Some Important Milestones in the Development of Quaternary Pollen Analysis 1916-2018

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Prague, October 2018
Introduction

Pioneer phase 1916–1950

Building phase 1950–1973 and mature phase 1973–present day

Where are we today and what about the future?

Conclusions

Acknowledgements
Introduction

Quaternary pollen analysis as we know it today is 102 years old. Several meetings, workshops, and journals celebrated the centenary in 2016.

Culminated in the major Special Issue publication of *Vegetation History and Archaeobotany* in 2018.
Contains 4 papers on history and development of pollen analysis and 5 research review-type articles.

The historical papers by Pim de Klerk, Kevin Edwards, and Christer Nordlund all provide valuable insights into our subject’s history.
Also a large review paper by Björn Berglund and myself (38 pages + 30 pages of supplementary material) on 100 years of Quaternary pollen analysis.

Veget Hist Archaeobot
DOI 10.1007/s00334-017-0630-2

One hundred years of Quaternary pollen analysis 1916–2016

H. John B. Birks¹²© · Björn E. Berglund³
Today I will discuss a few of the **major milestones** in the development of our subject. Inevitable **bias** towards north-west Europe and Minnesota where I have primarily worked and the types of palynology I am most interested in.

The milestones are grouped into **three major phases**

- Pioneer phase 1919 – 1950
- Building phases 1950 – 1973
- Mature phase 1973 – present day
Quaternary geologist fascinated by peat stratigraphy and associated macrofossils, mainly wood remains. Also fascinated by Gustaf Lagerheim’s (1902) observations of pollen preserved in peat. These important observations attracted much attention.

“This is a certain method for following carefully, with the aid of a microscope, layer after layer of both the immigration of all plants of which pollen or spores occur fossilised and also alterations with respect to the relative number of these plants” (NO Holst, 1909)

A very perspicuous, forward-looking comment! Holst (1846-1918) was an all-round geologist. Did not live to see pollen analysis take off.
1906
1927
1929
1929
1937
1938
1944
Tofsy von Post

Big man in many ways!

Du Rietz, von Post & Braun-Blanquet 1935

Birks & Berglund (2018)
Von Post presented pollen analysis to a wide audience at the 16th Scandinavian Meeting of Natural Scientists in Kristiania (now Oslo) in **July 1916** and then in Stockholm in November 1916. Published in Swedish in **1916** and **1918**. Translated into English by MB Davis and K Fægri in **1967**. However, key diagram from the lecture was never published.

Time-space diagram of 13 sites from NE Denmark to central Sweden

“think horizontally, act vertically”

“think horizontally, work vertically”

Birks & Berglund (2018)
Basic sampling design across vegetational boundaries, ecotones, species-range limits, and/or climate gradients very valuable; e.g.

- Itasca transect in NW Minnesota
- S–N transect in western Scotland
- W–E transect in northern Norway and Sweden
- S–N transect in S Norway
- SE–NW transect across central Norway
- Forest –tundra ecotone in Lapland

“I consider that this category of fossils [pollen], hitherto rather overlooked, can indeed, through systematic treatment, considerably widen our knowledge of the Late-Quaternary deposits and their history.” (von Post 1967)
International ‘explosion’ of pollen analysis

Very rapid spread

1918 Russia
1919 Norway
1920 Denmark
1921 Finland
1922 Færøe Islands
1922 Czechoslovakia
1923 Austria
1924 Germany
1925 Estonia
1925 Lativa
1925 Switzerland
1926 Poland
1927 Canada
1929 Patagonia
1929 New Zealand
In 13 years since von Post’s lecture, pollen analysis was well established in 15 countries and 3 continents!

Paul Sears (1891-1990)
Karl Rudolph (1881-1937)
Franz Firbas (1902-1964)
Lucy Cranwell (1907-2000)
Gunnar Erdtman 1897-1973 – palynology’s ‘evangelist’

Defended his doctoral thesis in 1921 (written in German).

