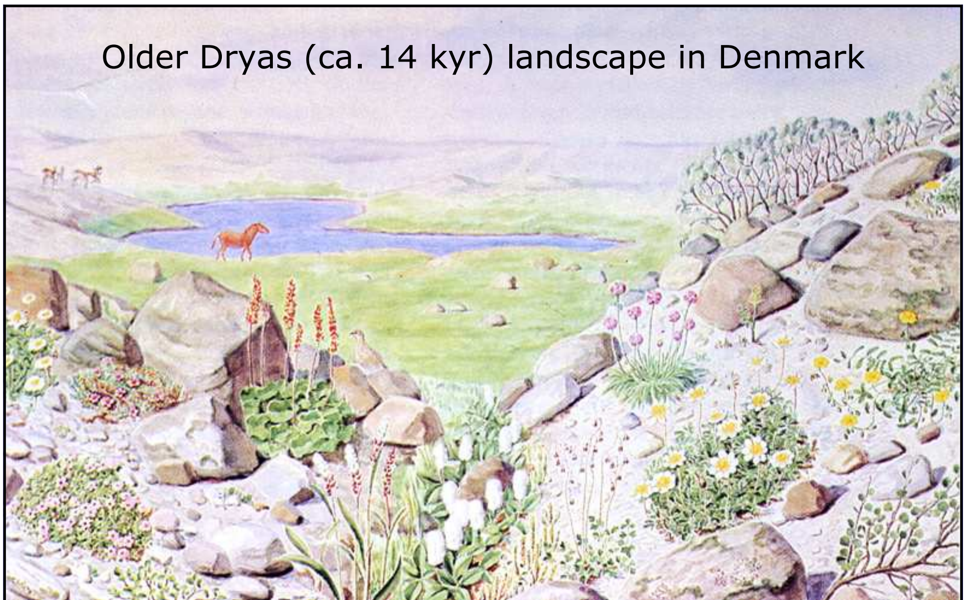


Vegetation 20 kyr ago

Widespread ice, tundra, and steppe in north and east; park-tundra in south, and forest confined to Mediterranean basin

Iversen (1973)

Older Dryas (ca. 14 kyr) landscape in Denmark



Abundant alpines along with species of steppe habitats (e.g. *Helianthemum, Hippophae, Ephedra*) and large herbivores

Iversen (1973)

Possible LGM landscape in central Europe

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

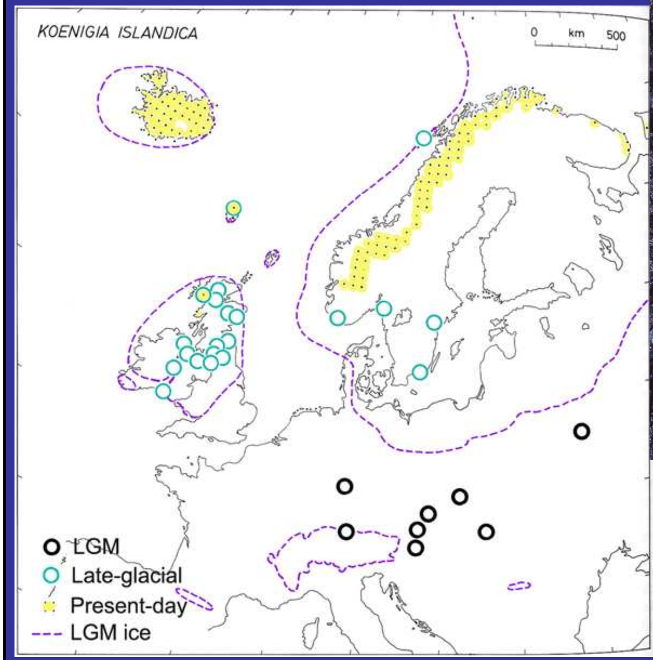
Alpines in LGM

Besides familiar arctic-alpines found commonly as fossils such as

Dryas octopetala	*Lychnis alpina*
Salix herbacea	*Saxifraga oppositifolia*
Salix reticulata	*Oxyria digyna*
Betula nana	*Bistorta vivipara*
Saxifraga cespitosa	*Silene acaulis*

also find fossils of plants not growing in central European mountains, only in northern Europe today

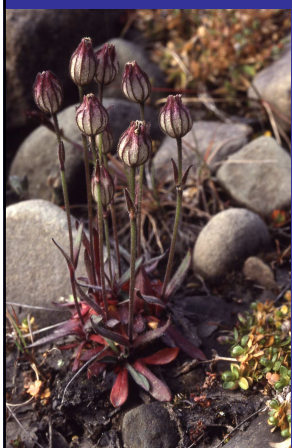
Ranunculus hyperboreus	*Campanula uniflora*
Salix polaris	*Koenigia islandica*
Silene uralensis	*Pedicularis hirsuta*



Koenigia islandica

Lang (1994)

Other northern plants found as fossils in central Europe in LGM



Silene uralensis

Salix polaris

Ranunculus hyperboreus

Pedicularis hirsuta

Common alpines in LGM throughout northern and central Europe

Dryas octopetala

Silene acaulis

Bistorta vivipara

Lychnis alpina

Betula nana

Saxifraga oppositifolia

"The arctic forms, during their long southern migration and re-migration northward, will have been exposed to nearly the same climate, and, as is especially to be noticed, they will have **kept in a body together**; consequently their mutual relations will not have been much disturbed, and, in accordance with the principles inculcated in this volume, they will not have been liable to much modification."

Charles Darwin (1859, p. 368 *On the Origin of Species*)

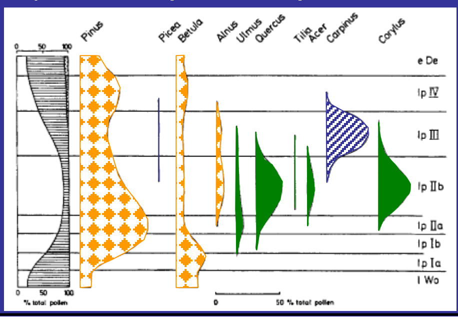
Darwin is suggesting that major climatic changes like glaciation may not cause 'modification' because as species shifted their distributions, they will have remained in the same communities ('**kept in a body together**'). Did they?

What do we Know about Tree Assemblages in Other Interglacials?

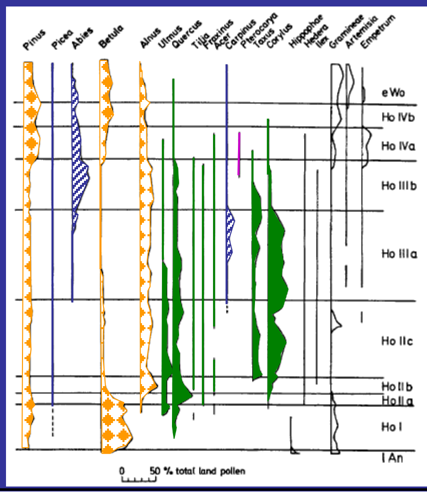
General Pattern:

NW Europe – many inter-glacial pollen stratigraphies, e.g. East Anglia

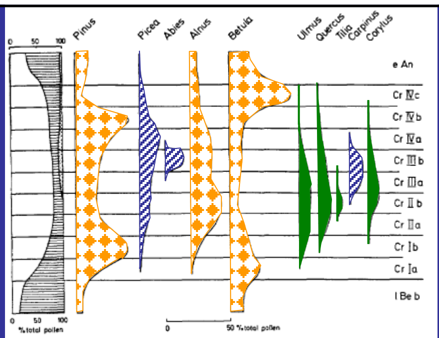
Ipswichian(=Eemian) MIS 5e



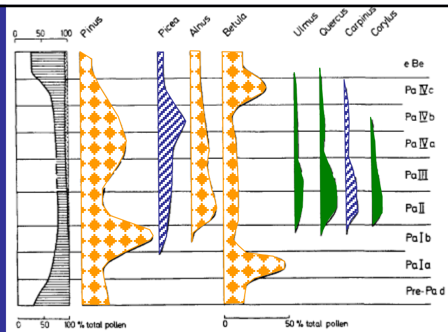
Hoxnian(=?Holsteinian) MIS 11c or 7c



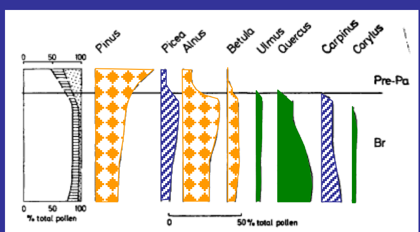
West (1980)



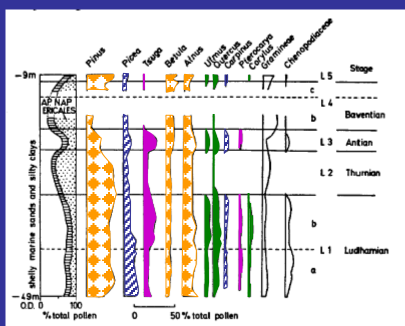
Cromerian MIS?



Pastonian MIS?



Bramertonian MIS?



West (1980)

Ludhamian, Thurnian, Baventian MIS?

