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

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**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).
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.

(Modified from Oldfield 1983)

Beyond Predictions: Biodiversity Conservation in a Changing Climate

Terence P. Dawson, Stephen T. Jackson, Joanna L. House, Colin Prentice, Georgia M. Mace

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.

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**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.
North Greenland Ice Core Project (NGRIP)

Subannual resolution of $\delta^{18}O$ and $\delta^D$, 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 ($\lambda$)

Annual resolution
Ramps shown as bars

Steffensen et al. 2008
δ¹⁸O - proxy for past air temperature: YD/H 10°C in 60 yrs
annual layer thickness (λ): increase of 40% in 40 yrs
d = δD - 8δ¹⁸O (deuterium excess) - past ocean surface
temperature at moisture source: changes in 1-3 yrs
Dust and Ca²⁺ - 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 2-4°C 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

[Map of Kråkenes Lake]

[Photo of Kråkenes Lake]
Kråkenes Lake and cirque with YD moraine in Mehuken Mountain

Coring
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
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

Percentages of Calculation Sum
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.
Landscape changes - became increasingly more stabilised within 300 years after YD
Terrestrial vegetation and landscape development

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

Nigardsbreen 'Little Ice Age' moraine chronology

Possible modern analogues

Knut Fægri
(1909-2001)
Doctoral thesis 1933

Photo: Bjørn Wold
Vegetation changes since ice retreat at Nigardsbreen

Timing of major successional phases

<table>
<thead>
<tr>
<th>Phase</th>
<th>Duration</th>
<th>Kråkenes Duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Pioneer phase</td>
<td>50-200 years</td>
<td>50 years</td>
</tr>
<tr>
<td>2. <em>Salix</em> and <em>Empetrum</em> phase</td>
<td>50-325 years</td>
<td>250 years</td>
</tr>
<tr>
<td>3. <em>Betula</em> woodland</td>
<td>200-350 years</td>
<td>645-720 years</td>
</tr>
</tbody>
</table>

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

![Kråkenes - Rate of Change](image)

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:
- $\alpha$: diversity in a sample plot, or 'point' diversity (or within-habitat diversity).
- $\beta$: 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.
- $\gamma$: diversity among parallel gradients or classes of environmental variables. Product of $\alpha$-diversity of communities and $\beta$-differentiation among them.
- $\delta$: the total regional diversity of an area: sum of all previous components. Applicable to broad biogeographical areas. 'Species pool'

In practice, $\gamma$ and $\delta$ diversities are rarely distinguished. $\gamma$ is often used to designate the total diversity of a landscape, geographical area, or island.

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**Kråkenes - estimated pollen richness**

Estimated by rarefaction analysis. Pollen richness probably closest to Whittaker's $\gamma$-diversity, namely diversity among parallel gradients within the lake's pollen-source area, or $\delta$-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.
No clear relationship between richness (α or γ-diversity) and turnover (β-diversity)

<table>
<thead>
<tr>
<th>Time (years)</th>
<th>Turnover (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kråkenes 2450 (total record)</td>
<td>2.75</td>
</tr>
<tr>
<td>720 (YD-Betula)</td>
<td>2.42</td>
</tr>
<tr>
<td>260 (first 260 yrs)</td>
<td><strong>1.91</strong></td>
</tr>
<tr>
<td>'Little Ice Age' 1750 moraines</td>
<td></td>
</tr>
<tr>
<td>Nigardsbreen 250</td>
<td>3.81</td>
</tr>
<tr>
<td>Bersetbreen 252</td>
<td>3.16</td>
</tr>
<tr>
<td>Bøyabreen 306</td>
<td>3.41</td>
</tr>
<tr>
<td>Åbrekkebreen 250</td>
<td>2.98</td>
</tr>
<tr>
<td>Bødalsbreen 250</td>
<td>2.82</td>
</tr>
<tr>
<td>Storbreen 250</td>
<td>3.72</td>
</tr>
<tr>
<td>Mean 260</td>
<td><strong>3.32</strong></td>
</tr>
</tbody>
</table>
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