Travelled and worked widely – British Isles, NW Germany, The Netherlands, Belgium, France, Russia, Canada, USA, New Zealand ...

Published in English, German, French, and native Swedish
Major falling out between von Post and Erdtman soon after Erdtman became palynology’s ‘evangelist’ and international ‘star’ in the late 1920s

“During the 30 years that elapsed from the publication of my thesis up to von Post’s death in 1951, I had practically no contact with him!” (Erdtman 1967)

Reason for this antagonism (largely, according to Fægri) on the part of von Post probably jealousy; sadly a common affliction in academia.
Knud Jessen 1884-1971 – pollen and macrofossils

One of the forgotten greats.

Outstanding botanist – floristics, ecology, taxonomy, plant geography, plant macrofossils, pollen analysis, conservation

First to combine plant macrofossils (his speciality) with pollen (as a dating tool) and archaeology in relation to Baltic Sea history in his doctoral thesis.
Major monograph in 2 volumes on 38 interglacials in Denmark and N Germany. Pollen and macrofossils – unbelievable work!
Worked in Ireland with his ‘student’ G Frank Mitchell

Gortian (?Holsteinian) interglacial

Detailed macrofossils (Jessen) and pollen (Andersen)

Showed presence of plants in Ireland now only found in eastern N America or Balkans
Appropriately honoured by his colleagues in a 1954 Festschrift and an honorary ScD from Cambridge University

Many important, and still relevant, papers by

Iversen
Fægri
Andersen
Krog

Iversen (Ed.) (1954)

Major turning point in development of pollen analysis
Fægri and Iversen met, shared a bedroom, and a life-long collaboration began.

As plant ecologists, we were unhappy (and a bit critical) of the strongly geological approach to pollen analysis of von Post.

Laid plans in 1933 to write a monograph about *botanical pollen analysis*, but both very busy and communication during World War 2 was almost impossible.

Within ~12 years of the Baltic Course, both had made major contributions:

- **Iversen**: 1934, 1936, 1941, 1942 (including “Landnam” classic), 1944
- **Fægri**: 1935, 1940, 1943, 1944, 1945
Several years of work (and disagreements according to Fægri!) with Fægri writing most of the book in the daytime and Iversen spending the night-time modifying it (and, as Fægri admitted, “Iver calmed my text down”). Resulted in the *Text-book*. 

**Johs Iversen (1904-1971)**

**Knut Fægri (1909-2001)**

**Text-Book of Modern Pollen Analysis**

1950
Iver and Jørgen Troels-Smith (‘Troels’) developed a useable (and sensible) terminology for pollen morphology that allowed Iver to devise the pollen key in the *Text-book*.

Iver and Fægri called the book *Text-book of Modern Pollen Analysis* and dedicated it to von Post. Emphasised the importance of botanical and ecological knowledge.

They worried about von Post’s likely reaction

But no need

“"It can hardly be an exaggeration to characterise the book as the banner for a new era in the science of pollen analysis ... I shall leave the pollen statistical stage” (von Post 1950)

Fægri and Iver elated!

Major paradigm shift in pollen analysis
Other pioneers in ecological pollen analysis

The idea of ecological pollen analysis was not confined to Fægri and Iversen. Several major contributions from Karl Rudolph, Franz Firbas, Karl Bertsch, Władysław Szafer, Harry Godwin, Max Welten, Leo Aario, Ed Deevey, and others.

Their work is less well known – mainly published in German, French, or Polish and/or in ‘obscure’ local journals or in broad American journals such as *American Journal of Science*.

Along with the 1950 *Text-book*, Firbas’ (1949) major synthesis, and outstanding papers by Welten (1944), Godwin (1940), Deevey (1939, 1943), Aario (1940), Szafer (1935), Bertsch (1935, 1940), and others, the **pioneer phase was over** and the **building phase could develop**.
Building Phase 1950-1973 and Mature Phase 1973-Present

Three major scientific developments were occurring during these periods but not directly within pollen analysis.