All show **four main phases**

1. Pre-temperate phase – **boreal** trees (e.g. *Betula*, *Pinus*)
2. Early-temperate phase – **deciduous** trees (e.g. *Ulmus*, *Quercus*, *Fraxinus*, *Corylus*)
3. Late-temperate phase – **mixed** deciduous and coniferous trees (e.g. *Carpinus*, *Abies*, *Picea*)
4. Post-temperate phase – **boreal** trees (e.g. *Betula*, *Pinus*, *Picea*) and **heathland** development

MIS1				
0.97	MIS5.5			
0.85	0.88	MIS7.5		
0.77	0.79	0.78	MIS9.5	
0.53	0.48	0.45	0.42	MIS11.3

Correlation coefficients between four interglacials at Velay, longest record in NW Europe

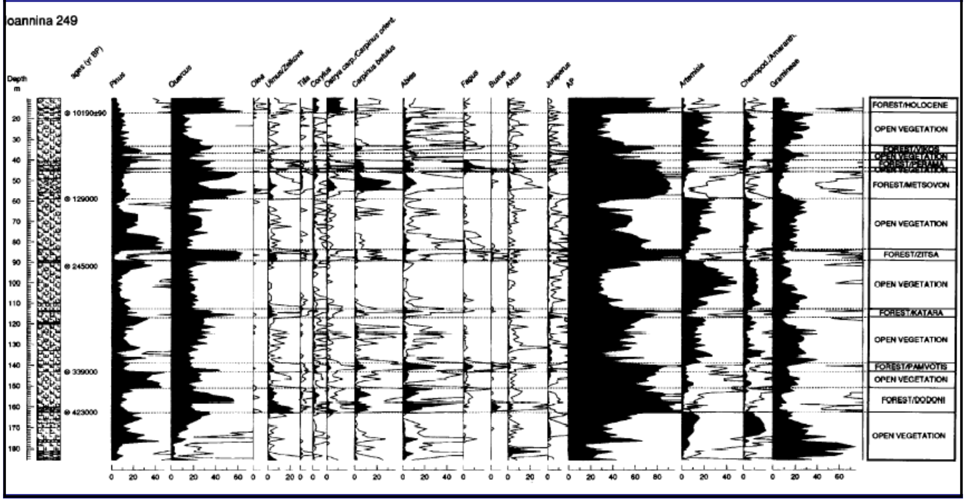
Chedaddi *et al*. (2005)

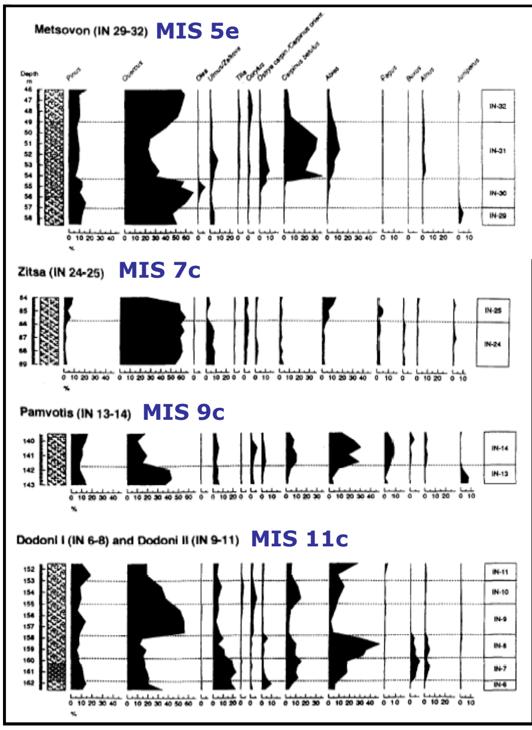
1. Marine Isotope Stage (MIS) 9c, 7c, and 5e closely correlated.
2. MIS 1 and 11c less well correlated even though they have **similar** precessional variations. MIS 11c is closest climatic analogue to Holocene.
3. General similar vegetation dynamics but different tree composition in all five interglacials even though their durations were very different and their solar insolation values were different.

Ioannina, Pindus Mountains, Greece

Tzedakis & Bennett (1995) Quat Sci Rev

180 m sequence, Holocene + 4 interglacials





	5e	7c	9c	11c
5e				
7c	- -			
9c	- -	- -		
11c	- -	- -	- +	

- climate different (solar insolation)

- pollen different

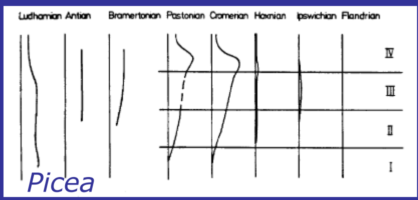
+ pollen similar

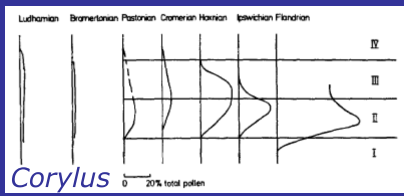
Different interglacials have **different solar insolation** values and **different pollen stratigraphies**, except for two interglacials with **similar** pollen stratigraphies.

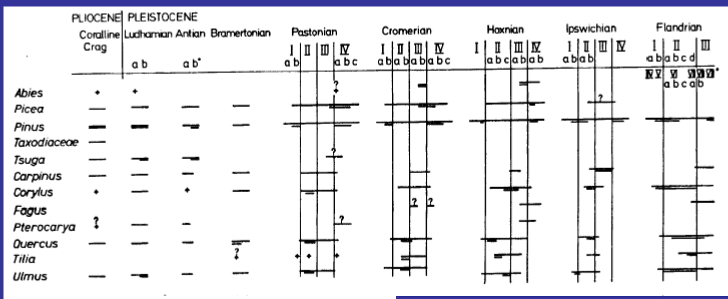
Tzedakis & Bennett (1995)

Differences between interglacials

Differences in relative abundance







Taxon occurrences

West (1980)

[+]*Abies* 3/8
[*]*Tsuga* 3/8
Fagus 2/8
[*]*Pterocarya* 4/8
[+]*Picea* 6/8
[*]Not native in Europe
[+]Not native in UK

These and other differences between interglacials may reflect **biotic responses** to

- differences in **climate** in different interglacials (insolation, precipitation, CO_2, etc)
- differences in **genetic variability** of taxa between interglacials (e.g. *Fagus*, *Corylus*)
- differences in biotic **interactions** in different interglacials (plant competitions, plant-animal interactions, etc)
- differences in location of **refugia** between glacials
- different probabilities of **extinction** after different interglacials or in glacials
- different probabilities of external **disturbance** factors (fire, pathogens, etc)
- **interactions** between some of all of these factors

Embarrassingly ignorant of nearly all these potential drivers, especially when we consider interglacials

Different interglacials had different climates in terms of **solar insolation values**. Interglacial pollen stratigraphies are surprisingly broadly **similar** at the **coarse** plant functional or ecological group **level** but are, not surprisingly, **different** at the **assemblage** or **individual taxon** level.

In general each interglacial begins with high summer and low winter insolation, then both summer and winter insolation reach present-day values, and finally summer temperature decreases and winter temperature increases.

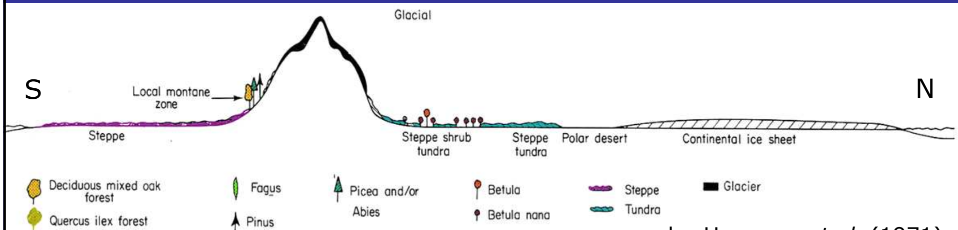
Main lesson from interglacials is the seemingly **wide** climatic tolerances of major tree taxa that dominate interglacials.

Virtually nothing is known about tree refugia prior to the Eemian (MIS 5e).

As regards the Weichselian, knowledge of **tree refugia** in Last Glacial Maximum (LGM) is greatly changing, thanks to an increasing emphasis on plant **macrofossil remains**.

What do we know about Tree Distributions in the LGM?

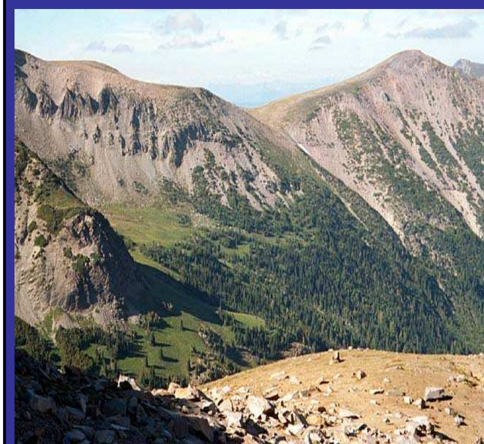
1. What about trees in southern and Mediterranean refugia during the LGM?

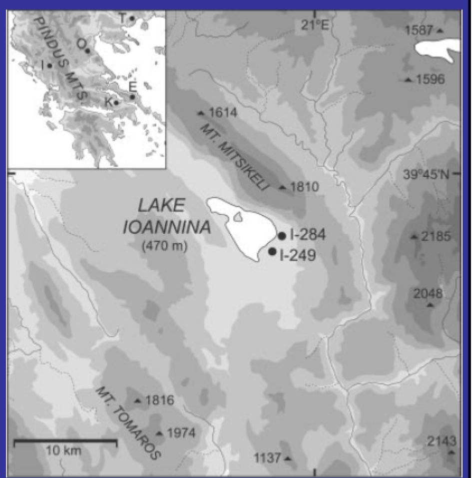


van der Hammen *et al*. (1971)

Traditional refugium model – narrow tree belt in southern European mountains and in the Balkan, Italian, and Iberian peninsulas

