Vegetation Responses to Rapid Climate Change at the Late-Glacial/Holocene Transition

John Birks

Nordforsk PhD course, Abisko 2011

Why is a Quaternary-time palaeoecological perspective relevant to questions of migration, persistence, and adaptation?

How did biota respond to past rapid climate change?

Younger Dryas/Holocene transition at 11,700 calibrated years BP at Kåkenes

- Terrestrial vegetation and landscape development
- Possible modern analogues
- Chironomid-inferred temperatures and delayed arrival of *Betula*
- Other biotic responses at the YD/H transition
- Lake development and aquatic changes
- Conclusions

What could have determined persistence, migration, or extinction in the past?

How can Quaternary palaeoecology provide insights to understanding migration and persistence?

What conclusions can Quaternary palaeoecology draw about vegetation dynamics?

Ecosystem functional change at YD/H transition

Novel ecosystems

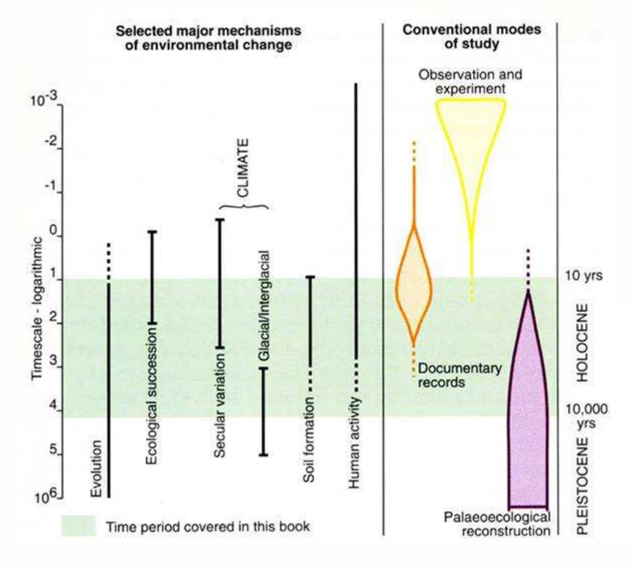
Conclusions

Why is a Quaternary Palaeoecological Perspective Relevant?

Long argued that to conserve biological diversity, **essential** to build an understanding of **ecological processes** into conservation planning

Understanding ecological and evolutionary processes is particularly important for identifying factors that might provide **resilience** in the face of **rapid climate change**

Problem is that many ecological and evolutionary processes occur on **timescales** that **exceed** even long-term observational ecological data-sets (~100 yrs)

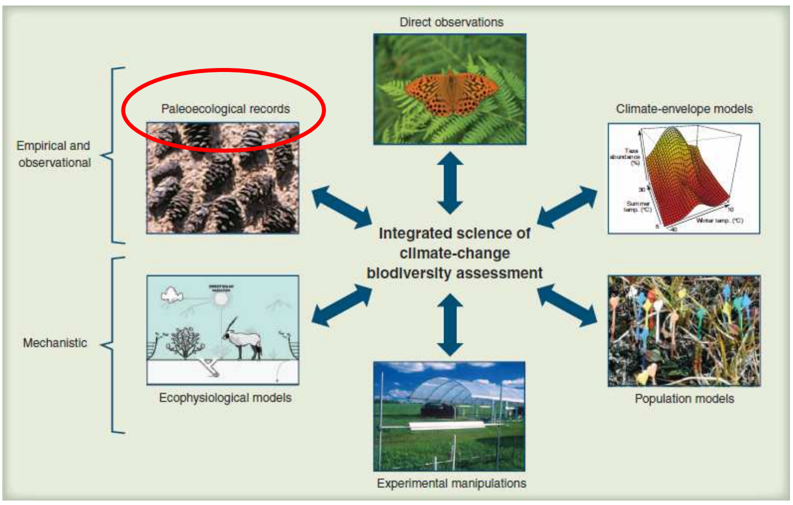


(Modified from Oldfield 1983)

Challenge for palaeoecological studies is to obtain the **temporal resolution** of documentary records and observational data. Needed if we are to evaluate biotic responses to rapid climate changes that may have occurred over 20-50 years and may occur in the future.

Beyond Predictions: Biodiversity Conservation in a Changing Climate

Terence P. Dawson,[1] Stephen T. Jackson,[2] Joanna I. House,[3] Iain Colin Prentice,[3,4,5] Georgina M. Mace[4,6]*



Dawson et al. (2011)

Integrated approach to climate-change biodiversity assessment

Dawson et al. (2011)

Modes of biotic response to environmental change
Very useful framework to view biotic responses

Major step forward

"Drawing on evidence from **palaeoecological observations**, recent phenological and microevolutionary responses, experiments, and computational models, we review the insights that different approaches bring to anticipating and managing the biodiversity consequences of climate change, including the extent of species' natural resilience."

Dawson et al. (2011)

One approach for dealing with the data-gap between ecological and evolutionary time-scales is to rely on **modelling.** These models focus on future spatial distributions of species and assemblages under climate change rather than the ecological responses to climate change. Many crippling assumptions and serious problems of scale. Strongly dismissed by Dawson et al. (2011).

High-resolution **palaeoecological records** provide unique information on species dynamics and their interactions with environmental change spanning 100s or 1000s years.

Review   *Trends in Ecology and Evolution* Vol.25 No.10

Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data

K.J. Willis[1,3,4], R.M. Bailey[2], S.A. Bhagwat[1,2] and H.J.B. Birks[1,2,3]

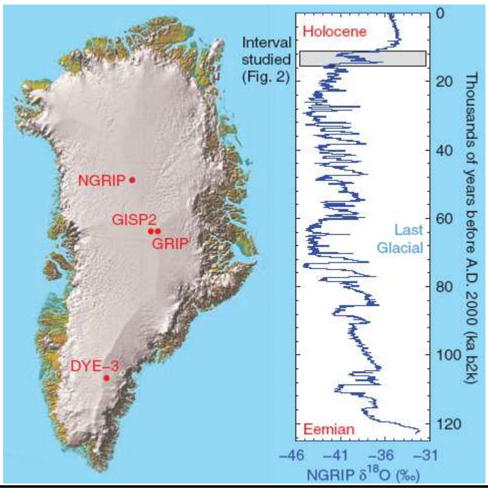
How did Biota Respond to a Past Rapid Climate Change?

Do biota migrate, persist, adapt, or go extinct locally or regionally?

The end of the Younger Dryas at 11700 years ago is a perfect '**natural experiment**' for studying biotic responses to rapid climate change

High-Resolution Greenland Ice Core Data Show Abrupt Climate Change Happens in Few Years

Jørgen Peder Steffensen,[1*] Katrine K. Andersen,[1] Matthias Bigler,[1,2] Henrik B. Clausen,[1] Dorthe Dahl-Jensen,[1] Hubertus Fischer,[2,3] Kumiko Goto-Azuma,[4] Margareta Hansson,[5] Sigfús J. Johnsen,[1] Jean Jouzel,[6] Valérie Masson-Delmotte,[6] Trevor Popp,[7] Sune O. Rasmussen,[1] Regine Röthlisberger,[2,8] Urs Ruth,[3] Bernhard Stauffer,[2] Marie-Louise Siggaard-Andersen,[1] Árný E. Sveinbjörnsdóttir,[9] Anders Svensson,[1] James W. C. White[7]

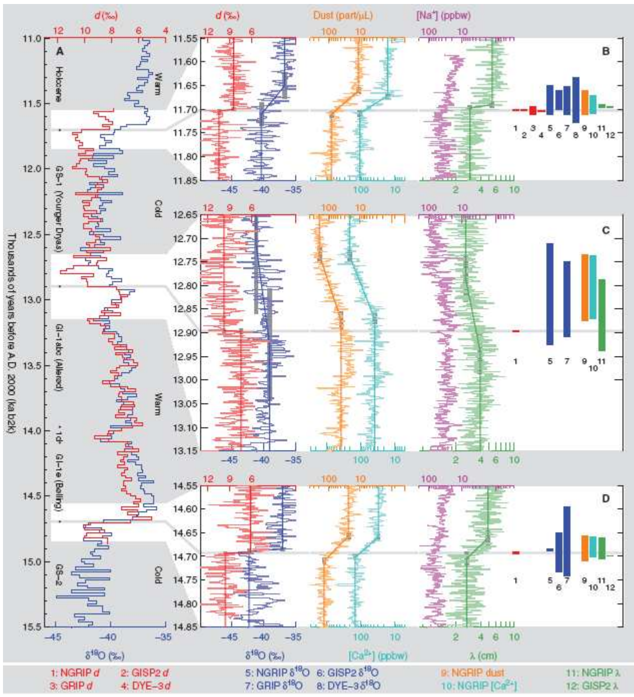


North Greenland Ice Core Project (NGRIP)

Subannual resolution of $\delta^{18}O$ and δD, Ca^{2+}, Na^{+}, and insoluble dust for 15.5-11.0 ka with every 2.5-5 cm resolution giving 1-3 samples per year.

Used 'ramp-regression' to locate the most likely timing from one stable state to another in each proxy time-series.

Steffensen *et al*. 2008
Science 321: 680-684



YD/Holocene at 11.7 ka

deuterium excess (d) ‰

$\delta^{18}O$ ‰

log dust

log Ca^{2+}

log Na^{+}

layer thickness (λ)

Annual resolution

Ramps shown as bars

Steffensen *et al*. 2008

$\delta^{18}O$ - proxy for past air temperature: YD/H 10ºC in **60 yrs**

annual layer thickness (λ): increase of 40% in **40 yrs**

d = $\delta D - 8\delta^{18}O$ (deuterium excess) – past ocean surface temperature at moisture source: changes in **1-3 yrs**

Dust and Ca^{2+} - dust content: decrease by a factor of 5 or 7 within **40 yrs** (plots are reversed)

Na^{+}: little change

Indicate change in precipitation source (δD) **switched mode in 1-3 yrs** and initiated a more gradual change (over 40-50 yrs) of Greenland air temperature

Changes of 2-4ºK in Greenland moisture source temperature from **1 year to next**

Ice-cores show how variable the last glacial period was – no simple Last Glacial Maximum