2. Development of high-quality optical microscopes and of electron and scanning microscopes, especially since about 1960.
3. Development of mainframe computers and, as a result, development of greater accessibility of multivariate numerical techniques from about 1968.

All important for developments within pollen analysis since 1950.
Selected **twelve methodological developments** in pollen analysis.

Not easy to separate the building and mature phases – scientific development is a continuum, like time.


Brought together many new and innovative studies on modern pollen representation. Pollen dispersal, vegetation dynamics at different scales, modern macrofossil representation, and palaeolimnology. Like to think it was a turning point in our subject. Provided a firmer, factual basis for interpreting pollen-analytical data.
Improved field and coring techniques

- essential!


Allowed coring of lake sediments (very rarely done until early 1960s) not only from ice but also from open water. First open-water coring was by Iversen in 1932 in Greenland and Deevey in 1936 in New England but from the ice.
Improved laboratory methodology, pollen reference collections, error estimation of counts, semi-automated counting, etc.

Plus – Keith Bennett, Sylvia Peglar, Jens Stockmarr, et al.
Greatly improved pollen morphology

Gunnar Erdtman (palynology’s ambassador)  
Wim Punt  
Jacqueline van Leeuwen
Estimation and interpretation of pollen-accumulation rates ‘influx’

Welten 1944; Deevey 1946; Davis & Deevey 1964; Davis et al. 1973

Max Welten

1944

Margaret Davis

Plus – Keith Bennett, Thomas Giesecke, Sheila Hicks, Heikki Seppä, et al.
Development of quantitative charcoal analysis and reconstruction of fire history

Jim Clark

Cathy Whitlock

Willy Tinner

Plus – Daniele Colombaroli, Dan Gavin, Phil Higuera, Feng Sheng Hu, et al.
Development of user-friendly computer software to handle and plot pollen-analytical data

TILIA, TILIA-GRAPH

Eric Grimm

Development of numerical methods

Summarising pollen-analytical data; estimating numerical properties (e.g. richness), reconstructing environmental variables (e.g. climate); testing hypotheses

Detailed modern pollen-representation studies

Development of pollen-representation and dispersal models; Landscape Reconstruction Algorithm; etc.

Svend Andersen, Colin Prentice, Henrik Tauber, Roel Janssen, Shinya Sugita, Rona Peck

Plus – Leo Aario, Jane Bunting, Margaret Davis, Franz Firbas, Marie-José Gaillard-Lemdahl, Steve Jackson, Pim van der Knaap, Petr Kuneš, Martin Theuerkauf, et al.
Resurrection of plant-macrofossil analysis

“Macrofossils are only useful for aquatic plants whose pollen record is so poor”  Johs Iversen (1969, pers. comm.)

“...”

Clement (and Eleanor) Reid
AG Nathorst
Knud Jessen
Bill Watts
Hilary Birks
Steve Jackson

Improved project design

Better formulation of research questions; careful site selection; etc.

Studies in sub-tropical and tropical areas

Thanks to improved coring techniques and extensive exploration, many sub-tropical and tropical areas have now been studied palynologically –

Amazonia Andes Bolivia Ecuador
Galápagos Madagascar Mauritius Panama
PNG Peru Sarawak Sumatra
Tanzania Tropical Africa Tropical Asia

Pioneered by Selling, Hedberg, and Livingstone.
Other important methodological developments

- Database development and palaeo-ecoinformatics – Neotoma, EPD, etc.
- Non-pollen palynomorphs (NPPs) – fungal spores, algae, phytoliths, etc.
- Pollen trapping and monitoring
- Hindcast dynamic vegetation modelling, biomisation, etc. with pollen data
- Integration of pollen analysis with multi-proxy projects involving diatoms, chironomids, geochemistry, isotopes, etc.
- Deep lake coring, long cores, laminated sediments, marine palynology
- Improved age–depth modelling, increasingly within a Bayesian framework
Where are we Today and What About the Future?