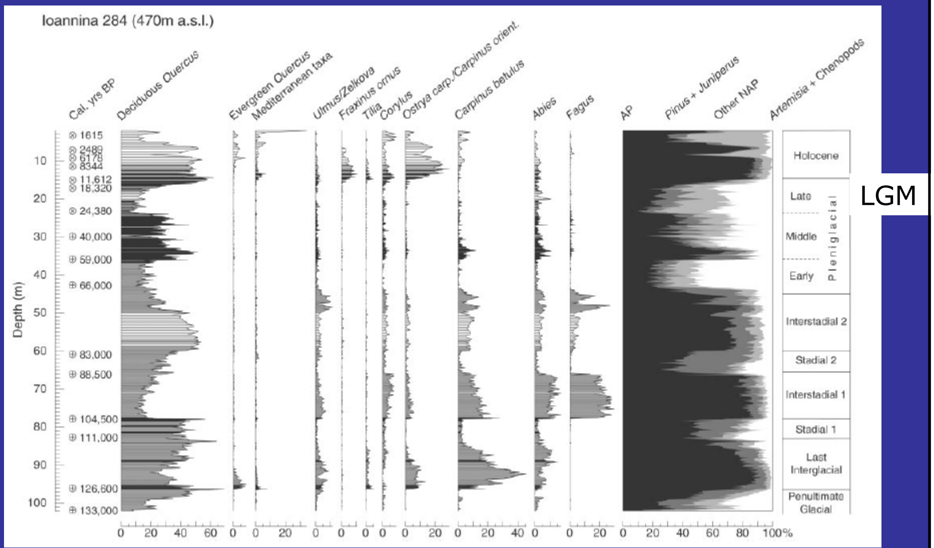
Pindus Mountains, NW Greece





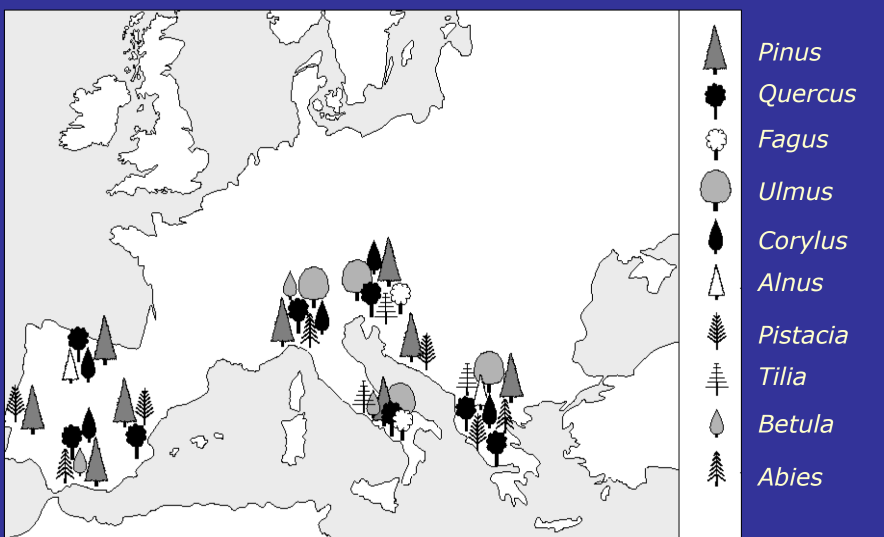
Location of Ioannina basin

Tzedakis *et al*. (2002)



Tzedakis *et al*. (2002)

Pollen evidence for traditional southern European LGM refugial model



Bennett *et al*. (1991), Birks & Line (1992)

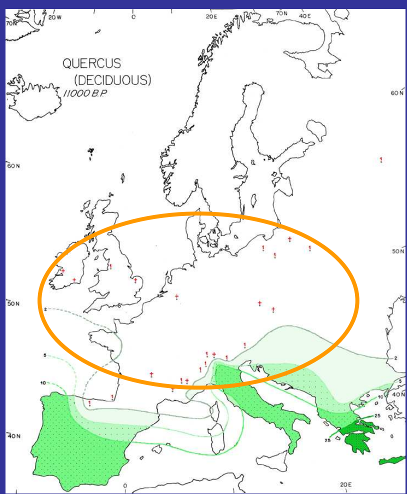
2. What about trees in central, eastern, and northern Europe during the LGM?

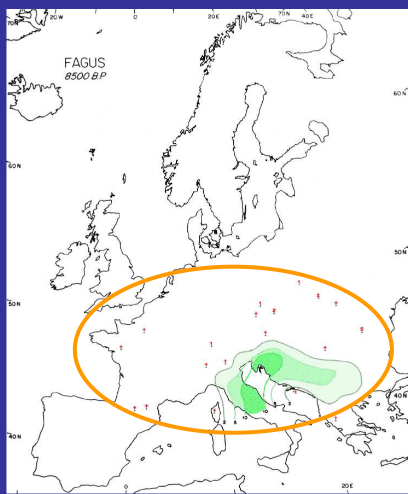
Detection difficult

1. **Low pollen values** – do these result from long-distance pollen transport or from small, scattered but nearby populations?

   Classic problem in pollen analysis since Hesselman's question to Lennart von Post in 1916. No satisfactory answer.

2. **Few continuous sites** of LGM age
3. **Pollen productivity** related to **temperature** and some trees cease producing pollen under cold conditions
4. **Pollen productivity** may also be reduced by l**ow atmospheric CO_2** concentrations





Low pollen values disregarded by Huntley & Birks (1983) following von Post (1916) and Fægri & Iversen (1964) but not Hesselman (1916)!

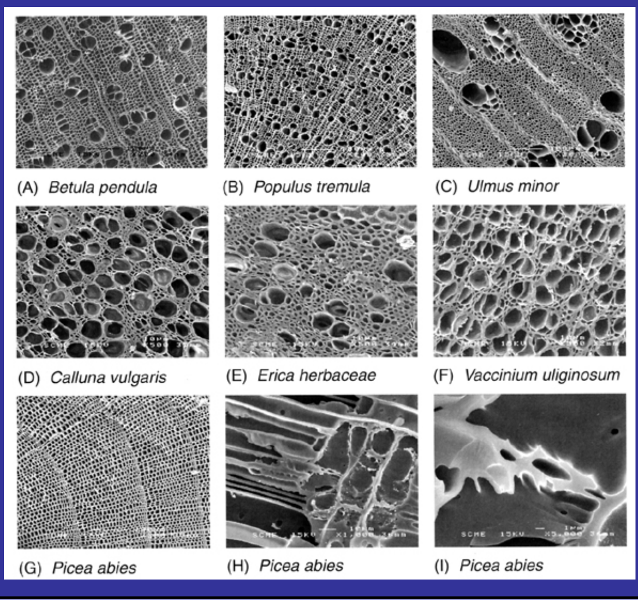
Need other lines of evidence to test the hypothesis that the low pollen values resulted from far-distance transport

- megafossils
- macrofossils
- macroscopic charcoal

and, least satisfactory,

- conifer stomata (easily reworked and can be blown for great distances across snow)

Fossil evidence for trees in central and eastern Europe during the LGM: macroscopic charcoal evidence

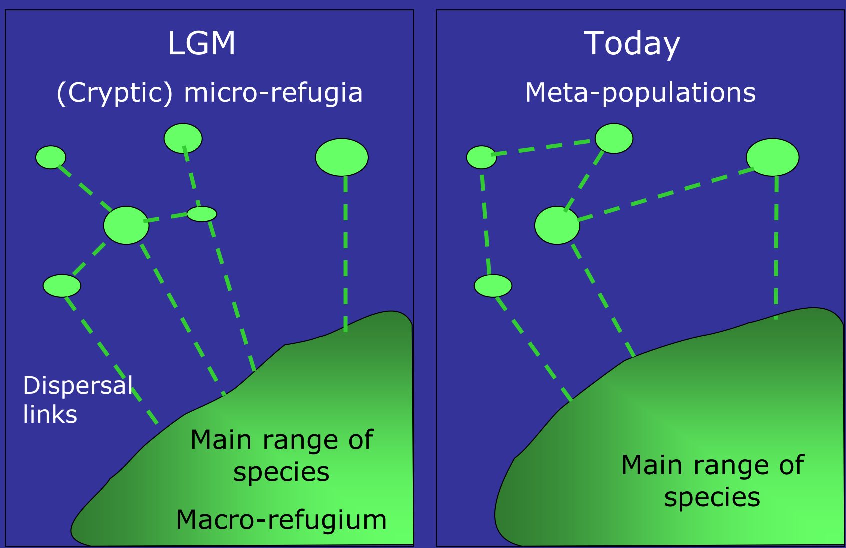


Scanning electron microscope images of wood charcoal

Tree taxa that have reliable macrofossil evidence for LGM presence in **central, eastern, or northern European refugia**, so-called micro-refugia or cryptic regugia

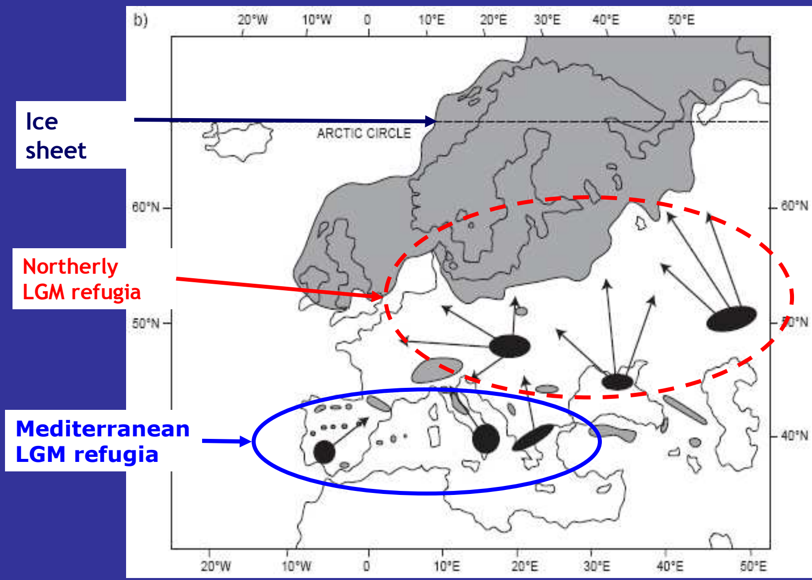
Abies alba
Alnus glutinosa
Betula pendula
Betula pubescens
Corylus
Carpinus betulus
Fagus sylvatica
Fraxinus excelsior
Juniperus communis
Picea abies
Pinus cembra
Pinus mugo
Pinus sylvestris
Populus tremula
Quercus
Rhamnus cathartica
Salix
Sorbus aucuparia
Taxus baccata
Ulmus