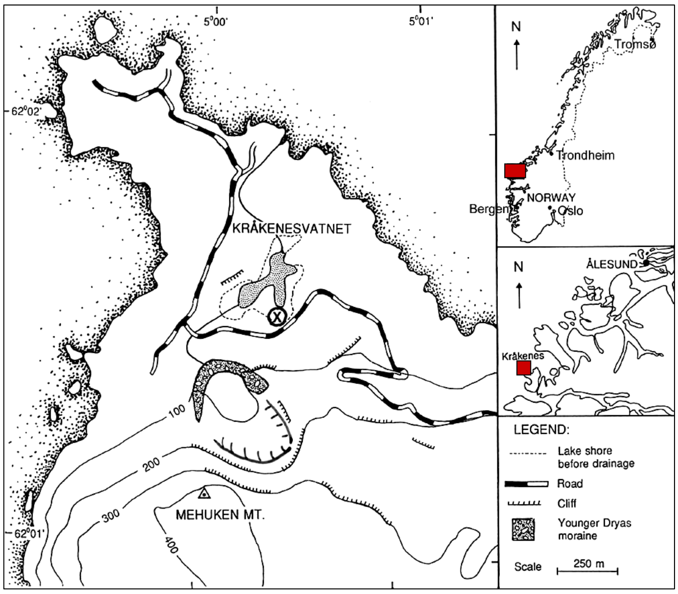
Younger Dryas/Holocene Transition at 11,700 Calibrated Years BP

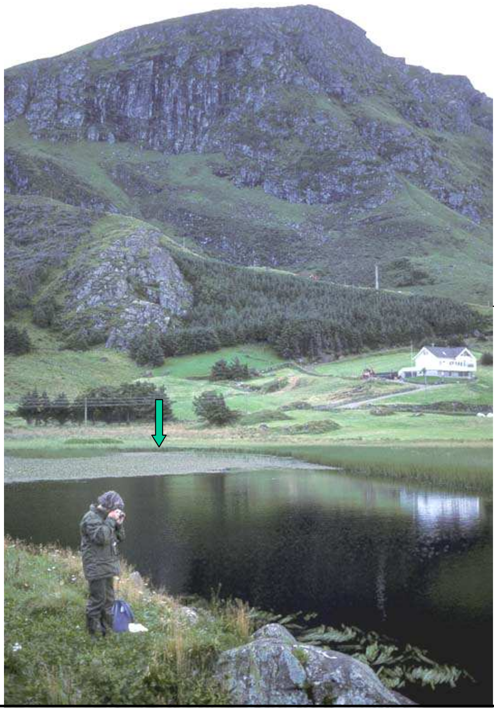
1. Remarkable climatic shift and rapid warming event felt over much of the Earth's surface
2. 'Global change' by any definition
3. Represents a global 'natural experiment' allowing us to investigate biotic responses to rapid climatic change

'Coaxing history to conduct experiments'
Deevey (1969)

'Using the geological record as an ecological laboratory'
Flessa & Jackson (2005)

Kråkenes Lake, Western Norway

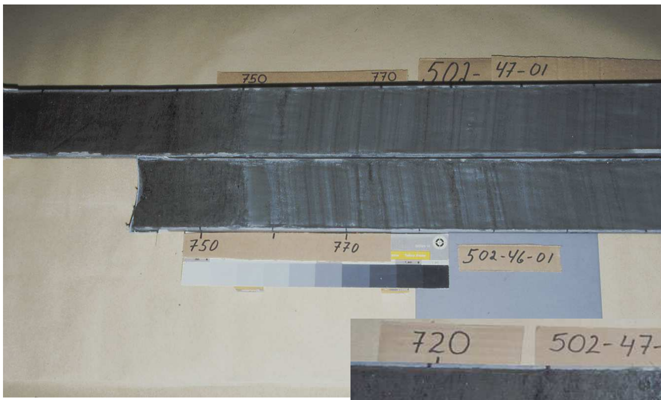




Kråkenes Lake and cirque with YD moraine in Mehuken Mountain

moraine

Coring



Kråkenes cores at the YD/Holocene transition

Detailed study of the Younger Dryas-Early Holocene transition designed to answer the following

- What were the biological responses?
- What happened on land and in the lake?
- How does the Kråkenes vegetational development compare with vegetational changes today?
- What were the rates of change and the magnitude of compositional turnover (beta-diversity)?
- What factors may have controlled the terrestrial vegetational development?

Part of multidisciplinary study of Kråkenes Lake led by Hilary Birks

KRÅKENES PROJECT

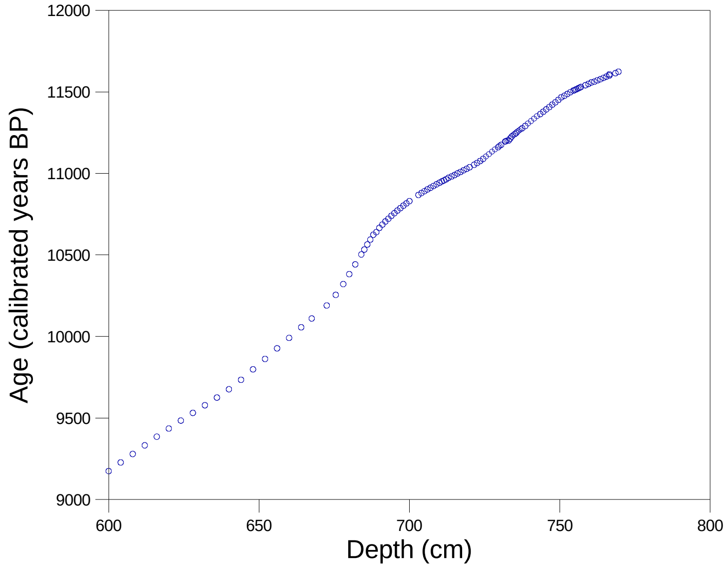
Palaeoecological Data

1. **Pollen analysis** by Sylvia Peglar
   600-769.5 cm 117 samples
   101 taxa 16 aquatic taxa
2. **Macrofossil analysis** by Hilary Birks
   Pollen analyses supplemented by plant macrofossil analyses that provide unambiguous evidence of local presence of taxa, for example, birch trees
3. **Diatom analysis**
   Aquatic changes in the lake studied by fine resolution diatom analyses by Emily Bradshaw
4. **Chironomid analysis**
   Past temperatures estimated from fossil chironomid assemblages by Steve Brooks and John Birks

5. **Radiocarbon dating** by Steinar Gulliksen
   Chronology based on 72 AMS dates, wiggle-matched to the German oak-pine dendro-calibration curve by Gulliksen *et al*. (1998 The Holocene 8: 249-259)
6. **Pollen sample resolution**
   Mean age difference = 21 years
   Median age difference = 14 years

   Chronology in **calibrated years** is the key to being able to put the palaeoecological data into a reliable and realistic time scale

Kråkenes Early Holocene pollen sample resolution

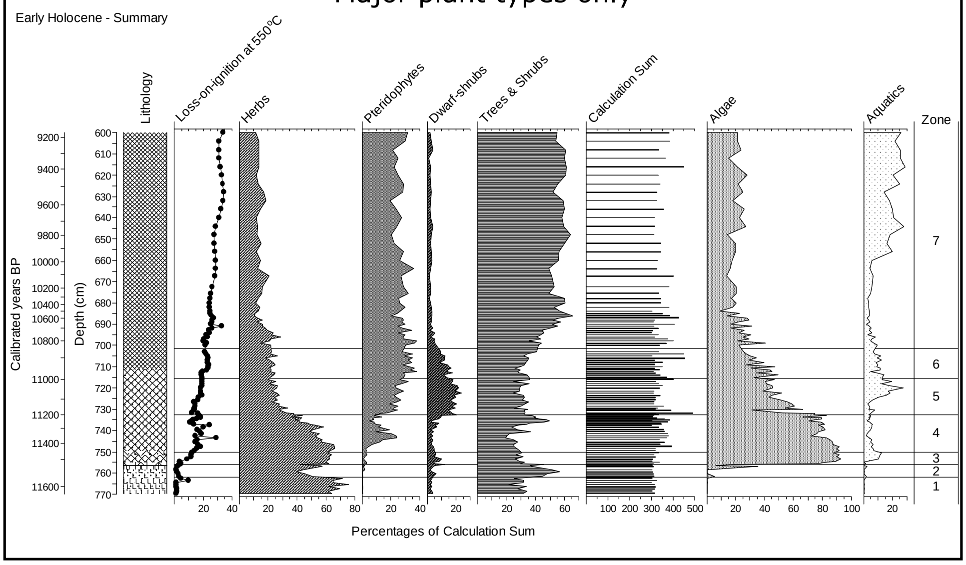


Terrestrial vegetation and landscape development

Krakenes

Early Holocene - Summary

Major plant types only



Major changes

Zone 1 Younger Dryas – herb-dominated, no aquatics or algae

Zone 1/2 Younger Dryas–Holocene transition at 11550 yr BP

Zone 2 Earliest Holocene – spread of *Salix* (willow) communities

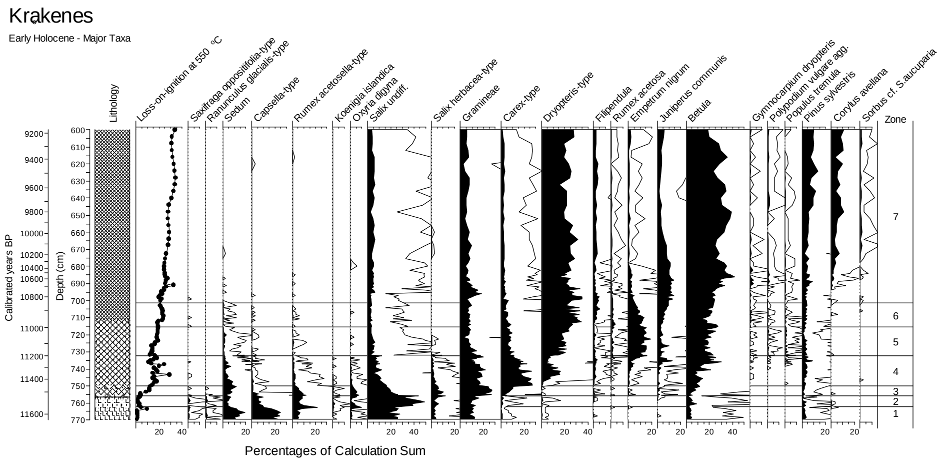
Zone 3 Major expansion of algae and beginnings of aquatic macrophytes **50 years** after end of Younger Dryas

Zone 4 Beginnings of expansion of ferns **110 years** after end of YD

Zone 5 Expansion of dwarf shrubs and beginning of decline of algae **370 years** after end of YD

Zone 6 Shrubs and some birch trees start to rise **575 years** after end of YD

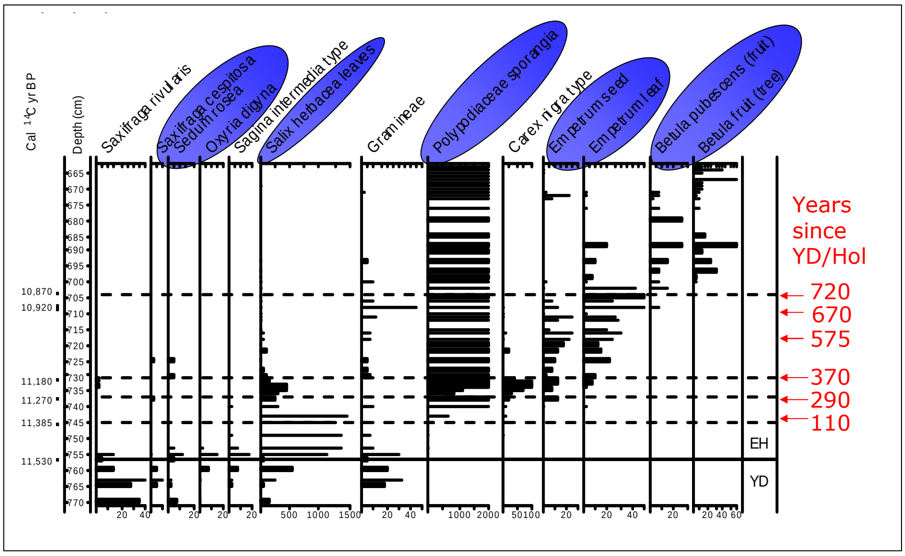
Zone 7 Tree, shrub, and fern dominance **720 years** after end of YD



Two statistically significant pollen zone boundaries in 110 years since YD, 3 zone boundaries in 370 years, 4 zone boundaries in 575 years, and 5 zone boundaries in 720 years (first expansion of *Betula*).