Methodological developments are not an end in themselves, they are a means to an end.

How have they been used to help our research on past vegetation and environment and to decipher “the geological record of ecological dynamics” (Flessa & Jackson 2005)?

In a non-experimental historical science, can distinguish three phases (Ball 1975; Fægri 1974)

- **Descriptive exploratory phase** (stage I *sensu* Fægri) with initial detection, description, and archiving of patterns

- **Narrative phase** (stage II) with plausible but largely untestable inductive explanations for the patterns detected in the descriptive phase

- **Analytical phase** (stage III) in which falsifiable hypotheses about the processes are proposed, evaluated, tested, and rejected
Descriptive phase

In last 50 years, many **new areas** explored palynologically

- Andes
- Easter Island
- Amazonia
Iran

1977

PALYNOLOGICAL INVESTIGATIONS IN WESTERN IRAN

W. van Zeist & S. Bottema

THE PLEIGLACIAL, LATE GLACIAL AND EARLY POSTGLACIAL VEGETATIONS OF ZERIBAR AND THEIR PRESENT-DAY COUNTERPARTS

H. Freitag

SE USA

1980

THE LATE QUATERNARY VEGETATION HISTORY OF THE SOUTHEASTERN UNITED STATES

W. A. Watts

Department of Botany, Trinity College, Dublin, Ireland and Limnological Research Center, University of Minnesota, Minneapolis, Minnesota 55455

Tropical Asia and Africa

1979

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY OF LONDON

B. BIOLOGICAL SCIENCES

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10 July 1979

Late Quaternary vegetational history of the Enga Province of upland Papua New Guinea

by D. Walker and J.R. Flenley

1995


Orbital forced frequencies in the 975,000 year pollen record from Tenagi Philippon (Greece)

HJPM Mommersteeg1, MF Loutre2, R Young1, TA Wijmstra1, H Hooghiemstra1

1 The Netherlands Centre for Geo-Ecological Research (ICG), Hugo de Vries Laboratory, Department of Palynology and Paleo/Actuo-Ecology, University of Amsterdam, Kruislaan 318, NL-1098 SM Amsterdam, Netherlands

2 Institut d’Astronomie et de Géophysique Georges Lemaître, Université Catholique de Louvain, Chemin du Cyclotron 2, B-1348 Louvain-la-Neuve, Belgium

Greece

2011
Major advances in study of long interglacial sequences in Colombia, Greece, Russia, France, Italy, etc.

Fantastic source of information – ‘natural long-term ecological experiments’ (IGNEX)
Narrative Phase

Three examples: one site; 32 sites; 828 sites

1. One site – Gerzensee, Swiss Plateau, 603 m

Unique ultra-detailed multi-proxy study of late-glacial, particularly Termination 1A. Ecosystem reconstruction with 8-year resolution

Brigitta Ammann
<table>
<thead>
<tr>
<th>Age (cal yr BP)</th>
<th>Duration (cal yrs)</th>
<th>Stable oxygen isotopes</th>
<th>Physiognomy of past vegetation</th>
<th>Reconstructed vegetation</th>
<th>Pollen accumulation rates (grains cm(^{-2}) yr(^{-1}))</th>
<th>Rates of palynological change (per 70 yrs)</th>
<th>Palynological richness (taxa cm(^{-2}) yr(^{-1}))</th>
<th>Inferred soils</th>
<th>Soil changes</th>
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<tbody>
<tr>
<td>15675 – 14665</td>
<td>1010</td>
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<td>Shrub-tundra: Artemisia,</td>
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<td>++ Regosols or lithosols</td>
<td>Minrogenic P &amp; N ↓</td>
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<td>14565 – 14445</td>
<td>220</td>
<td></td>
<td></td>
<td>Juniperus, Hippophae</td>
<td>+</td>
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<td></td>
<td>+ Humus accumulation</td>
<td>N fixation</td>
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<tr>
<td>14445 – 13835</td>
<td>610</td>
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<td></td>
<td>scrub with birch</td>
<td>+</td>
<td></td>
<td></td>
<td>+++ Mosaic of xeric &amp; mesic soils</td>
<td>Humus, P, &amp; N ↑</td>
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<tr>
<td>13835 – 12710</td>
<td>1125</td>
<td></td>
<td></td>
<td>Birch forest</td>
<td>+</td>
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<td></td>
<td>+++ Cambisols (brown earths)</td>
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<td>12710 – 12500</td>
<td>210</td>
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<td>Birch-pine forest,</td>
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<td>+ + + ?</td>
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<td>followed by pine-birch</td>
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<td></td>
<td>forest</td>
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</tbody>
</table>