Birks & Willis (2008)

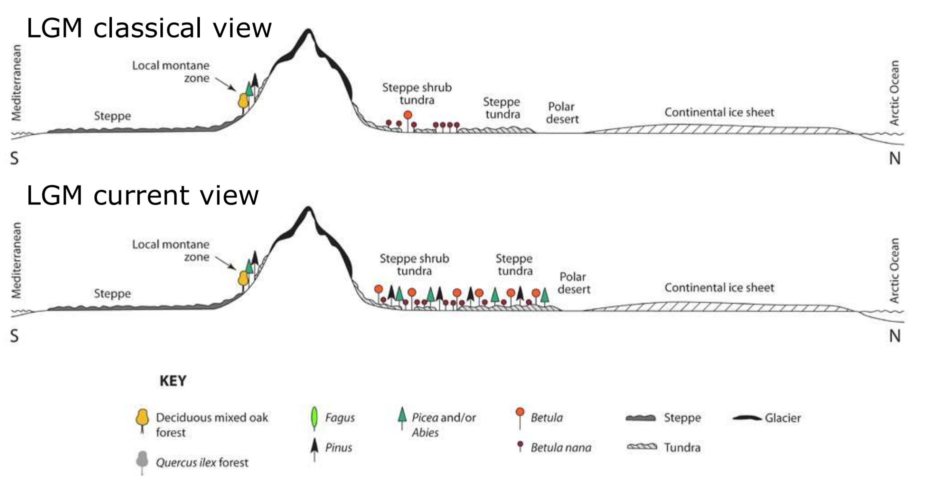


See Mosblech et al. (2011) J Biogeogr 38: 419-429

Current model of trees in LGM based on all available fossil evidence



Birks & Willis (2008)



Birks & Willis (2008)

What might LGM ‘cryptic’ refugia have looked like?

Picea crassifolia, Sichuan 3600 m

Picea <3%

Artemisia and Poaceae >75%

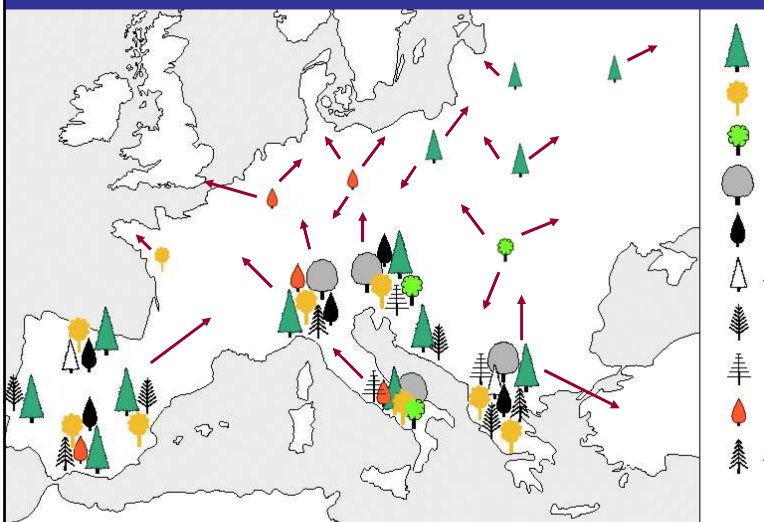
John Birks unpublished

Picea glauca, Alaska

Picea <1%

Petit *et al*. (2008)

Possible scenarios for earliest Holocene
based on available palaeobotanical data



Birks & Willis unpublished

Quaternary ice ages environmentally distinctive and presumably produced **unusual biotic patterns** that could be thought of as unusual in Earth's history.

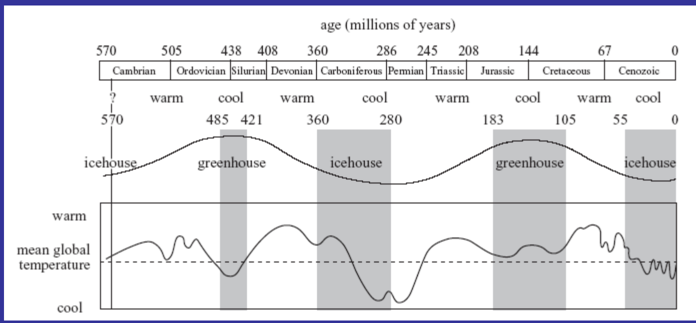
Repeated redistribution and isolation of plants in micro-environmentally favourable locations during periods of adverse climatic conditions ('**refugia**') may have important evolutionary implications.

These are:

- allopatric **speciation** – isolation resulted in genetic differentiation among populations so that they were unable to interbreed on re-expansion
- **extinction** – isolation resulted in populations too small to survive
- species **persistence** – species ranges were fragmented and re-expanded with each glacial-interglacial cycle but there was no genetic differentiation when fragmented or it was lost when populations re-expanded and mixed. **Evolutionary stasis**

Remember that **ice-house** Earth is not confined to Quaternary or Cenozoic.

Over the last 600 Myr, at least three intervals of 'ice-house' Earth with widespread continental glaciation, global cooling, and increased ariditiy.



Willis & Niklas (2004)

Are speciation rates during these 'ice-house' intervals different to those in 'greenhouse' periods?

Is there Evidence for Allopatric Speciation in the Quaternary?

Eldredge and Gould's view that fossil record shows **long periods** of **little change** in lineages interspaced with **brief periods** of relatively **rapid change** ('punctuated equilibria') as speciation takes place through geographical isolation (allopatric and peripatric speciation).

Gould (1985) proposed evolutionary theory includes processes of **three** separable **tiers of time**

1. 'Ecological moments' - microevolution
2. 'Geological time' (millions of years) - macroevolution
3. Mass extinctions

Challenged by Bennett (1990, 1997)

Evolutionary insights from Q-Time. Bennett (1990, 1997)

1. If we accept that Milankovitch cycles have been a major factor in pacing climate history throughout Earth's history, can expect **disruption** of communities to have been a permanent factor at time scales of 20-100 k yr. Leads to frequent population crashes, range shifts, and gene flow.
2. As species have responded **individually** to climatic changes forced by Milankovitch cycles in the Quaternary, likely that they have responded in a similar way to pre-Quaternary Milankovitch cycles.
3. Milankovitch cycles affect Earth on time scales much longer than the **generation times** of any organisms but shorter than most, if not all, **species durations**.
4. Over ecological time with relatively stable climate, adaptation and evolution by **natural selection** may take place. As climate changes in response to Milankovitch cycles, communities break up, and new communities form.

5. A**daptations** accumulated are likely to be **lost** unless they also prove useful (so-called exaptations) under the new conditions.
6. G**ene pools** are thus being **stirred** by recombining temporarily separated populations. Gradualistic speciation is thus difficult.
7. Quaternary fossil record has very little evidence for **rates of macroevolution** being higher than in earlier geologic periods. Surprising given the clear and dramatic environmental changes.
8. Orbital forcing of climate undoes much of any evolutionary progress accumulated at a **microevolutionary level** in ecological time. Mass extinctions will undo any lineage trends resulting from peripatric speciation occurring in 1-20m yr scale.

9. **Levels of processes** controlling evolutionary patterns

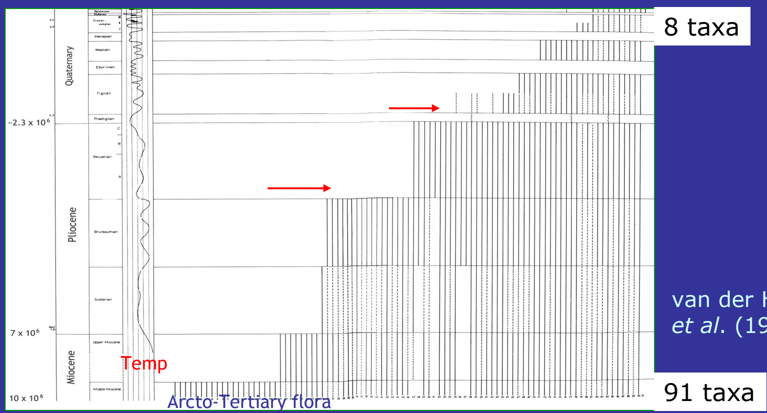
Level	Periodicity	Cause	Process
First	-	Natural selection	Microevolution within species through natural selection. Ecological time
Second	20-100 k yr	Milankovitch	Disruption, loss of accumulated microevolution changes
Third	-	Isolation	Macroevolution through geographic isolation created by second level (e.g. sea-level changes). Geological time
Fourth	~26 M yr	Mass extinctions	Loss of species and higher taxa

Milankovitch level is the 'missing level' in Gould's original analysis

10. Reinforces concept of **punctuated equilibrium** and makes it more difficult to maintain hypothesis of Darwin that processes visible in ecological time gradually build up into macroevolutionary trends.
11. Quaternary instability may not have led to increased speciation rates. Most species appear to **pre-date** the Quaternary.
12. No convincing evidence for macroevolution (morphological species) during the Quaternary. Microevolution (e.g. *Hieracium*, *Primula*, and *Taraxacum*) and cryptic speciation (e.g. *Conocephalum*) may have occurred.

Are there Plant Extinctions in the Quaternary?

Well known that the European flora, especially trees and shrubs, has become increasingly **impoverished** from Miocene to Holocene.