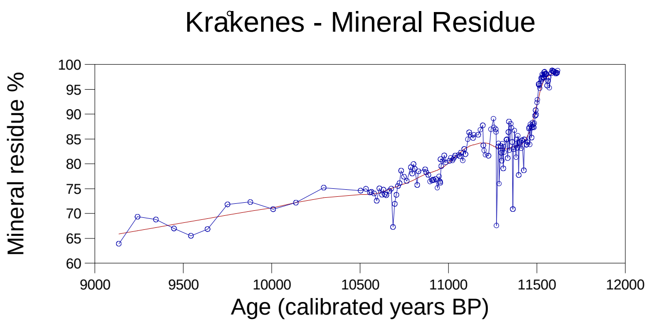
Very rapid pollen stratigraphical changes and hence **rapid vegetational dynamics.**

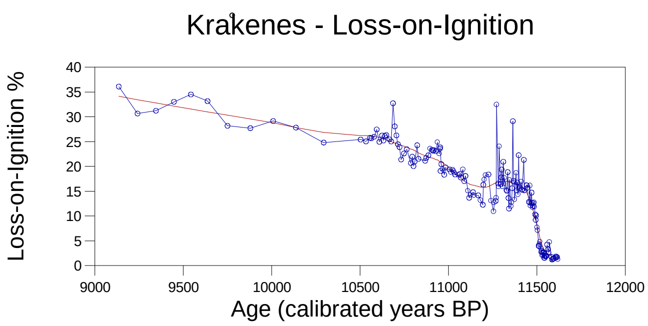
Kråkenes terrestrial macrofossils – summary diagram



Analyst: Hilary Birks

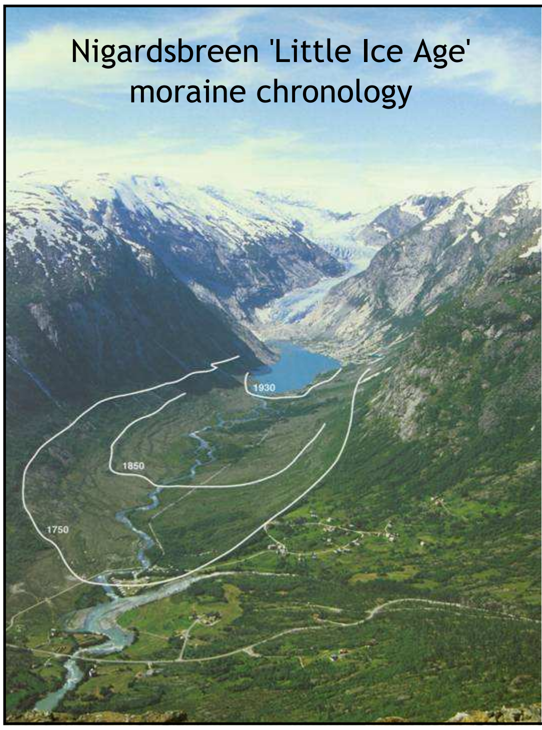
Landscape changes – became increasingly more stabilised within 300 years after YD



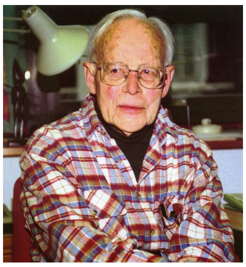


Terrestrial vegetation and landscape development

Zone	Age (cal yr BP)	Years since YD	
7	10830	720	*Betula* woodland with *Juniperus*, *Populus*, *Sorbus aucuparia*, and later *Corylus*. Abundant tall-ferns. *Betula* macrofossils start at 10880 BP
6	10975	575	Fern-rich *Empetrum-Vaccinium* heaths with *Juniperus*
5	11180	370	*Empetrum-Vaccinium* heaths with tall-ferns. Stable landscape
4	11440	110	Species-rich grassland with tall-ferns, tall-herbs, and sedges. Moderately stable
3	11500	50	Species-rich grassland with wet flushes and snow-beds
2	11550	0	*Salix* snow-beds, much melt-water and instability
1	YD		Open unstable landscape with 'arctic-alpines' and 'pioneers', amorphous solifluction



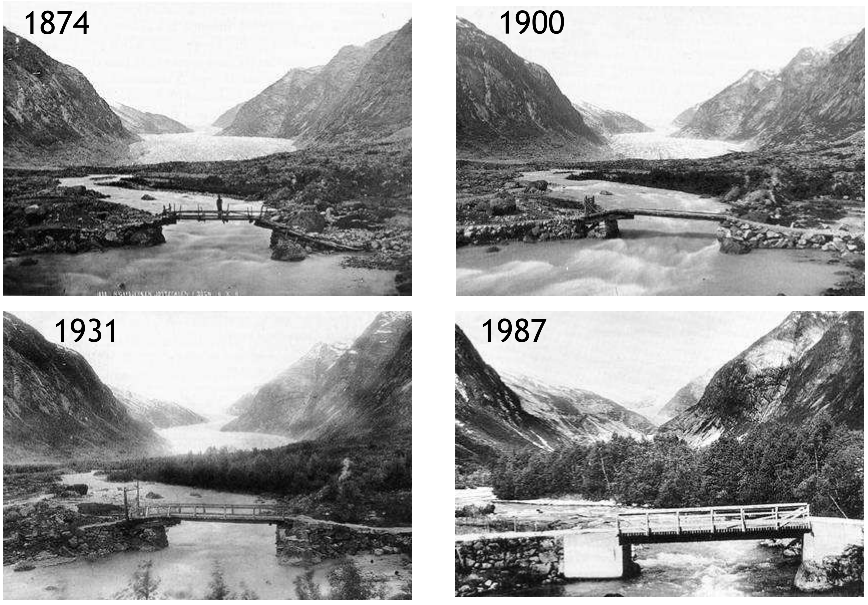
Possible modern analogues



Knut Fægri
(1909-2001)
Doctoral thesis 1933

Photo: Bjørn Wold

Nigardsbreen, Jostedalsbreen



Matthews (1992)

Nigardsbreen, Jostedalsbreen

2002

Vegetation changes since ice retreat at Nigardsbreen

20 years

80 years

150 years

220 years

Timing of major successional phases

	'Little Ice Age' glacial moraines	Kråkenes
1. Pioneer phase	50-200 years	50 years
2. *Salix* and *Empetrum* phase	50-325 years	250 years
3. *Betula* woodland	200-350 years	645-720 years

Why the lag in *Betula* woodland development at Kråkenes?

Dispersal limitation?

Unfavourable environment?

Available-habitat limitation?

Chironomid-inferred mean July air temperatures and the delayed arrival of *Betula*

11520 yr BP	30 yr after YD-H	>10°C
11490 yr BP	60 yr after YD-H	>11°C

If these temperatures are correct, suggest that summer temperatures were suitable for *Betula* woodland 610-640 years **before** *Betula* arrived or 640-670 years **before** *Betula* expanded.

Simplest explanation for delayed arrival of *Betula* is a lag due to

1) landscape development (e.g. soil development) processes

2) tree spreading delays from areas further south

3) interactions with other, unknown climate variables

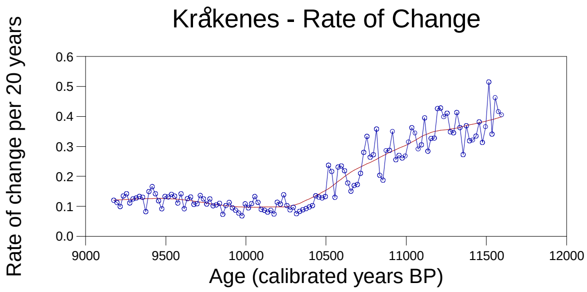
4) no-analogue climate in earliest Holocene

5) surprising amount of macroscopic charcoal suggesting local fires in the early Holocene (zone 6 – *Empetrum* zone)

6) Interactions of some or all these factors

Other biotic responses at the YD/H transition

1. Rate of pollen assemblage change



Rate of pollen assemblage change (estimated by chi-square distance as in correspondence analysis) standardised for 20 years. Changes in percentage values as well as changes in species composition (cf. turnover).

See decreasing rate of change until about 10500 years, 1000 years since YD, when *Betula* woodland was well developed.

Birks & Birks 2008

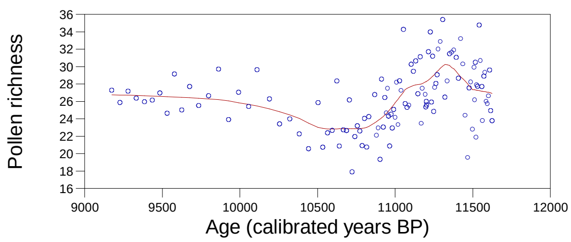
2. Richness and turnover

R.H. Whittaker proposed several concepts of **diversity**:

- α: diversity in a sample plot, or 'point' diversity (or within-habitat diversity).
- β: diversity or **turnover** along ecological gradients (or between-habitat diversity). Differentiation diversity. Many meanings - poorly understood. Cannot be estimated unless there are known environmental or temporal gradients or the underlying latent structure of the data has been recovered.
- γ: diversity among parallel gradients or classes of environmental variables. Product of α-diversity of communities and β-differentiation among them.
- δ: the total **regional** diversity of an area: sum of all previous components. Applicable to broad biogeographical areas. 'Species pool'

In practice, γ and δ diversities are rarely distinguished. γ is often used to designate the **total** diversity of a landscape, geographical area, or island.