Ammann et al. (2015); Birks et al. (2016)
2. Thirty-two Holocene sites – in six major vegetation zones in Norway. Consistent methodology and pollen taxonomy throughout

Reconstructions of past

pollen richness as Hill’s N0;
pollen diversity as Hill’s N1; and
pollen diversity of most abundant taxa as Hill’s N2

Investigating impact of Homo sapiens phase (Birks 1986) on richness and diversity. Piece-wise regression before phase and in phase

Vivian Felde
3. Based on 828 sites – pollen maps at 500-year intervals for 54 taxa

Pollen mapping initiated and developed in Europe by von Post, Rudolph, Szafer, Godwin, Firbas, and Huntley & Birks. Now with the European Pollen Database, Brewer et al. have presented state-of-the-art pollen maps. Hope that phylogeographers studying DNA of extant tree populations will use these maps and not the out-dated maps of Huntley & Birks!
Mapping Lateglacial and Holocene European pollen data

Corylus

Common name: Hazel
Family: Betulaceae
Plant type: Deciduous broadleaved trees and shrubs
Species included: Corylus avellana L., Corylus maxima L., Corylus colurna L.

Map projection: Lambert Azimuthal Equal-Area
Projection center: 12°E, 48°N
Data source: European Pollen Database
Mapping Lateglacial and Holocene European pollen data

Tilia

Common name: Lime
Family: Malvaceae
Plant type: Deciduous broadleaved trees and shrubs
Species included: Tilia platyphyllos Mill., Tilia cordata Scop., Tilia tomentosa Moench, Tilia rubra DC, Tilia dasystyla Steven

Map projection: Lambert Azimuthal Equal-Area
Projection center: 12°E, 48°N
Data source: European Pollen Database

© Journal of Maps, 201x
Mapping
Lateglacial and Holocene
European pollen data

Picea

Common name: Spruce
Family: Pinaceae
Plant type: Evergreen coniferous trees
Species included: Picea abies (L.) H. Karst., Picea omorica Panic

Map projection: Lambert Azimuthal Equal-Area
Projection center: 12°E, 48°N
Data source: European Pollen Database

© Journal of Maps, 201x
Palaeobotanical and molecular data combined

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

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) in extant populations
Molecular data from extant populations –

chloro plast haplotypes

microsatellite data

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

Magri et al. (2006)
Nuclear genetic markers (isozymes) from extant populations

Isozyme data – 9 groups
- Italian group,
- southern Balkans,
- Iberian Peninsula,
- rest of Europe

Magri et al. (2006)
Palaeobotanical data (pollen and macrofossils)

Magri et al. (2006)

● = >2%  ▲ = macrofossil
Combine palaeobotanical and chloroplast haplotype data

Chloroplast haplotypes

- **Type 1** – spread from several refugia
- **Type 2** – only in Italy
- **Other types** – mainly in Balkans

Magri et al. (2006)
Combine palaeobotanical and isozyme data

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

Magri et al. (2006)
Suggested Holocene refugial areas and main colonisation routes

Magri et al. (2006)
Multiple LGM population centres (microrefugia), up to 45°N. Some, but not all, of these contributed to the Holocene expansion. Others, especially in the Mediterranean region (macrorefugia) did not expand.