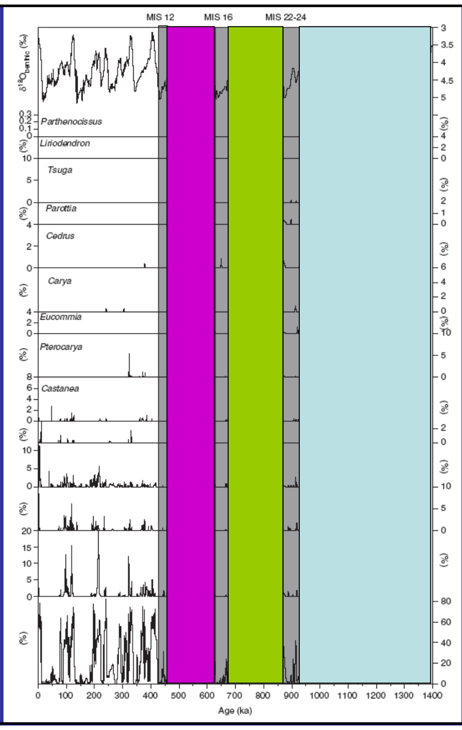


van der Hammen *et al.* (1971)

Losses in NW Europe

Weichselian	2 taxa	*?Bruckenthalia (=Erica) spiculifolia, Picea omorika*
Eemian	5 taxa	*Dulichium arundinaceum, Brasenia schreberi, Chamaecyparis thyoides, Cotoneaster acuticarpa, Aldrovanda vesiculosa*
Holsteinian	7 taxa	*Azolla filiculoides, Pterocarya, Nymphoides cordata, N. peltata, Rhododendron ponticum, Osmunda cinnamomea, Osmunda claytoniana*
Cromerian	6 taxa	*Eucommia, Celtis, Parthenocissus, Liriodendron, Tsuga, Aesculus*

Many of these appear to be **less frost-tolerant** than currently widespread European plants. Extinction **may** have occurred in **glacial** rather than interglacial stages. Surprising number of aquatics or marsh plants.



Tenaghi Philippon 1.4 myr

1. More diverse flora before MIS 22-24
2. Remaining taxa extinct in MIS 16 or soon after (e.g. *Cedrus*, *Carya*, *Eucommia*)
3. No extinctions in MIS 12 (maximum extent of ice sheets based on benthic ^{18}O isotopes)

Tzedakis *et al*. (2006)

Global extinction of *Picea critchfieldii*, abundant in LGM of south-eastern US, occurred during last deglaciation (16,000-10,000 yr BP), a time of rapid climate change (Jackson & Weng 1999).

Glacial stages are highly dynamic climatically with cold, dry conditions in response to Heinrich events and Dansgaard-Oeschger interstadial-stadial variability. **High amplitude** fluctuations during glacial stages may be responsible for **extinctions**.

All other late-Quaternary extinctions are thought to be the result of **human activity** (e.g. Easter Island palm).

Regional late-Quaternary **extinctions** are surprisingly rare (e.g. *Koenigia islandica* from central Europe in LGM, *Larix sibirica* from central Sweden in mid-Holocene, *Picea omorika* from north-west Europe).

One global extinction (other than human-induced extinctions). About **100 taxa gone extinct** from Europe in last 1-2 Myr but are still found growing in Asia or North America, and 15 taxa extinct from Europe in last 250 thousand years.

No plant known from NW Europe to have gone globally extinct during the Quaternary. Extinction **not a major factor** in Quaternary plant diversity

Ecological implications of '41 kyr' and '100 kyr' worlds within the Quaternary

100 kyr world
Late Pleistocene

41 kyr world
Early Pleistocene

Blue = glacial

Green = interglacial

Interglacials much shorter in the Late Pleistocene 100 kyr world than in the Early Pleistocene 41 kyr world. Greater potential mixing of genes in Late Pleistocene world with longer glacials.

- Number of cycles and hence major floristic and vegetational change 2.5 times greater in Early Pleistocene than in Middle-Late Pleistocene
- Differences between glacial and interglacial conditions probably less extreme than in Middle-Late Pleistocene with less drastic glacial stages
- Chances of losing species in Early Pleistocene in refugial areas greater because of more dynamic conditions and many more high amplitude fluctuations
- Changes in amplitude of climate changes
- More extinction in '41 kyr' world than in '100 kyr' world

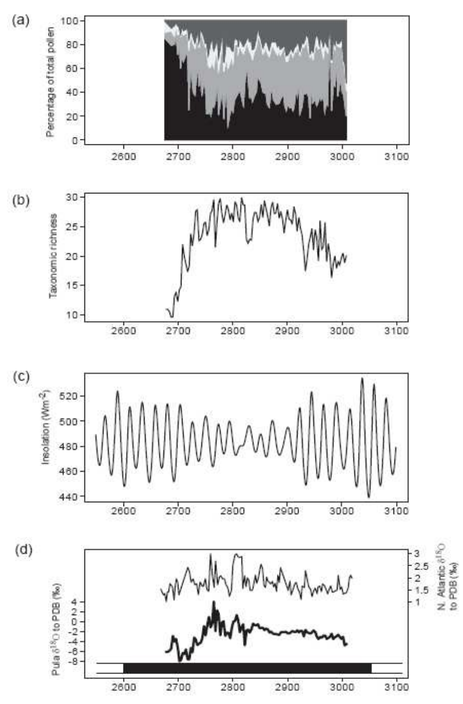
Extinctions in Late Pliocene

Late Pliocene pollen record from Pula Maar, Hungary, 320,000 year record

Kathy Willis *et al.*

Pula Maar, Hungary

- sediments composed of finely laminated oil-shales, each couplet represents a single year of accumulation
- sequence contains c. 320,000 years in annual layers between c. 3.0-2.67 Myr
- analysed for pollen, isotopes, and geochemistry at interval of every 2500 years



Fossil pollen %

Dark grey = warm temperate
White = herbs
Light grey = cool temperate
Black = boreal

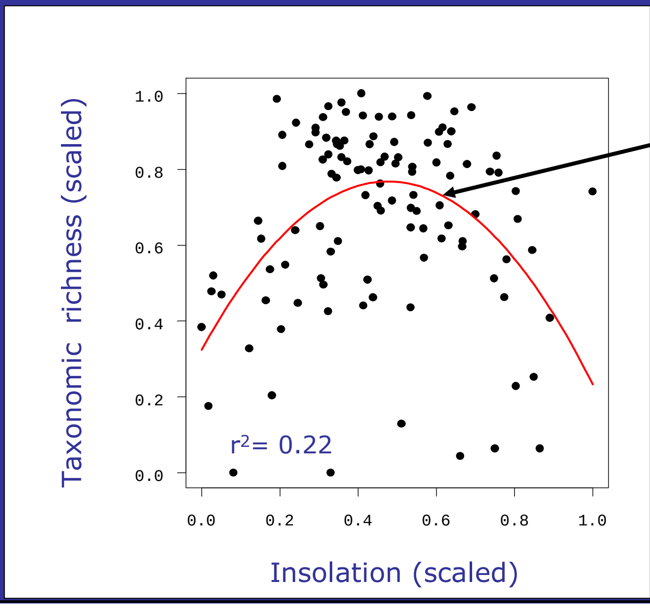
Palaeo-richness

Palaeo-energy (Laskar's 2004 insolation calculations)

Palaeo-water balance ($\delta^{18}O$)

Willis *et al*. (2007) Ecology Letters 10: 673-679

Energy-based model – Laskar energy calculations vs pollen richness

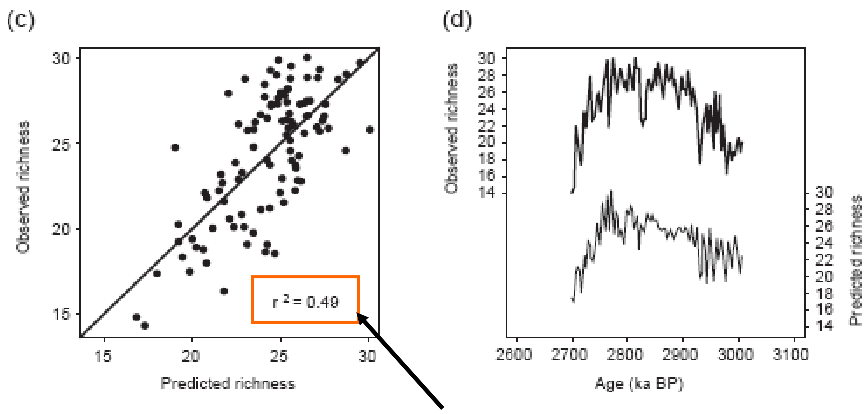


Highest richness corresponds to intermediate insolation

Non-linear relationship

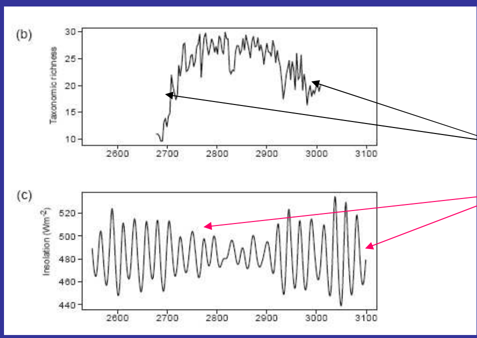
Willis *et al*. (2007)

Combined water-energy model (energy^2 + water)



Combined water-energy model provides much better predictor of richness than water or energy alone

Willis *et al*. (2007)



High amplitude fluctuations appear to lead to low taxonomic richness

Local extinctions of *Sequoia, Nyssa, Parrotia, Fagus*, etc. occur in periods of **high amplitude** fluctuations – reductions of regional species pool

See Svenning (2003) Ecology Letters for trait analysis of species that went extinct in Europe

Willis *et al*. (2007)

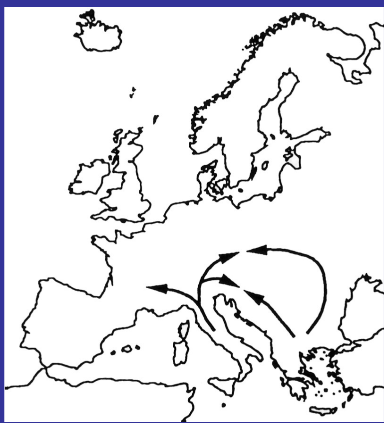
Main feature of Ice Ages are

- **No** evidence for speciation
- **Little** evidence for global extinctions
- **Much** evidence for **stasis**

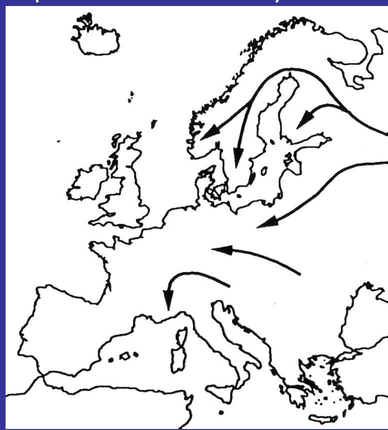
Main effect of Quaternary ice ages on plants is **species persistence** and **evolutionary stasis** retained by rapid migrations and resulting mixing of gene pools

What are the Main Biological Responses to Repeated Quaternary Glacial-Interglacial Cycles?