Kråkenes – estimated pollen richness



Estimated by rarefaction analysis. Pollen richness probably closest to Whittaker's γ-diversity, namely diversity among parallel gradients within the lake's pollen-source area, or δ-diversity, the total regional diversity – 'landscape diversity'

Maximum richness in zones 2-4 (species-rich grasslands and moderately stable landscape) 50-370 years after the YD (11,500-11,180 yr BP). Drops with the expansion of *Betula* woodland about 10,830 yr BP, rises to near constant level by 10,000 yr BP.

Maximum richness at 'intermediate' productivity or intermediate 'disturbance'

Beta diversity and turnover

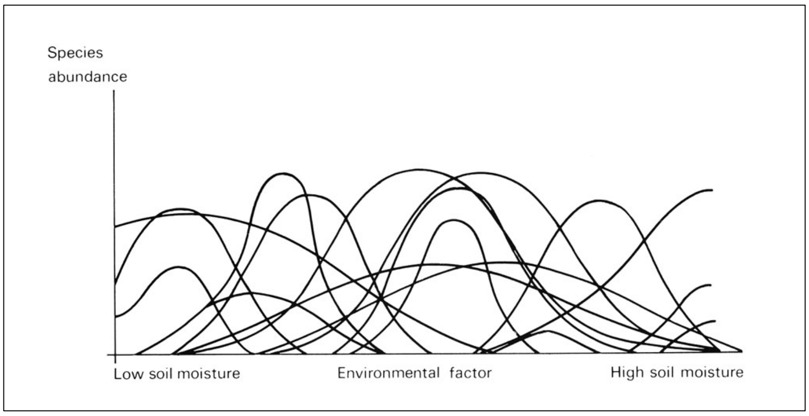
Many (too many!) meanings of beta diversity in ecology

Change in community composition (**turnover**) along gradients in space. Requires gradients to be **measured** or the **underlying latent structure** of the data to be recovered.

What are we talking about when we consider beta diversity in palaeoecology?

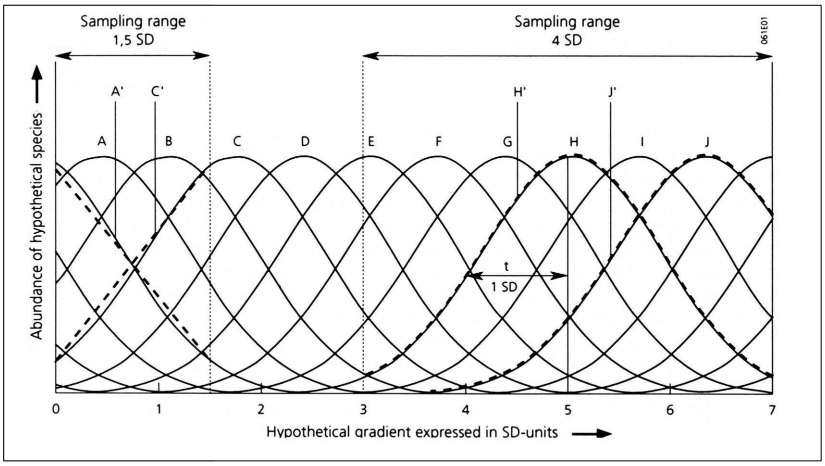
Change in assemblage composition (turnover) along a temporal gradient, namely a stratigraphical sequence.

Species responses along environmental gradients



Overlapping Gaussian unimodal curves of species responses to an environmental factor. Can also be a **temporal gradient**.

Kent & Coker (1992)

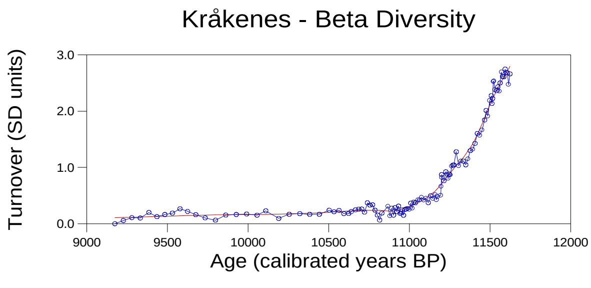


Hypothetical diagram of the occurrence of species A-J over an environmental gradient. The length of the gradient is expressed in standard deviation units (SD units). Broken lines (A', C', H', J') describe fitted occurrences of species A, C, H and J respectively. If sampling takes place over a gradient range <1.5 SD, this means the occurrences of most species are best described by a linear model (A' and C'). If sampling takes place over a gradient range >3 SD, occurrences of most species are best described by an unimodal model (H' and J').

van Wijngaarden *et al.* (1995)

Turnover

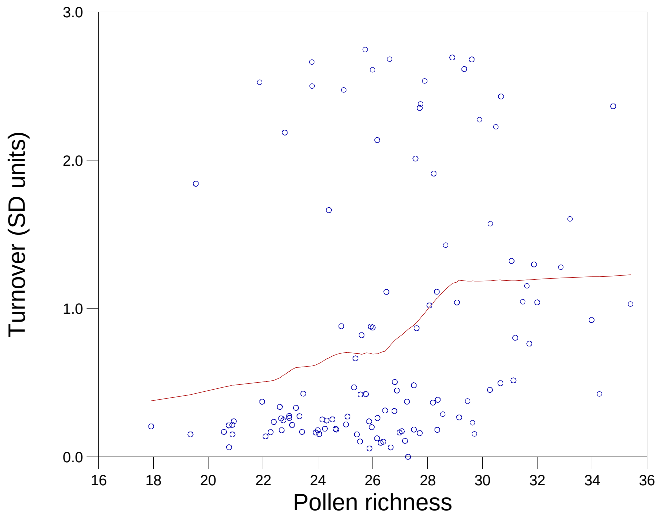
Can estimate turnover or β-diversity within the frame-work of multivariate direct gradient analysis using detrended canonical correspondence analysis and Hill's scaling in units of compositional change or 'turnover' (standard deviation units) along a temporal gradient.



High compositional turnover until 11,180 years BP, 370 yrs since YD with the development of *Empetrum* heaths.

Species composition changes for 370 years since YD. Species turnover very low after 11,000 years BP.

Kråkenes - richness and turnover



No clear relationship between richness (α or γ-diversity) and turnover (β-diversity)

Turnover (β-diversity) estimates (standard deviation units)

	Time (years)	Turnover (SD)
Kråkenes	2450 (total record)	2.75
	720 (YD-*Betula*)	2.42
	260 (first 260 yrs)	**1.91**
'Little Ice Age' 1750 moraines		
Nigardsbreen	250	3.81
Bersetbreen	252	3.16
Bøyabreen	306	3.41
Åbrekkebreen	250	2.98
Bødalsbreen	250	2.82
Storbreen	250	3.72
Mean	260	**3.32**

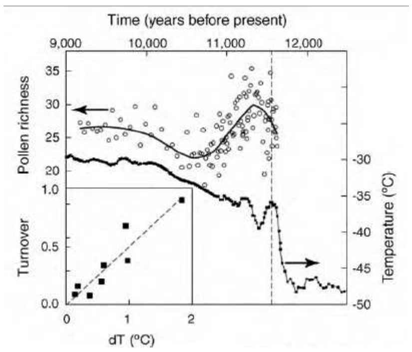
Less turnover (1.91 SD) in 260 years at Kråkenes than in the same time duration on 'Little Ice Age' moraines in western Norway (3.32 SD).

Betula arrived at Kråkenes 670 years after the YD-Holocene transition and expanded 720 years after transition.

On 'Little Ice Age' moraines *Betula* present and abundant about 200 years after moraine formation.

Betula arrival and expansion at Kråkenes **later** than one would expect from modern ecological observations.

3. Richness-climate and turnover-climate relationships



Pollen richness

Chironomid-inferred temperature

Pollen turnover in 250 year intervals and changes in chironomid temperatures in same intervals

Highest richness in earliest Holocene, decreases with expansion of *Betula* about 10,830 yr BP, rises to constant level by 10,000 yr BP. Maximum richness at 'intermediate' temperatures (= productivity)

Increase in compositional turnover with rapid climate change

Willis *et al*. 2010

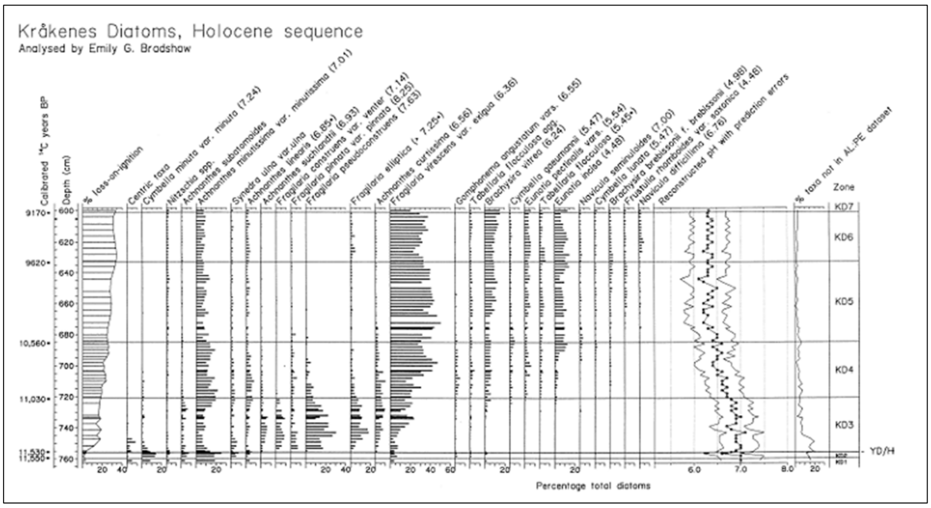
4. Biotic responses at Kråkenes YD/H transition

- Compositional change, regime shifts, and turnover (**persistence, re-adjustment, interactions**)
- Local extinction (e.g. *Saxifraga rivularis*) (**emigration**)
- Expansion (e.g. *Betula*) (**immigration**)
- Natural variability (? noise or biotic change or cyclicity) (**persist**)
- Habitat shift (e.g. *Salix herbacea*)

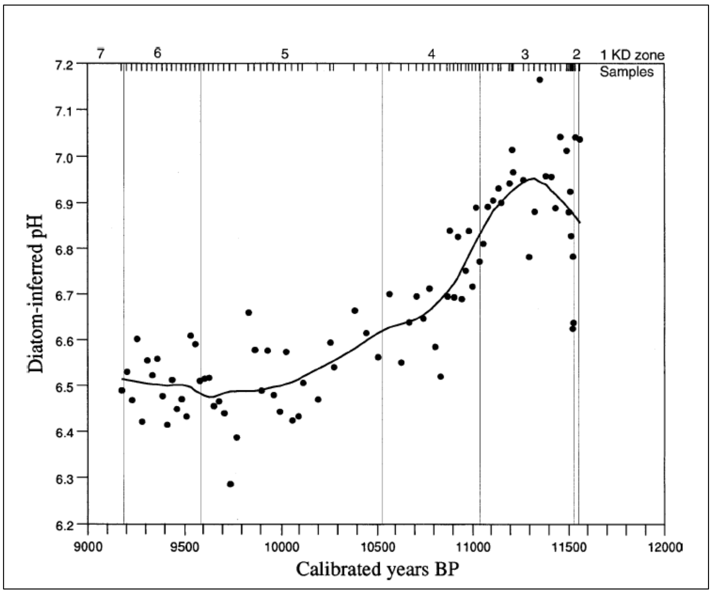
In terms of Dawson et al. (2011) modes of population and species-range response to YD/H climate change we have