See some populations expanded considerably, whereas others hardly expanded.

Much to be done along the lines of this unique study.
Making major contributions to ecology and biogeography, some discussed in my ‘Conundrum’ talk – extinction, migration, stasis, adaptation, persistence, evolutionary and ecological processes in the Quaternary.

Other major contributions include

- Glacial–interglacial cycle, long-term soil development in glaciated and unglaciated areas, role of mycorrhiza in vegetation dynamics
- Realised environmental space, potential niches, and no-analogue pollen assemblages (and by inference no-analogue vegetation)
• Nature of vegetation, community concept, individualistic behaviour
• Past forest structure, extent of forest cover, and landscape openness
• Megafaunal extinctions in context of past vegetation and ecosystem dynamics
• Providing a catchment history in palaeolimnological studies. Taken a time for palaeolimnologists to follow Ed Deevey’s idea that a lake does not exist without its catchment!

Steve Jackson  Kathy Willis  Jack Williams
Analytical phase

Three examples, all involving direct testing of explicit hypotheses about underlying ‘drivers’ or processes of patterns in pollen data.

“Coaxing history to conduct experiments” (Deevey 1969)

i) Diss Mere and the *Ulmus* (elm) pollen decline
Diss Mere pollen percentage diagram. The scale at the base of the diagram gives percentages for the hatched silhouettes: unshaded silhouettes are exaggerated x 10 scale. All curves plotted to the same scale, as the sum of determinable pollen grains and spores of all extant vascular plants (except obligate aquatic taxa).

Peglar (1993)
Principal hypotheses to explain the NW European *Ulmus* decline

1. **Climate change** - climate became less favourable for elm and for elm only over a large area of N.W. Europe
   
   Predictions - other taxa affected; 
   
   **slow** decline (? 100-150 years)

2. **Soil change** - soils became less favourable for elm and for elm only over a large area of N.W. Europe
   
   Predictions - other taxa affected; 
   
   **slow** decline (? 100-150 years)

Peglar & Birks (1993)
<table>
<thead>
<tr>
<th></th>
<th>Competitive exclusion</th>
<th>Human impact</th>
<th>Pathogenic attack</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predictions</td>
<td>exclusion by later tree arrivals</td>
<td>selective clearance of elm or pollarding or shredding of elm for animal fodder</td>
<td>widespread attack by a pathogen specific to elm</td>
</tr>
<tr>
<td>Predictions</td>
<td>new taxa arrive at time of elm fall; <strong>slow</strong> decline (? 100-150 years)</td>
<td>not synchronous over large areas; <strong>slow</strong> decline given Neolithic population size and available technology (? 250 years)</td>
<td><strong>rapid</strong> decline (? 10-20 years)</td>
</tr>
</tbody>
</table>

Peglar & Birks (1993)
Interactions of possible causative processes

Predicted rate of decline

Climate + Human impact
- SLOW

Climate + Disease
- RAPID

Disease + Human impact
- RAPID

Climate + Disease + Human impact
- RAPID

Rate of decline key parameter to estimate

Peglar & Birks (1993)
Annual pollen influx of *Ulmus* pollen as deviations from the mean
Population halving time = 5 years

Peglar (1993)
Predicted rate of *Ulmus* decline for major hypotheses

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Predicted rate of decline</th>
</tr>
</thead>
<tbody>
<tr>
<td>Climate</td>
<td>SLOW</td>
</tr>
<tr>
<td>Human impact</td>
<td>SLOW</td>
</tr>
<tr>
<td>Disease</td>
<td>RAPID</td>
</tr>
<tr>
<td>Climate + Human impact</td>
<td>SLOW</td>
</tr>
<tr>
<td>Climate + Disease</td>
<td>RAPID</td>
</tr>
<tr>
<td>Disease + Human impact</td>
<td>RAPID</td>
</tr>
<tr>
<td>Climate + Disease + Human impact</td>
<td>RAPID</td>
</tr>
</tbody>
</table>

**Hypotheses not falsified**

<table>
<thead>
<tr>
<th>Disease</th>
<th>Disease + Human impact</th>
</tr>
</thead>
<tbody>
<tr>
<td>Climate + Disease</td>
<td>Climate + Disease + Human impact</td>
</tr>
</tbody>
</table>

Peglar & Birks (1993)
No evidence for any climatic change at this time.