1. Interglacial **spread** of biota from glacial 'refugia' in individualistic pattern at rates of up to 100-2000 m yr^{-1}

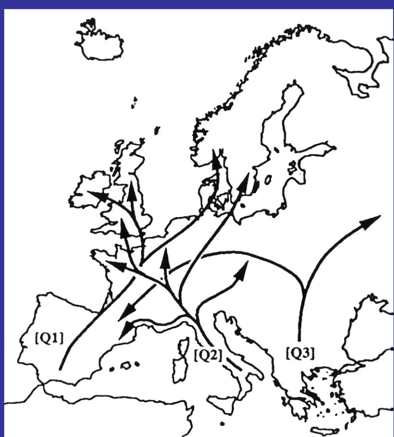


Post-glacial colonisation routes for *Abies alba*

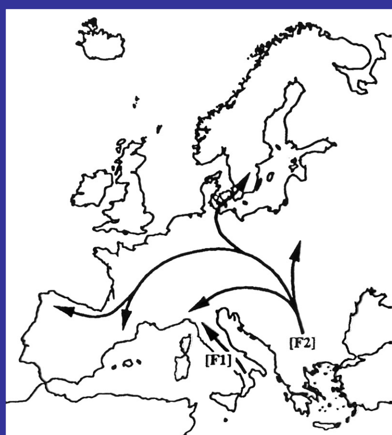


Post-glacial colonisation routes for *Picea abies*

Taberlet (1998)



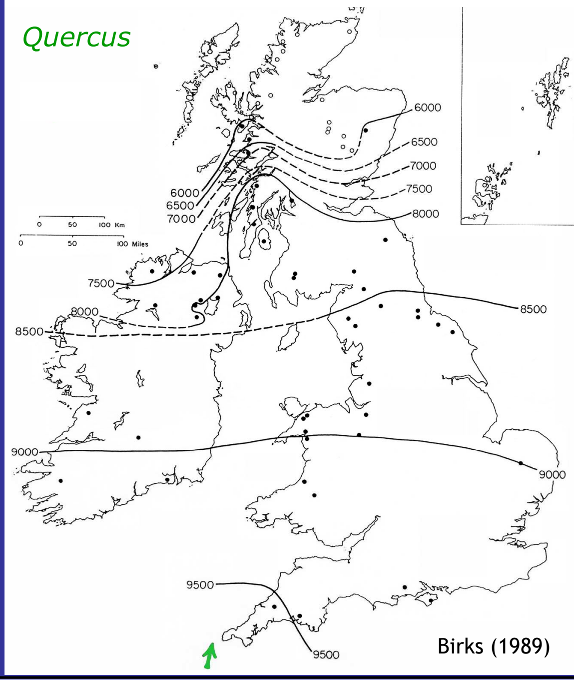
Post-glacial colonisation routes for *Quercus* spp.



Post-glacial colonisation routes for *Fagus sylvatica*

Taberlet (1998)

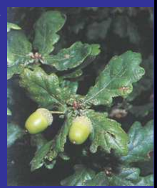
Isochrones for British Isles

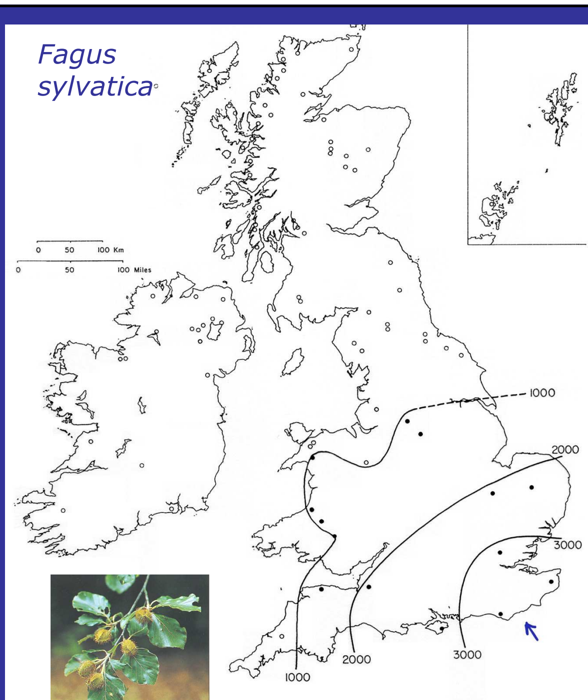


***Quercus*, oak**

Isochrone map of the rational limit of *Quercus* pollen in the British Isles. The isochrones are based on data from the sites indicated by dots and are shown as radiocarbon years BP. Sites where there is no pollen-analytical evidence for local presence are shown as open circles.

Spread quickly throughout England and Ireland. Slowed down in Scotland and reached its distributional limit (climate, soil).

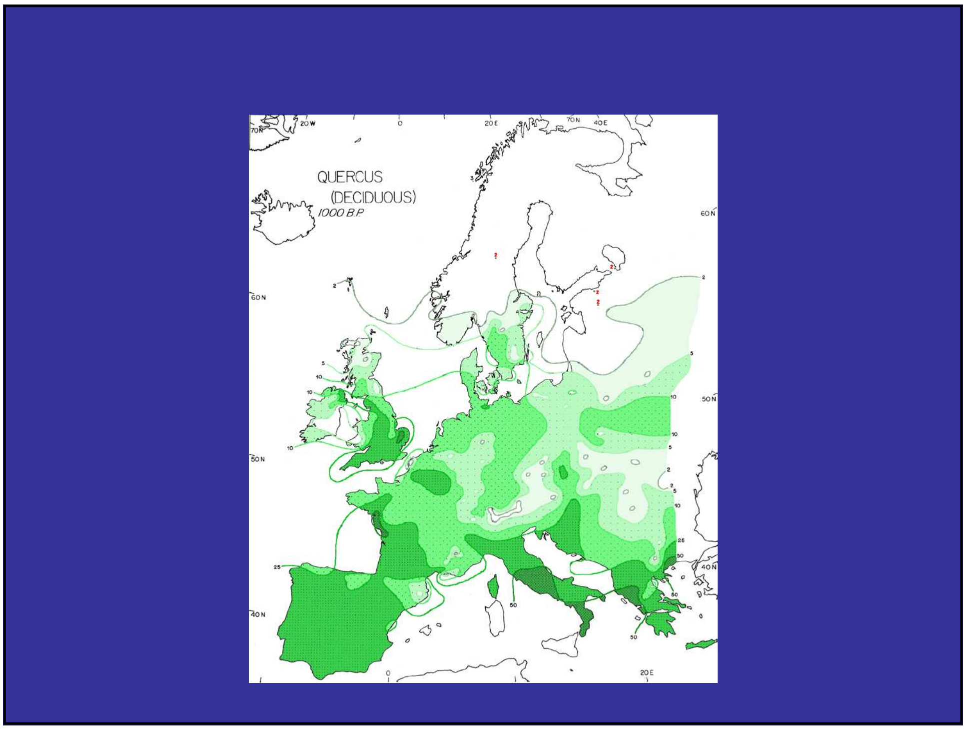


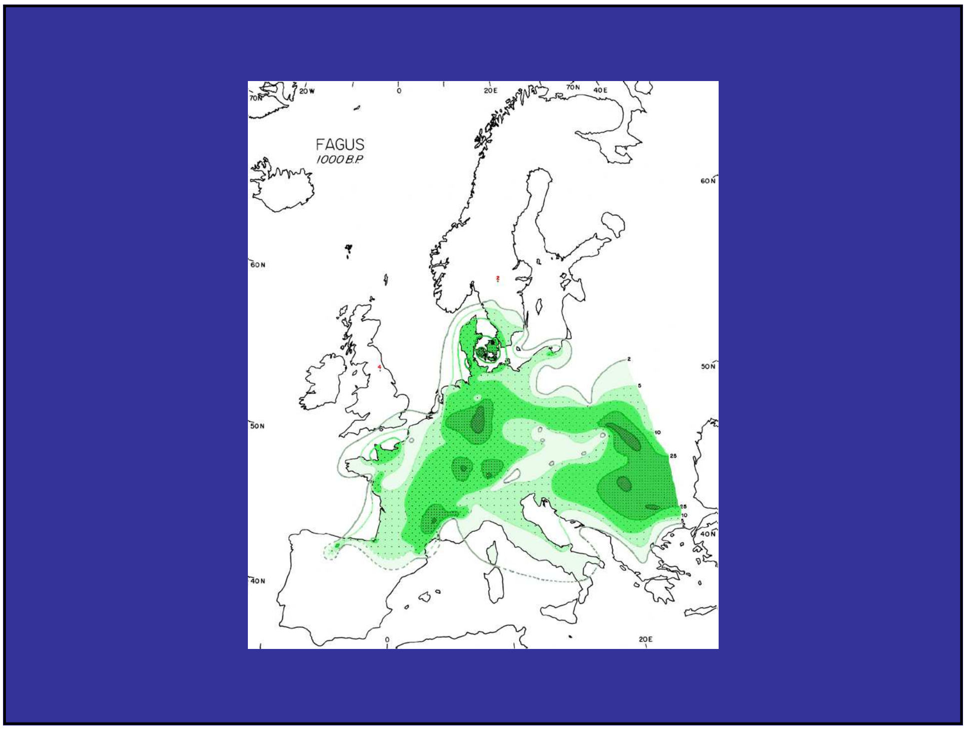


Spread of ***Fagus***, beech

The spread was late and restricted to southern England. However, planted *Fagus* flourishes beyond its natural limit, e.g. throughout UK and in Bergen.