Persistence (tolerance)	*Salix* spp., *Carex* spp., *Empetrum nigrum*
Habitat shift	*Salix herbacea, Rhodiola rosea*, (snow-bed to exposed sea-cliffs)
Migration	*Betula pubescens, Corylus avellana*
Extinction (local)	Cold-demanding arctic-alpines (e.g. *Ranunculus glacialis, Koenigia islandica*)

Lake development and aquatic changes



Bradshaw *et al*. (2000)



Bradshaw *et al*. (2000)

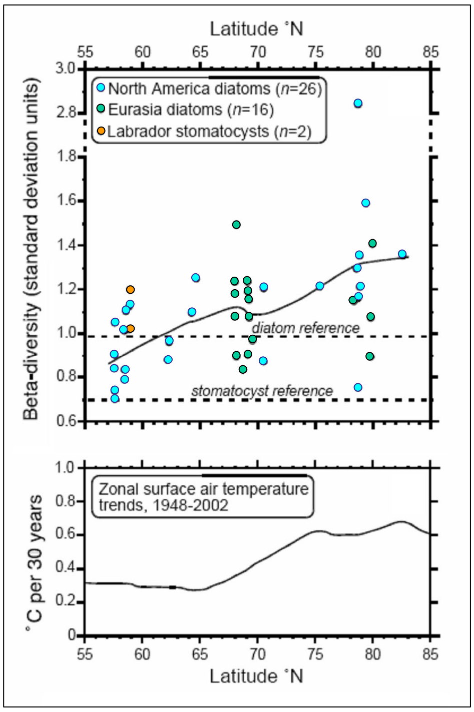
Diatom compositional turnover (DCCA)

2440 years since YD-H   2.89 SD
150 years since YD-H   2.81 SD

Chose 150 yr to allow comparison with analysis of recent (last 150 yr) diatom changes in 42 Arctic lakes – Smol *et al*. (2005) PNAS 102: 4397-4402.

Diatoms	42 Arctic sites	0.70 – 2.84 SD
Diatoms	11 'control' sites not in Arctic or impacted by acidification or eutrophication	0.72 – 1.39 SD median = 1.02 SD
Kråkenes	150 yr	2.81 SD

Turnover in 150 yr at Kråkenes about the same as has occurred in last 150 yr in Arctic Canada (Ellesmere) in response to recent climate change



Smol *et al*. (2005)

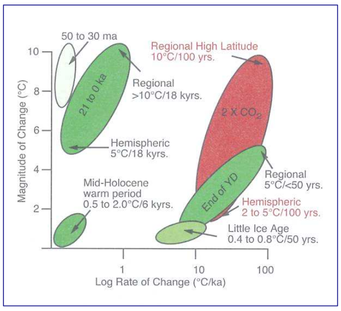
Conclusions from Kråkenes study

1. **Rapid** initial terrestrial vegetational and diatom **responses** to rapid climatic change at the Younger Dryas-Holocene transition.
2. **Sustained changes** in compositional turnover in terrestrial pollen assemblages for about 370 years and significant rates of assemblage change for about 1000 years since the YD-H transition. Highly dynamic system.
3. **Compositional turnover** in terrestrial pollen assemblages in 260 years (1.91 SD) much less than in vegetation in primary succession on 'Little Ice Age' moraines (3.32 SD) in same time period.
4. **Lags** (about 400-450 years) in the arrival of *Betula*, possibly due to delays in landscape (e.g. soil) development, migration delays, fire, or unique climate and/or interaction of climate variables, or an interaction of some or all of these factors.

   This 400-450 year lag contrasts with model predictions for Alaskan and alpine tree-line responses with lags of 150-250 years (Chapin & Starfield 1997, Rupp *et al*. 2000) in relation to predicted future climate warming.

5. **Diatom assemblages** show the major amount of their compositional turnover in the first 150 years since the onset of the Holocene. No detectable lags.
6. **Different responses** to rapid climate change at the Younger Dryas-Holocene transition in different biological systems. Terrestrial and limnic systems. Different spatial scales and life-cycle temporal scales.
7. **Fine-resolution analyses** of several palaeoecological proxies at key sites such as Kråkenes are a means of linking the temporal scales of palaeoecology with the scales of modern landscape ecology and process-based ecological modelling.

8. **Important** to put the Younger Dryas-Holocene transition in context of other past climate changes and projected future change. **Magnitude of change** and **log rate of change**.



Alverson *et al.* (2003)

The YD/H is of comparable rapidity to projected regional high latitude change but about half the estimated magnitude for future change.

Magnitude of future regional temperature change could well exceed any previous widespread changes in the Quaternary. 'Lessons from the past' may have limited relevance to the future.

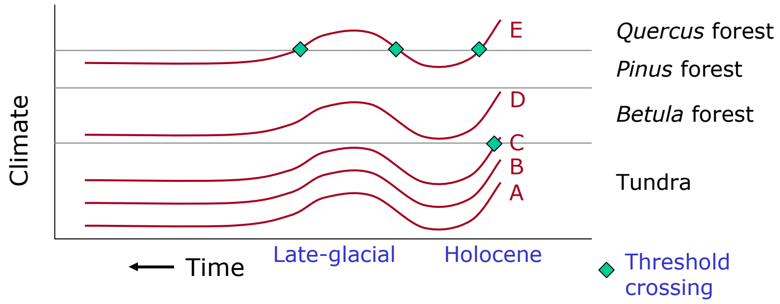
What could have Determined Persistence, Migration, or Extinction in the Past?

Ecological thresholds where an ecosystem switches from one stable regime state to another, usually within a relatively short time-interval (**regime shift**), can be recognised in palaeoecological records.

Much information potentially available from palaeoecological records on alternative stable states, rates of change, possible triggering mechanisms, and systems that demonstrate **resilience** to thresholds.

Key questions are what combination of environmental variables result in a regime shift and what impact does it have on biodiversity?

Conceptual model based on Fægri and Iversen (1964)



Climate change at five different localities
- A, B, D - no thresholds crossed
- C - one threshold crossed
- E - three thresholds crossed

Critical threshold can be a function of regional climate, local climate, bedrock and soils, aspect, exposure, etc

Absence of vegetational changes does not mean no climate change, only that **no ecological threshold** was crossed

Responses depend on thresholds being or not being crossed

What combinations of biotic and abiotic processes will result in **ecological resilience** to climate change and where might these combinations occur?

Late-glacial palaeoecological records demonstrate
(1) rapid turnover of communities
(2) novel biotic assemblages
(3) migrations, invasions, and expansions
(4) local extinctions

They do **not** demonstrate the broad-scale extinctions predicted by models. In contrast there is strong evidence for **persistence**.

Evidence that some species expanded their ranges slowly or largely failed to expand from their refugia in response to rapid climate warming in the early Holocene. No obvious ecological reason for this.

Palaeoecological data suggest that

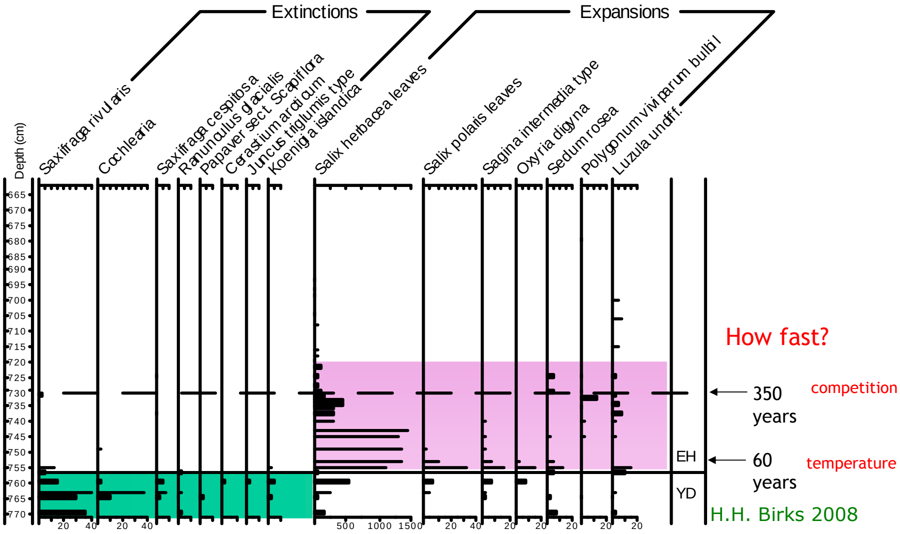
1. rapid rates of spread of some taxa
2. realised niche often broader than those seen today
3. landscape heterogeneity in space and time, and
4. the occurrence of many small populations in locally favourable habitats (microrefugia)

might all have contributed to persistence during the rapid climate changes at the onset of the Holocene

Kråkenes YD/Holocene

Impact of Holocene on YD plants

Species dynamics first driven by temperature rise, later by competition



H.H. Birks 2008

Local extinctions of high-altitude arctic-alpines within 60 years of Holocene, others expand in response to climate change and then decline, probably in response to competition from shrub vegetation.

Can Quaternary Palaeoecology Provide Insights to Understanding Migration and Persistence?

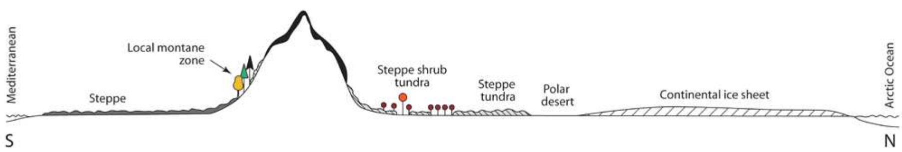
1. Migration

Long thought that major last glacial maximum refugia for plants and animals were confined to southern Europe (Balkans, Iberia, Italian peninsula).