Lamination thickness remains constant, so no very warm or very cold summers or extreme winters.

Reject Climate + Disease

Climate + Disease + Human Impact

Left with Disease

Disease + Human Impact

Peglar & Birks (1993)
Favour disease + human impact
but alternative of disease alone not rejected
ii) Origin of a landscape mosaic in the Rocky Mountains, USA

Park-forest mosaic, Wyoming

Aerial photo showing core sites in Fish Creek Park and surrounding forest (1:40,000).

Location of Fish Creek Park, Wind River Range, Wyoming.
Park-forest mosaic, Wyoming
Hypotheses of park origin and expected vegetation histories from park and forest sites.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Expected vegetation sequence at present park and forest sites</th>
</tr>
</thead>
</table>
| Permanent site (e.g. soil factors) | Park: Park vegetation throughout  
                             Forest: Forest vegetation throughout * |
| Remnant (e.g. once all park) | Park: Park vegetation throughout  
                             Forest: Park, then forest * |
| Replacement (e.g. disturbance)  | Park: Forest,* then park  
                             Forest: Forest vegetation throughout * |

* Forest vegetation may have short intervals of non-forested vegetation following disturbance, but revert to forest vegetation soon after.

Studied 2 forest sites and 3 park sites – all small and shallow, <30 m diameter ponds

Lynch (1998)
Vegetation changes inferred from pollen assemblages at five sites. Gaps represent periods with no sediment record. Problem of small shallow ponds

Lynch (1998)
### Hypotheses of park origin and expected vegetation histories from park and forest sites.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Expected vegetation sequence at present park and forest sites</th>
<th>Outcome</th>
</tr>
</thead>
<tbody>
<tr>
<td>Permanent site</td>
<td>Park: Park vegetation throughout</td>
<td>Rejected</td>
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<tr>
<td>(e.g. soil factors)</td>
<td>Forest: Forest vegetation throughout *</td>
<td></td>
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<tr>
<td>Remnant</td>
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<td></td>
</tr>
</tbody>
</table>

* Forest vegetation may have short intervals of non-forested vegetation following disturbance, but revert to forest vegetation soon after.

**Why forest replaced by park about 2500 B.P.?** Climate change, disturbance regime. Positive feedback between vegetation and microclimate may maintain park once forest is removed.

Lynch (1998)
iii) Are there migrational lags in *Betula* trees in the earliest Holocene?

Birks et al. (2000)
Palaeoecological data

1. **Pollen analysis** by Sylvia Peglar
   - 600–769.5 cm  117 samples
   - 101 taxa       16 aquatic taxa
   - Mean age difference: 21 years
   - Median age difference: 14 years

2. **Macrofossil analysis** by Hilary Birks
   - Pollen analyses supplemented by plant macrofossil analyses to provide unambiguous evidence of local presence of taxa, e.g. birch trees

3. **Chironomid analysis** by Steve Brooks and John Birks
   - Past temperatures estimated from fossil chironomid assemblages

4. **Radiocarbon dating** by Steinar Gulliksen
   - Chronology based on 72 AMS dates, wiggle-matched to the German oak–pine dendrocalibration curve by Gulliksen *et al.* (1988 Holocene 8: 249-59). Chronology in calibrated years is the key to being able to put the palaeoecological data into a reliable and realistic time scale
Five statistically significant pollen zone boundaries in 720 years since YD to the first expansion of *Betula* as shown by macrofossils.