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

<table>
<thead>
<tr>
<th>Mode</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Persistence (tolerance)</td>
<td><em>Salix</em> spp., <em>Carex</em> spp., <em>Emetrum nigrum</em></td>
</tr>
<tr>
<td>Habitat shift</td>
<td><em>Salix herbacea</em>, <em>Rhodiola rosea</em>, (snow-bed to exposed sea-cliffs)</td>
</tr>
<tr>
<td>Migration</td>
<td><em>Betula pubescens</em>, <em>Corylus avellana</em></td>
</tr>
<tr>
<td>Extinction (local)</td>
<td>Cold-demanding arctic-alpines (e.g. <em>Ranunculus glacialis</em>, <em>Koenigia islandica</em>)</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Diatoms</th>
<th>42 Arctic sites</th>
<th>0.70 - 2.84 SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diatoms</td>
<td>11 'control' sites not in Arctic or impacted by acidification or eutrophication</td>
<td>0.72 - 1.39 SD</td>
</tr>
<tr>
<td></td>
<td></td>
<td>median = 1.02 SD</td>
</tr>
<tr>
<td>Kråkenes</td>
<td>150 yr</td>
<td>2.81 SD</td>
</tr>
</tbody>
</table>

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**.

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.

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**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?
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

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

Ice sheet  
Northerly LGM refugia  
Mediterranean LGM refugia  

Birks & Willis (2008)
Tree taxa that have reliable macrofossil evidence for LGM presence in multiple central, eastern, or northern European microrefugia

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies alba</td>
<td></td>
</tr>
<tr>
<td>Abies sibirica*</td>
<td></td>
</tr>
<tr>
<td>Alnus glutinosa*</td>
<td></td>
</tr>
<tr>
<td>Betula pendula*</td>
<td></td>
</tr>
<tr>
<td>Betula pubescens*</td>
<td></td>
</tr>
<tr>
<td>Corylus</td>
<td></td>
</tr>
<tr>
<td>Carpinus betulus</td>
<td></td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td></td>
</tr>
<tr>
<td>Fraxinus excelsior</td>
<td></td>
</tr>
<tr>
<td>Juniperus communis*</td>
<td></td>
</tr>
<tr>
<td>Larix sibirica*</td>
<td></td>
</tr>
</tbody>
</table>

* = 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

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Revised rates</th>
<th>Over-estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies alba</td>
<td>60</td>
<td>x5</td>
</tr>
<tr>
<td>Alnus</td>
<td>1000</td>
<td>x2</td>
</tr>
<tr>
<td>Betula</td>
<td>1430</td>
<td>x1.4</td>
</tr>
<tr>
<td>Carpinus betulus</td>
<td>250</td>
<td>x4</td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>60</td>
<td>x5</td>
</tr>
<tr>
<td>Picea</td>
<td>250</td>
<td>x2</td>
</tr>
<tr>
<td>Pinus</td>
<td>750</td>
<td>x2</td>
</tr>
<tr>
<td>Quercus</td>
<td>50</td>
<td>x10</td>
</tr>
<tr>
<td>Salix</td>
<td>750</td>
<td>x2</td>
</tr>
<tr>
<td>Corylus avellana</td>
<td>500</td>
<td>x3</td>
</tr>
<tr>
<td>Populus</td>
<td>750</td>
<td>x1.3</td>
</tr>
</tbody>
</table>

Willis, Bhagwat & Birks unpublished
**Isopollen mapping for Europe**

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

Huntley & Birks 1983

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**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)

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

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

B. Molecular-based migration rates

McLachlan *et al.* 2005
Possible scenarios for earliest Holocene based on available palaeobotanical data

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.

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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.

**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


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 (δ¹⁵N) 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.
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.
Complex data, complex results

1. High disturbance (fire, herbivores) and cool climate - grasses out-compete *Quercus*  
2. Low disturbance and climate warming - stable co-existence between oak and grass  
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.

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.
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

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.

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**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, and 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.
Acknowledgements

Hilary Birks        Kathy Willis
Sylvia Peglar      Christian Körner
Steve Brooks       Donatella Magri
Shonil Bhagwat    Lizzie Jeffers