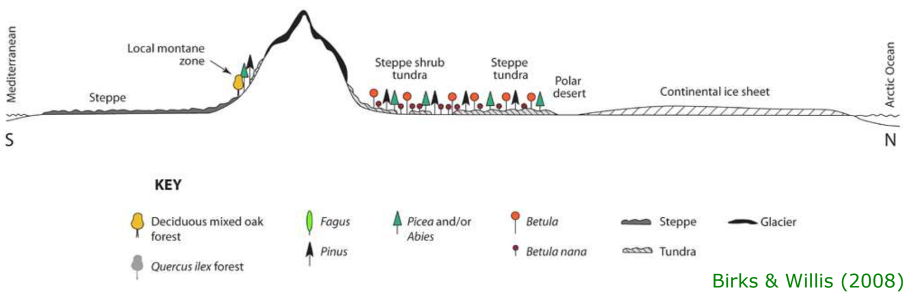
Now increasing evidence for tree taxa in **microrefugia** elsewhere in Europe. These microrefugia may have moved in response to climate change during last glacial stage – may explain why there may be a lag of 670 yrs at Kråkenes but almost no lag somewhere else in *Betula* expansion. Considerable stochasticity.

Scattered microrefugia similar to concept of **metapopulations** in population biology – discrete but with some connectivity and dynamic.

LGM classical view - Traditional refugium model – **narrow tree belt** in S European mountains and in Balkan, Italian, and Iberian peninsulas



LGM current view - Current refugium model – scattered tree populations in **microrefugia** in central, E, and N Europe



Birks & Willis (2008)

What might LGM microrefugia have looked like?

Picea crassifolia,
Sichuan 3600 m

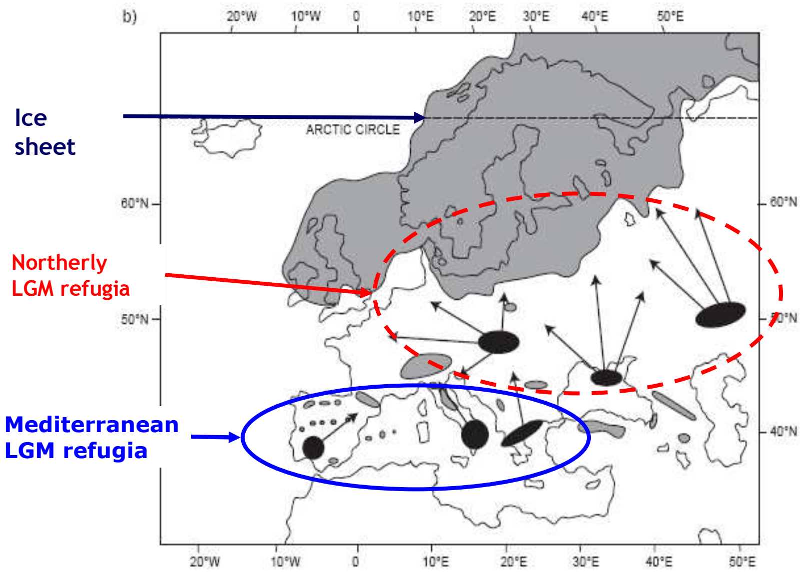
Picea <3%
Artemisia and Poaceae >75%
John Birks unpublished

Picea glauca, Alaska

Picea <1%

Petit *et al*. 2008

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



Birks & Willis (2008)

Tree taxa that have reliable macrofossil evidence for LGM presence in multiple **central, eastern, or northern European microrefugia**

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

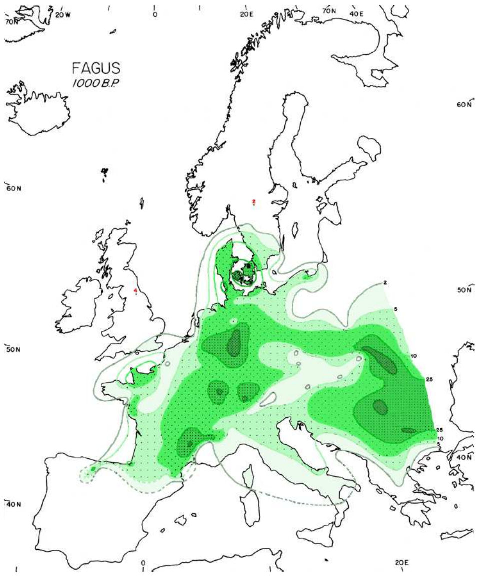
* = taxa near to Fennoscandian ice sheet in or soon after LGM

Revised European tree-spreading rates in light of available LGM macrofossil and macroscopic charcoal evidence

	Huntley & Birks 1983 (m yr^{-1})	Revised rates (m yr^{-1})	Over-estimate
Abies	300	60	x5
Alnus	2000	1000	x2
Betula	>2000	1430	x1.4
Carpinus betulus	1000	250	x4
Fagus sylvatica	300	60	x5
Picea	500	250	x2
Pinus	1500	750	x2
Quercus	500	50	x10
Salix	1000	750	x2
Corylus avellana	1500	500	x3
Populus	1000	750	x1.3

Willis, Bhagwat & Birks unpublished

Isopollen mapping for Europe



Suggests spreading rates of 200-300 m yr^{-1}

Huntley & Birks 1983

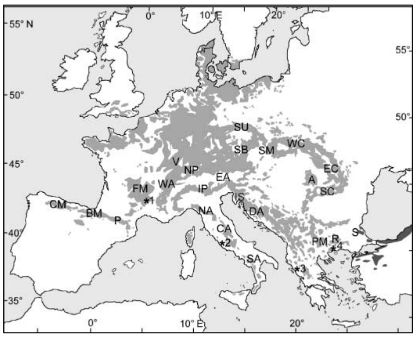
Is there other evidence for microrefugia?

Palaeobotanical and Molecular Data Combined 'The Way Forward in Palaeoecology'

Magri *et al*. 2006 New Phytologist 171: 199-221

Jackson 2006 New Phytologist 171: 1-3

Fagus sylvatica



Combination of palaeobotanical and molecular data

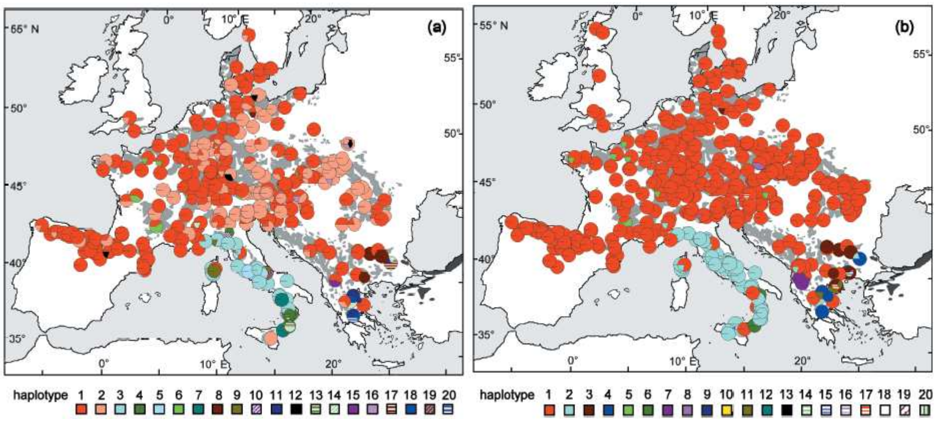
408 pollen sites with ^{14}C dates

80 macrofossil sites

468-600 sites for chloroplast DNA and nuclear genetic markers (isozymes)

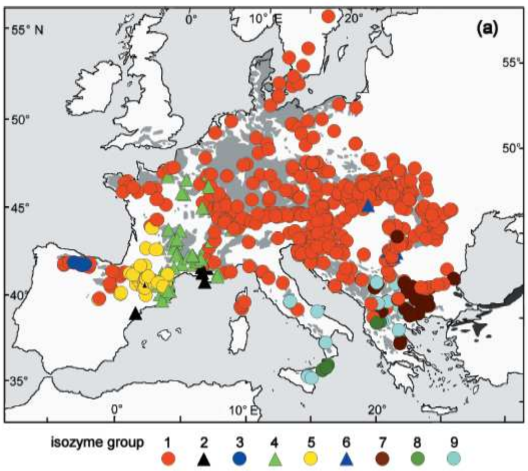
Molecular data –

Chloroplast haplotypes and Satellite data



20 different haplotypes detected. Three in more than 80% of trees.
(1) Italian peninsula, (2) southern Balkans, (3) rest of Europe.

Nuclear genetic markers (isozymes)



Isozyme data – 9 groups

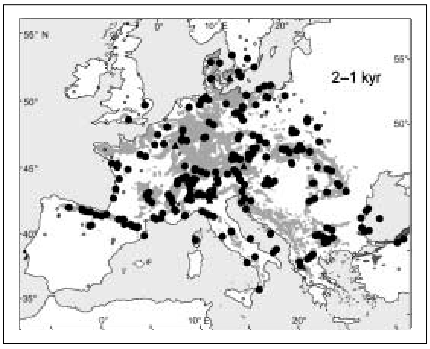
Italian group,

southern Balkans,

Iberian Peninsula,

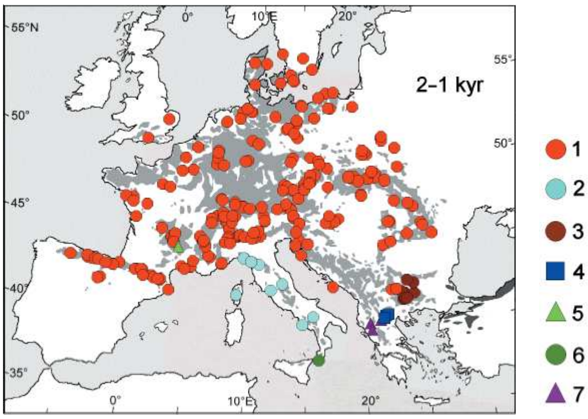
rest of Europe

Palaeobotanical data (pollen and macrofossils)



● = >2%   ▲ = macrofossil

Combine palaeobotanical and molecular data



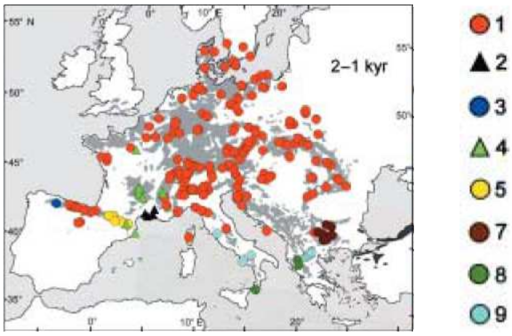
Chloroplast haplotypes

Type 1 – spread from several refugia

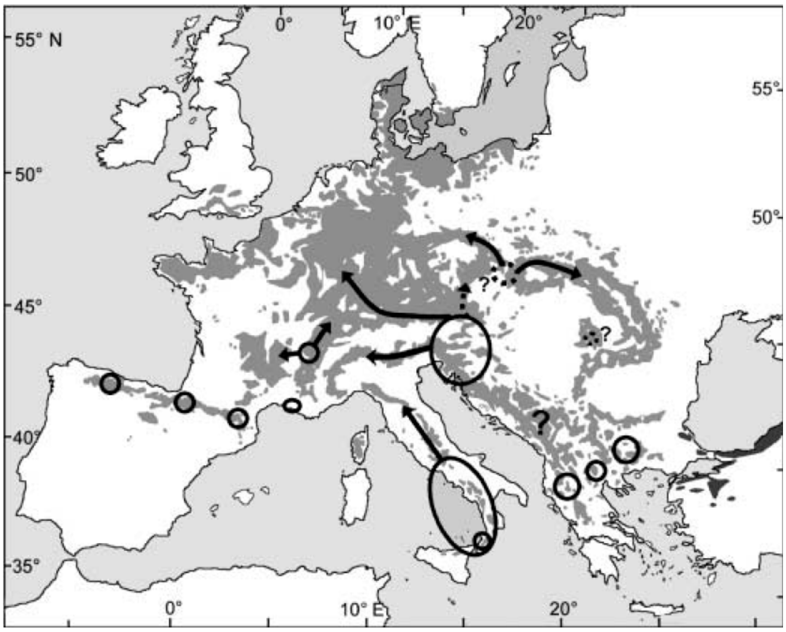
Type 2 – only in Italy

Other types – mainly in Balkans

Isozyme groups



Type 1 – spread from several refugia
Type 9 – only in Italy
Type 7 – mainly in Balkans
Type 5 - Iberia