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

Birks & Birks (2008)
Kråkenes terrestrial macrofossils – summary diagram
Six main phases

Hilary Birks, unpublished
## Terrestrial vegetation & 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><em>Betula</em> woodland with <em>Juniperus</em>, <em>Populus</em>, <em>Sorbus aucuparia</em>, and later <em>Corylus</em>. Abundant tall-ferns. <em>Betula</em> macrofossils start at 10880 BP, <strong>670 years</strong> since YD and expands <strong>720 years</strong> since YD</td>
</tr>
<tr>
<td>6</td>
<td>10975</td>
<td>575</td>
<td>Fern-rich <em>Empetrum-Vaccinium</em> heaths with <em>Juniperus</em></td>
</tr>
<tr>
<td>5</td>
<td>11180</td>
<td>370</td>
<td><em>Empetrum-Vaccinium</em> 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><em>Salix</em> snow-beds, much melt-water and instability</td>
</tr>
<tr>
<td>1</td>
<td>YD</td>
<td>0</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
Timing of major successional phases

<table>
<thead>
<tr>
<th>Phase</th>
<th>‘Little Ice Age’ glacial moraines</th>
<th>Kråkenes early Holocene</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><strong>670-720</strong> years</td>
</tr>
</tbody>
</table>

Why the lag in *Betula* woodland development at Kråkenes?
Chironomid-inferred mean July air temperatures & the delayed arrival of *Betula*

Chironomids show steep temperature rise of 0.3°C per 25 yr in earliest Holocene

<table>
<thead>
<tr>
<th>Year BP</th>
<th>Interval after YD-H</th>
<th>Temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td>11520</td>
<td>30 yr</td>
<td>&gt;10°C</td>
</tr>
<tr>
<td>11490</td>
<td>60 yr</td>
<td>&gt;11°C</td>
</tr>
</tbody>
</table>

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 hypotheses for delayed arrival of *Betula* are lags due to:

1) landscape development (e.g. soil development) processes
2) tree spreading delays from refugial areas further south or east
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

Cannot be satisfactorily resolved at present
Conclusions

Von Post’s (1916) conclusion that
“I consider that the category of fossils [pollen grains], hitherto rather overlooked, can indeed through systematic treatment, considerably widen our knowledge of late-Quaternary deposits and their history”

has, I feel, been convincingly demonstrated to be correct!
Ed Deevey’s (1967) proposal that 
“von Post’s simple idea that a series of changes in pollen proportions in accumulating peat was a four-dimensional look at vegetation, must rank with the double helix as one of the most productive suggestions of modern times”
is certainly supported by the achievements of palynologists in the last 50–60 years
The Future?

Much as I would like to discuss the next 50 years, it is not appropriate for me to do so as I will not be here in 50 year’s time!

Just conclude by saying that I feel that pollen analysis in 2018 with its ever-broadening links with phylogeography, ecosystem science, island biogeography, tropical forest ecology, archaeology, conservation and restoration ecology, and community and population ecology is in very good health and can address challenging and imaginative research questions. I hope it will maintain its good health, vitality, and live for at least another 100 years! What is needed is for young palynologists to ask interesting and important research questions and be prepared to do a lot of basic work.

Von Post has every reason to be immensely proud of his ‘simple idea’ of pollen analysis. It certainly has turned out to be a ‘most productive suggestion of modern times’.
## Acknowledgements

<table>
<thead>
<tr>
<th>Harry Godwin†</th>
<th>Jim Ritchie†</th>
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<tr>
<td>Knut Fægri †</td>
<td>Ed Cushing</td>
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<tr>
<td>Herb Wright †</td>
<td>Frank Oldfield</td>
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<tr>
<td>Svend Th Andersen †</td>
<td>Brigitta Ammann</td>
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<tr>
<td>Roel Janssen †</td>
<td>Hilary Birks</td>
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<tr>
<td>Bill Watts †</td>
<td>Björn Berglund</td>
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<td>Cathy Jenks</td>
<td>Kathy Willis</td>
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