Birks (1989)

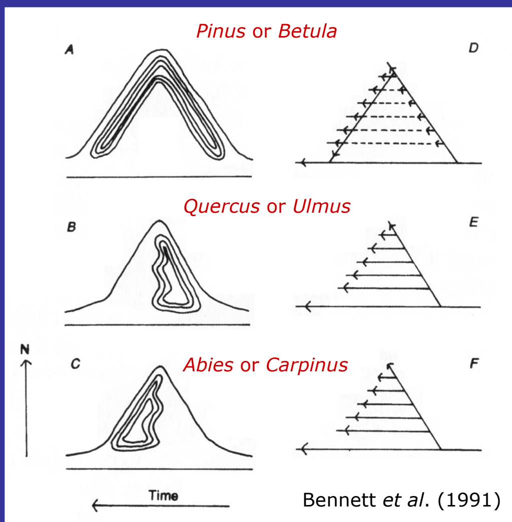

QUERCUS
(DECIDUOUS)
1000 B.P.


FAGUS
1000 B.P.

2. Each taxon appears to have responded **individually**.
3. Forest vegetation of N America and Europe has **no history longer than 10 k yr** (at best).
4. **Tropical vegetation** also experienced substantial change during late Quaternary climate shifts.
5. Same rapid mixing and subsequent separation also known for **mammals and beetles**.
6. Present-day terrestrial and freshwater communities have **no long history**. Communities have broken up and reformed in different configurations repeatedly and perhaps regularly on time scales of a few thousand years.
7. **Marine organisms** have similarly been highly mobile on spatial scales of whole oceans with Quaternary climatic changes.

8. At end of a warm interglacial and climate deteriorates, no evidence that trees migrate southwards. **Northern European populations decrease** and disappear *in situ*.

   Almost all northern European trees also occur in the south – 'long-term' persistence.

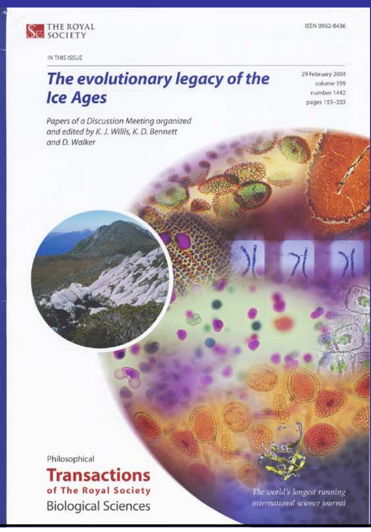


Diagrammatic representation of the spatial extent, variation in time, abundance, and ancestry of populations of tree taxa in Europe during an interglacial. A-C: Variation in northerly extent of range with time (outer lines) and abundance (contours); D-F: Ancestry of selected populations, extinct at end of lines.

9. It is the failure of a species' **southern** populations to survive during either an interglacial or glacial that will lead to its **extinction** from Europe.

10. The W-E orientation of southern and central **European mountains** unlikely to have led to the loss of many Tertiary species as a barrier to spread. The greater rate of extinction in Europe relative to N America is more likely a function of the **much reduced area** available for survival of refugial populations south of the Alps. Trees probably survived in suitable microhabitats in mid-latitude zones and in locally moist sites in lowlands and coastal areas. Tree biodiversity a result, in part, of **Quaternary history**.

Why is there no Evidence for Increased Genetic Diversification and Speciation During the Quaternary?



Willis *et al*. (2004)

Two possible explanations:

1. Fossil data incomplete, based largely on pollen. Pulses of genetic differentiation and resulting speciation may go unrecorded in the fossil record. Molecular techniques potentially valuable here but need a calibrated ‘molecular clock’.
2. Isolation in cold stages simply too short for speciation events.

Deep-Time records for last 410 Myr show average duration of fossil angiosperm species is **3.5 Myr** and new species appear every **0.38 Myr**.

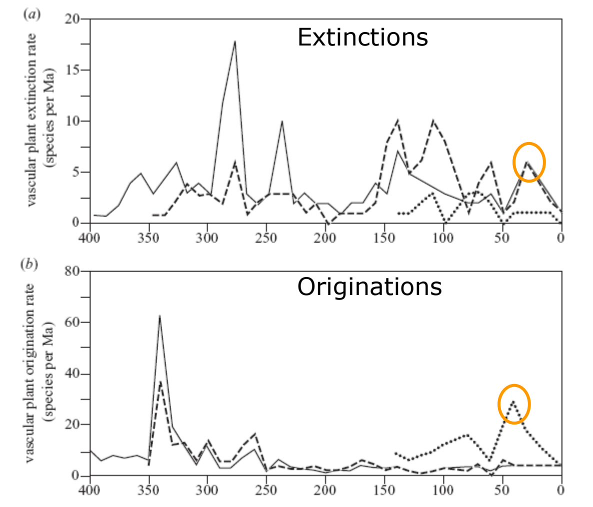
One new species every 10% of an average species’ lifetime.

Speciation event will occur about **once** in every 76000 generations.

Possible that **no apparent increase** in speciation rates in Quaternary because the **duration of isolation was simply too brief**, especially for trees.

Important therefore to consider speciation and patterns not in the Quaternary but in the past 50 Myr, the onset of the current ice-house Earth.

Are there differences between speciation rates in ice-house and greenhouse Earth?



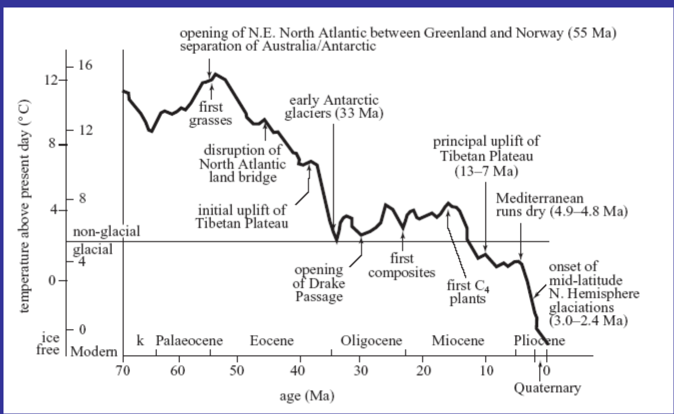
Willis & Niklas (2004)

Highest angiosperm speciation rate occurred between 40 and 35 Myr

High gymnosperm and pteridophyte extinctions at this time too, at the onset of ice build-up in the Southern Hemisphere

·····	angiosperms
– –	gymnosperms
——	pteridophytes

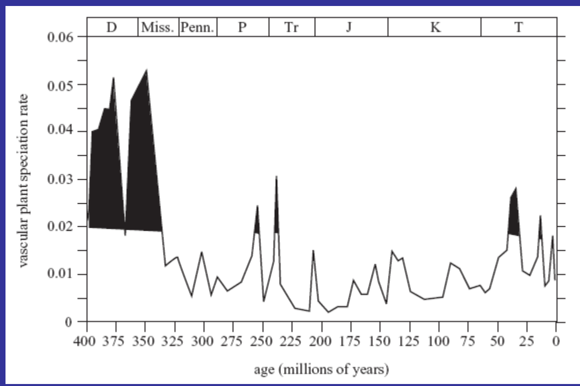
Suggestive that long-term climate change may have increased **diversification** and **speciation** at time of build-up of ice in the Southern Hemisphere from 50 Myr ago (ice-house Earth). Changes at scale of 1-2 Myr of Quaternary not detectable or not present. Data not detailed enough.



Willis & Niklas (2004)

What about previous ice-house Earths?

Speciation rate



Willis & Niklas (2004)

Speciation rate greatly increased

May have resulted from environmental changes at time-scales **much longer** than Milankovitch cycles

Stasis – An Important but Unexpected Response

If there is little speciation or extinction in response to Milankovitch oscillations, **stasis** is the major response in evolutionary terms for the Ice Ages.

Species and lower categories have appeared and persisted for longer or shorter lengths of time during the Quaternary as well as during earlier periods.

Uncertain if frequency of speciation has changed or not relative to the Palaeogene/Neogene. Species clearly persist unchanged (at least morphologically) over multiple glacial-interglacial cycles.

Stasis exists despite **considerable environmental change**. Major evolutionary response to Quaternary climate changes. Stability of species through these oscillations is amazing.

Stasis is interesting because it came about in **unlikely** circumstances when one would have **expected responses of speciation and extinction** to be important in response to Milankovitch oscillations.

" 'Is there any point to which you would wish to draw my attention?'

'*To the curious incident of the dog in the night-time*.'

'The dog did nothing in the night-time.'

'*That was the curious incident*,' remarked Sherlock Holmes."

Arthur Conan Doyle (Silver Blaze)

Molecular data and Q-Time

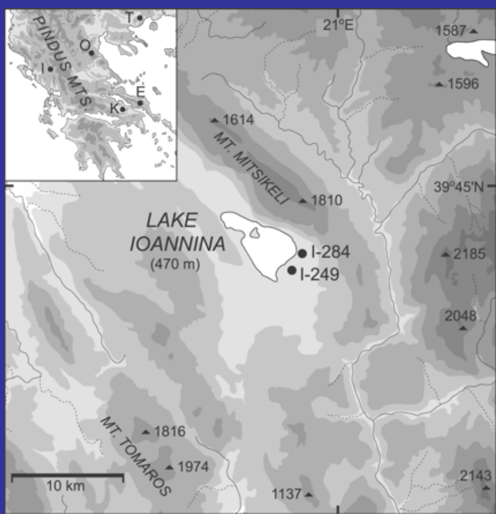
1. Considerable divergence between populations of many species in **southern refugial centres** such as Greece and Iberia. Took several glacial-interglacial cycles to accumulate.
2. **DNA divergence** data in animals suggest that species have continued forming through Pleistocene and such divergence has occurred apparently unhindered in places where environment has been relatively stable.
3. DNA divergence indicates that while in lowland tropical forests most species formed before the Quaternary, clusters of recently diverged lineages along with older species are found in **tropical mountain regions**.