Suggested refugial areas and main colonisation routes during the Holocene

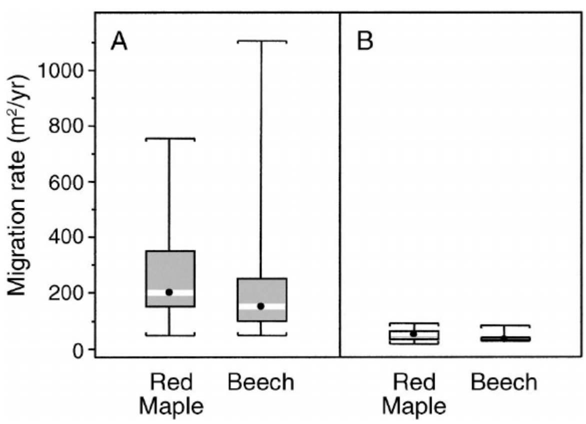
Multiple LGM population centres, up to 45°N. **Some**, but not all, of these contributed to the Holocene expansion. Others, especially in the Mediterranean region did not expand.

Early and vigorous expansion in Slovenia, southern Czech Republic, and southern Italy. Iberian, Balkan, Calabria, and Rhône populations remained restricted.

See **some populations expanded considerably**, whereas others **hardly expanded**. Mountain chains were not major barriers for its spread – may have actually **facilitated** its spread.

Shows complex genetics of *Fagus sylvatica*. Also had a complex history in quaternary interglacials. Very much a tree of the Holocene. Questions of adaptation arise.

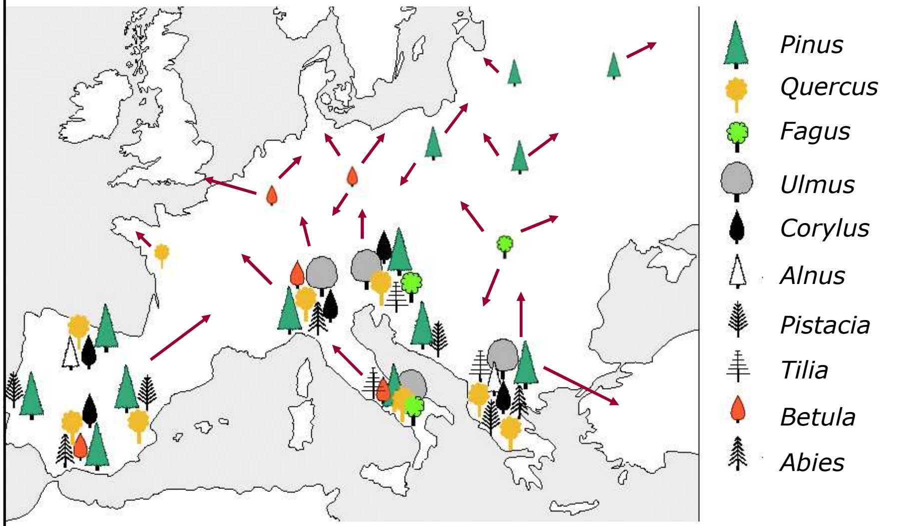
Eastern North America



McLachlan *et al*. 2005

A. Pollen-based migration rates for *Acer rubrum* and *Fagus grandifolia*
B. Molecular-based migration rates

Possible scenarios for earliest Holocene based on available palaeobotanical data



Birks & Willis unpublished

Significantly affects our predictions about how trees may respond to rapid climate change in the future

500 or 50 m yr^{-1}?

Very relevant to current discussion about 'assisted migration' and 'assisted colonisation' in conservation biology

2. Persistence

Extinction due to climate change **very rare** in Late Quaternary except at **local** scale.
Considerable evidence for persistence of arctic-alpine mountain plants.

Since LGM, **regional** extinction in central Europe of **11** species

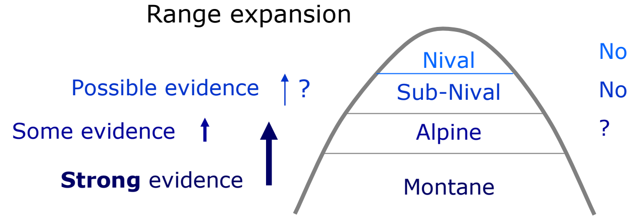
Campanula uniflora	*Diapensia lapponica*	*Koenigia islandica*
Pedicularis hirsuta	*Pedicularis lanata*	*Ranunculus hyperboreus*
Salix polaris	*Saxifraga cespitosa*	*Saxifraga rivularis*
Silene furcata	*Silene uralensis*	

One global extinction - *Picea critchfieldii*

Possible explanation for persistence comes from contemporary studies on summit floras and botanical resurveys

Very good evidence from many re-surveys of floristic analyses made in the 1900s-1950s and recently in Europe and N America that

1. Summit floras are becoming **more species-rich** as Montane species (e.g. dwarf-shrubs, grasses) move up mountains, presumably in response to climate warming
2. But evidence for **local extinction** of high-altitude alpine or sub-nival species is almost **non-existent.** Why?



Why is there little or no evidence for local extinction of high-altitude species?

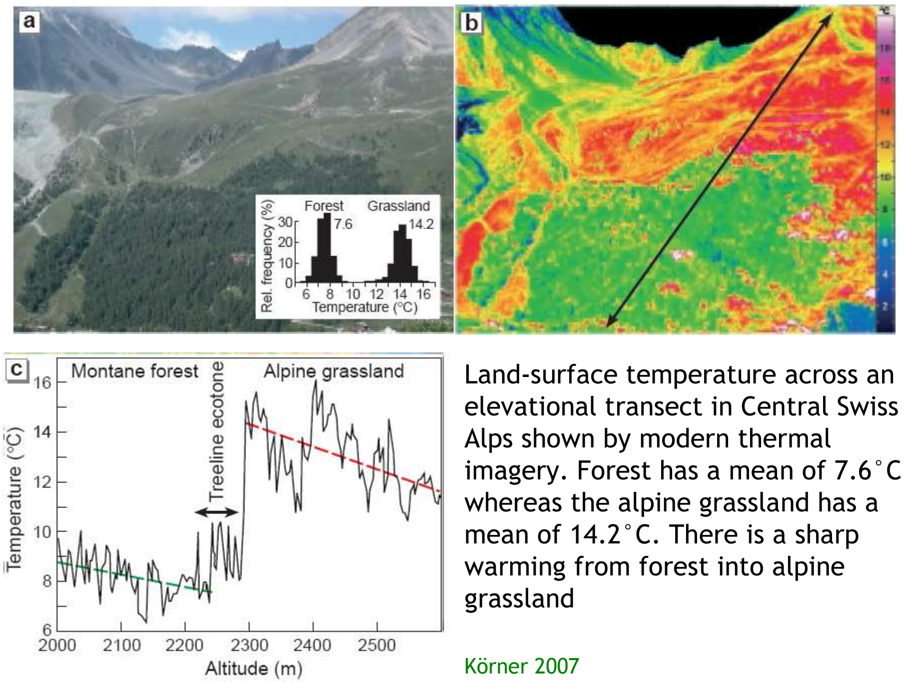
Need to assess an alpine landscape not at a climate-model scale or even at the 2 m height of a climate station, but at the plant level.

Use thermal imagery technology to measure **land surface temperature**.

Körner 2007 *Erdkunde*

Scherrer & Körner 2010 *Global Change Biology*

Scherrer & Körner 2011 *Journal of Biogeography*



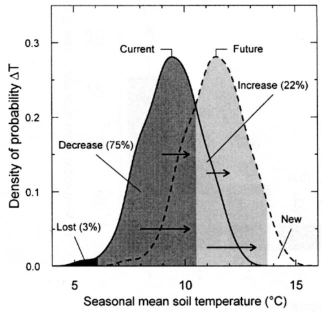
Land-surface temperature across an elevational transect in Central Swiss Alps shown by modern thermal imagery. Forest has a mean of 7.6°C whereas the alpine grassland has a mean of 14.2°C. There is a sharp warming from forest into alpine grassland

Körner 2007

In two alpine areas in Switzerland (2200-2800 m), used infrared thermometry and data-loggers to assess variation in plant-surface and ground temperature for 889 plots.

Found growing season mean soil temperature range of 7.2°C, surface temperature range of 10.5°C, and season length range of >32 days. Greatly exceed IPCC predictions for future, just on one summit.

IPCC 2°C warming will lead to the loss of the coldest habitats (3% of current area). 75% of current thermal habitats will be reduced in abundance (competition), 22% will become more abundant.



Scherrer & Körner 2011

Warn against projections of alpine plant species responses to climate warming based on a broad-scale (10’ x 10’) grid-scale modelling approach.

Alpine terrain is, for very many species, a much ‘safer’ place to live under conditions of climate change than flat terrain which offers no short distance escapes from the new thermal regime.

Landscape local heterogeneity leads to local climatic heterogeneity which confers biological resistance or inertia to change.

What Conclusions can Quaternary Palaeoecology make to Vegetation Dynamics?

Biotic responses to major climatic changes in the Late Quaternary have been mainly:

- distributional shifts
- high rates of population turnover
- changes in abundance and/or richness
- stasis

Much **less** important have been

- extinctions (global, regional, or local)
- speciations (? any evidence except for micro-species in, for example, *Primula, Alchemilla, Taraxacum, Meconopsis, Pedicularis, Calceolaria*)

Biotic responses have been **varied, dynamic, complex**, and **individualistic**. Very difficult to make useful generalisations.

Important issues of spatial and temporal **scales** in bridging Quaternary-time and Near-time studies.