Hewitt (1996,1999, 2000)

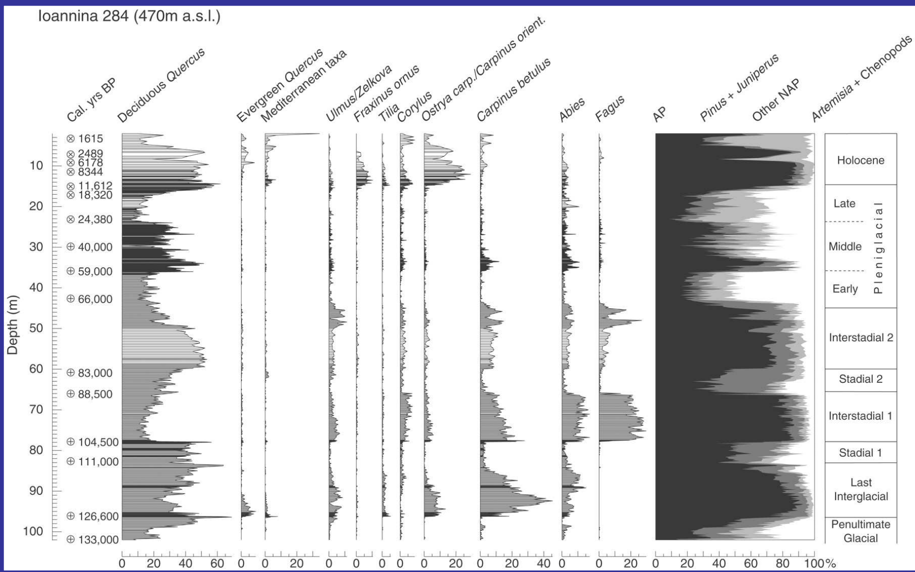
4. Such regions are **centres for speciation** because they provide a relatively stable habitat through minor climatic oscillations in which 'old' species survive and 'new' lineages are generated.
5. Such **long-term stability** may be a function of continued moisture availability and varied topography.
6. **Revised view** is such that while climatic instability mostly inhibited (or undid) speciation, species continued to form in places where presumed ecological stability allowed accumulation of genetic divergence through several glacial-interglacial cycles.

Hewitt (1996, 1999, 2000)

One such place may be the Balkans



Topographic map showing the Ioannina basin and surrounding area.



Pollen diagram of the top 102 m from Ioannina, showing % of selected taxa

Current hypothesis for high biodiversity in southern Europe

Tzedakis *et al.* (2002) Science

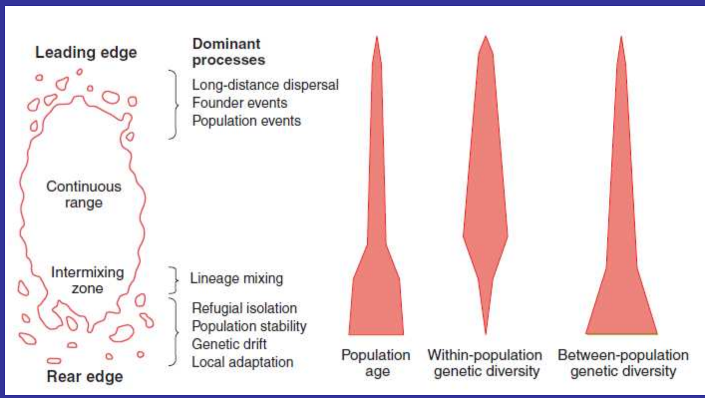
1. Iberian, Italian and Balkan peninsulas and their biota have remained **genetically isolated** over several glacial-interglacial cycles, thereby preserving the products of microevolutionary processes and peripatric, allopatric, or geographical speciation.
2. During **glacials**, reduced populations survived in isolated habitats and may have differentiated through selection and genetic drift. Micro-allopatry mixed with range expansion, varying selection, and hybridisation would be repeated in each interglacial cycle. Each taxon would follow its own individualistic pathway of divergence and speciation.

3. **Richness** of the Mediterranean biota with its unusually high endemism is, in part, a reflection of its geographical position and geological history as well as the extent to which Tertiary species could survive there.
4. Ioannina pollen data suggest **local buffering** from extreme climatic events. May have led to reduced extinction rates and favoured speciation. 150 species of spider in the area, highest in Balkans. Over 50% are woodland species. Persistence of tree populations there over the last 130 k yr may have promoted genetic divergence by providing relatively stable conditions (but not totally stable nor strongly unstable – 'intermediate' stability).

Leading edge and read edge of species range-limit

Bioclimate models used to predict dynamics of leading edge of species-range margins and the potential space that will be needed for future reserve boundaries.

The **rear-edge** is rarely considered by ecologists or modellers even though the rear-edge contains the source populations from which the leading-edge populations migrate.



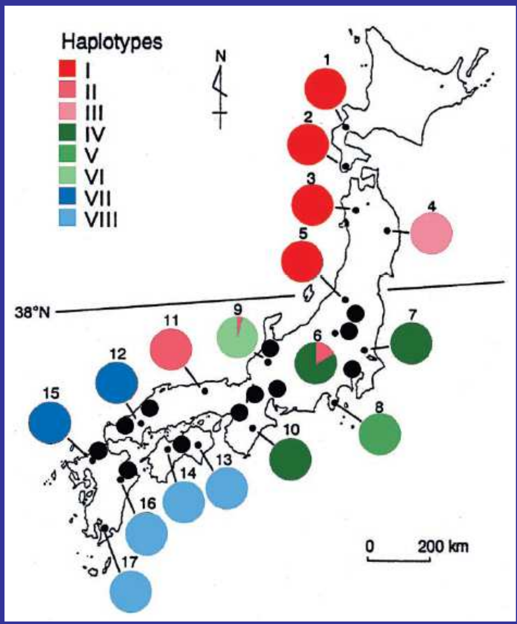
Willis & Birks (2006)

Palaeoecological and genetic evidence suggest that the rear-edge populations are important in the conservation of long-term genetic diversity and hence in speciation. Rear-edge is often in or near presumed LGM macro-refugia in, e.g. Balkans, Iberia, Italian peninsulas, or Carpathians.

Range shifts and adaptive responses to Quaternary climate change

"Tree taxa shifted latitude or elevation range in response to changes in Quaternary climate. Because many modern trees display adaptive differentiation in relation to latitude or elevation, it is likely that ancient trees were also so differentiated, with environmental sensitivities of populations throughout the range evolving in conjunction with migrations. Rapid climate changes challenge this process by imposing stronger selection and by distancing populations from environments to which they are adapted. The unprecedented rates of climate changes anticipated to occur in the future, coupled with land use changes that impede gene flow, can be expected to disrupt the interplay of adaptation and migration, likely affecting productivity and threatening the persistence of many species."

Davis & Shaw (2000) Science



Davis & Shaw (2000)

Phylogeographic analysis of *Fagus crenata*, a Japanese montane beech species, based on mitochondrial DNA haplotypes. Beech survived the glacial interval in small populations along the coast south of the 38th parallel, but by 13,000 calibrated calendar years before present, populations had expanded at the sites indicated by black dots. Pie diagrams indicate haplotype frequencies in 16 modern populations in nearby refuges at low elevations. Northern populations appear the have descended from populations near the northern limit of beech distribution 13,000 years ago. Populations 6 and 9 are related to other northern populations but include haplotypes resulting from hybridisation with eastern populations; the latter may have had their origin in refugial populations along the eastern coast.

Much to be done on adaptive response to environmental change using molecular techniques

Good evidence for genetic variation in

Abies alba	*Picea abies*
Fagus sylvatica	*Pinus sylvestris*
Quercus robur	*Quercus petraea*

Is this variation adaptive?

Main Conclusions

1. Considerable **climatic fluctuations** and environmental changes in the Quaternary with many glacial-interglacial cycles
2. **Biotic responses** to major climatic changes
   - distribution changes
   - high rates of population turnover
   - changes in abundance and/or richness
   - extinctions (global, regional, or local)
   - speciations
   - stasis
3. Biotic responses have been **varied**, **dynamic**, **complex**, and **individualistic**.

4. Interglacial–glacial records show that biotic responses to rapid climate change were mainly **redistribution** of species, genera, families, and vegetation types, high turnover, abundance changes often resulting in local or regional extinctions but very **rarely any global extinctions**. **No** evidence for **speciation**. Vegetation types often have **no** convincing **modern** palynological **analogue**.
5. A **combined use** of these Q-Time results and molecular phylogenies could help understand **rates** and **thresholds** of climate-biodiversity interactions and provide some **independent tests** of current models and predictions of biodiversity response to future climate change.

6. The Quaternary Ice Ages, contrary to popular opinion, were **not** periods of major plant speciation or extinction but were periods of evolutionary stasis and extensive changes in range dynamics. Milankovitch cycles may be the missing level in evolutionary theory, between microevolution by natural selection and macroevolution through allopatric speciation.
7. Need to consider both **Q-Time** and **Deep-Time** to understand the evolutionary legacies of the Ice Ages.

8. Many exciting **potential links** in the future between Q-Time, Deep-Time, molecular phylogeography, and evolutionary biology.

   "There is no more positive guide to the past occupation of any area by a particular species than the discovery of fossils. Nevertheless, we may garner a great deal of information from … genecological studies of well-chosen species."

   Baker (1959)

9. Can **now answer** Charles Lyell's big question of 1856 to Darwin. Result of repeated Milankovitch-forced migrations. Any natural selection that had occurred during interglacials or glacials did not accumulate over longer time periods to bring about speciation in the Darwinian sense. Stasis is the answer, Q-Time climate changes are the process.

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