What about ecosystem functioning?

Ecosystem Functional Changes at Younger Dryas/Holocene Transition

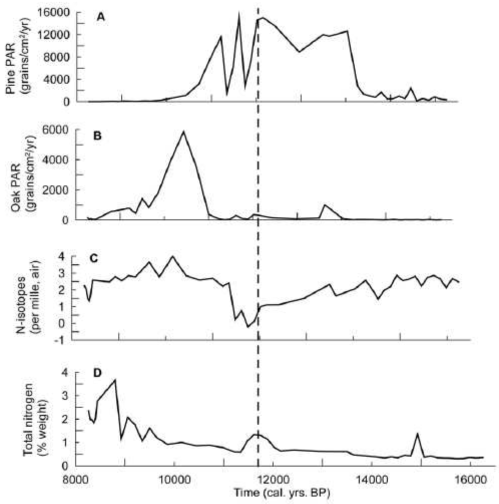
Jeffers *et al*. 2011 PLoS One 6: e16134

Role of N availability in influencing vegetational change at LG/YD transition.

Classical ecological theory predicts that changes in availability of essential resources like N should lead to vegetation change. What is unclear is the extent to which climate change will alter the vegetation-nitrogen cycle relationship.

During intervals of climate change, do changes in N cycling lead to vegetation change **or** do vegetation changes alter the N dynamics?

Need palaeoecological data to answer these questions.



Mohos To, S Hungary

10°C warming in 60 yrs (dashed line)

Pollen accumulation rate (PAR) of pine and oak

N (δ^{15}N) isotopes

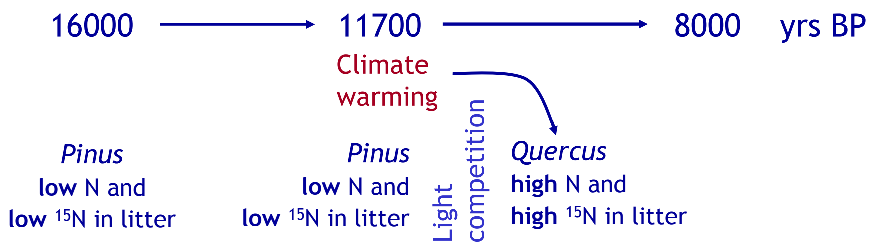
Total N

Jeffers *et al*. (2011)

Fitted a series of simple ecological **mechanistic models** to model tree dynamics, N changes, and climate. Used AIC to assess the relative amount of support for each mechanistic model.

'Best' model – nitrogen-independent population growth with feedback effects, namely **plant-derived nitrogen cycle** where interactions are between tree population dynamics and N cycle occurs via declining plant litter.

As oak replaced pine due to warming climate, **N cycling rates increased** but the mechanism by which trees interacted with N remained stable across the threshold change in climate and in the dominant tree.



Dynamics associated with **ecosystem functioning** can remain relatively stable following a **major change in climate.**

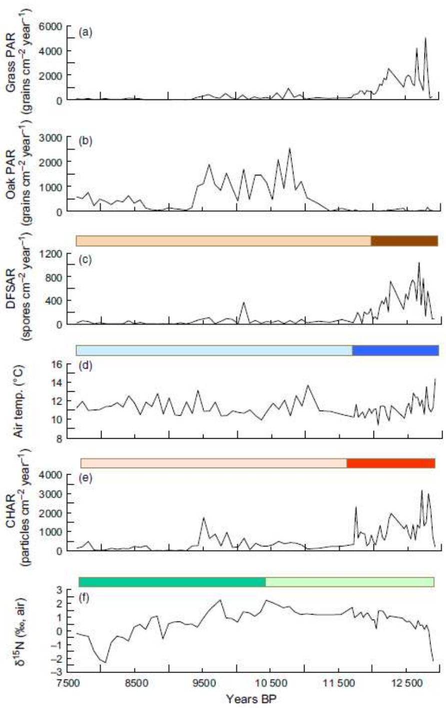
Succession occurred independently of change in N availability. Good evidence that forest ecosystems are not limited by available N over long time-scales.

Contrasts with many dynamic global vegetation models where N is assumed to limit tree growth during climate warming.

Jeffers *et al*. 2011 J Ecol 99: 1063-1070

Plant-plant interactions in response to climate change, plus changes in fire and changing nitrogen availability, and herbivore density. Complex series of 'natural experiments'.

Mechanistic ecological models, AIC criterion to select model to determine which environmental variables had greatest impact on *Quercus*-grass interaction.



Grass pollen

Quercus pollen

Dung-fungal spores

Chironomid-inferred temperature

Charcoal

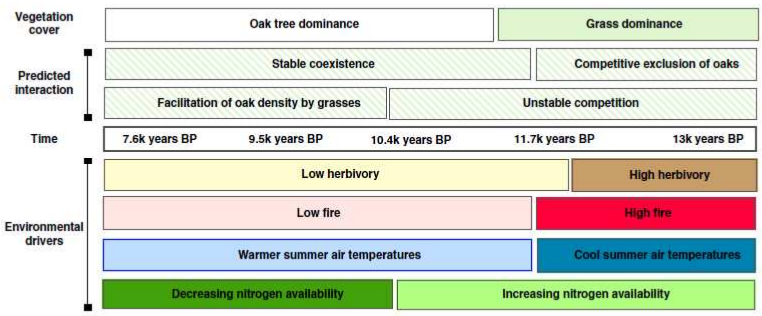
$\delta_{15}N$

Jeffers *et al*. (2011)

Complex data, complex results

1. High disturbance (fire, herbivores) and cool climate – grasses out-compete *Quercus* N ↑
2. Low disturbance and climate warming – stable co-existence between oak and grass N ↓
3. Changes in N cycle correspond with these two scenarios

Simplest model proposes a temporary period of unstable competition preceded by the shift to stable co-existence. Consistent with regime shift between alternative stable states.



Jeffers *et al.* (2011)

Abrupt changes in environment lead to abrupt changes in grass-tree interaction outcomes. Vary in direction with respect to resource or non-resource variables.

Shows how **complex** an ecological change can be when one considers more than one ecological driver.

Novel Ecosystems

By 2020, up to 48% of Earth's land surface will experience **novel climates**

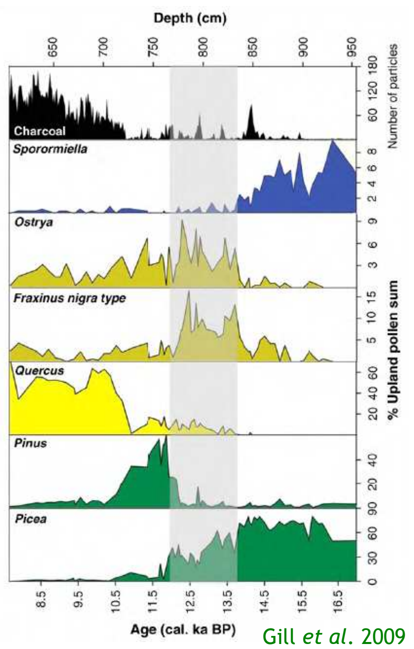
Novel climates will result in unexpected biotic associations or 'novel ecosystems'

Have **novel ecosystems** occurred in the past?

Fossil assemblages with **no modern analogues** may reflect novel ecosystems

What conditions do they occur under?

Appleman Lake, Indiana



Gill *et al*. 2009

Shaded area 11900-13700 BP is time of no-analogue pollen assemblages

Also charcoal (fire) and dung fungus *Sporormiella* (mega-fauna indicator)

- High spores before 13700 BP = many mega-fauna
- Low spores after 13700 BP = few mega-fauna. Deciduous trees such as *Fraxinus* increase
- By 11000 BP *Quercus* rises – high fire regime

Release from mega-herbivory in addition to novel climate (highly seasonal insolation and temperature) led to novel vegetation 13700 years ago. As climate shifted, *Quercus* expanded in the early Holocene.

Palaeoecology shows that **environmental and ecological changes** are perhaps the most common feature of a world in continual climate flux.

Management of **novel ecosystems** should be guided by looking through the telescope to the past. Can see what have been stable states, what might be possible novel ecosystems in the future, and what conditions lead to novel ecosystems.

Palaeoecology can also guide **restoration ecology** as well as nature management for the future.

Conclusions

Biotic responses to major climatic changes mainly been

- Distribution shifts as a result of migration from macrorefugia and microrefugia
- High rates of population turnover
- Changes in abundance and/or richness, some regime shifts
- Stasis or stability, very little extinction or emigration except at local, or more rarely, regional scales
- Changing plant-plant and plant-animal interactions resulting in novel or no-analogue assemblages
- Surprising amounts of resistance or inertia to change
- Habitat shift – difficult to detect (e.g. *Salix herbacea*)

Conclusions

Associated changes in **ecosystem functioning**

- Changes in N cycling and availability of N
- Plant-animal balances changed

Conclusions

Responses have been

Varied

Dynamic

Individualistic

Complex

Major challenge to **decipher** the palaeoecological record

Understanding complex ecological systems

Why does ecology need Quaternary palaeoecology?

1. Ecology

Modern-day observations and experiments ⇄ Modelling

Limited number of alternative states and no consideration of history, conditions absent today, and ecological legacies from past conditions (properties of an ecological system that can only be explained by events or conditions that are not present in the system today). Very limited opportunities to test hypotheses about ecological systems (few or no replicates, each system has its own unique history, legacies, etc.).

2. Ecological palaeoecology

Modern-day observations and experiments ⇄ Modelling

Palaeoecological data

Quaternary palaeoecology brings in information about past systems (variation in rates, states, and composition, different boundary conditions including those with no modern analogues), spatial and temporal scaling, long-term perspectives (longer than ecological observations and monitoring programmes).

Quaternary palaeoecology's major potential contributions to ecological and environmental science

1. The palaeoecological record as a long-term ecological laboratory or observatory
2. The palaeoecological record of ecological responses to past environment, particularly climate change
3. The palaeoecological record and deciphering of ecological legacies from human activities and recent environmental change (e.g. 'Little Ice Age') – 'missing dimension' in ecology

Unique view on ecological dynamics in response to a rapid climate change about 11,700 years ago.

'**Natural experiment**'

Challenges some of our ideas about biotic responses and ecosystem functioning in response to rapid environmental change.

As we move into the future, we need to predict what lies ahead. Just as early 17th century European map-makers applied for terra incognita the label 'Here there may be dragons', we should be aware that dragons may or may not lurk in our future.

However, whether dragons exist or not, we must consider **all** the data we have from Quaternary-time and Near-time studies to '**help future ecological predictions**' to avoid making too many incorrect predictions.

The Younger Dryas-Holocene transition is a remarkable 'natural experiment'. Much still to be done to understand all the records from this experiment. **Major challenge** for Quaternary researchers and much to contribute to Near-time ecology.

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