Past forests of Europe

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European forests have varied in their composition, structure, and extent over the last 5 million years or more in response to global climate changes. European forests have also undergone very major changes due to the alternating glacial-interglacial cycles of the Quaternary (last 2.6 million years). European forests have greatly changed in their extent and structure in the last 5,000 years due to human activities (the Homo sapiens phase) in the current Holocene interglacial in which we live. Contemporary ecologists and foresters can learn from 'lessons from the past' about forest responses and resilience to environmental changes in the past.

Introduction

Were European forests 500, 5,000, 15,000, 150,000, 1.5 million, 2.5 million, and 5 million years ago similar in species composition, structure, and extent to the forests of Europe today? As we cannot directly observe the forests of the past, to answer these questions we need to reconstruct past forests indirectly using the fossil record. This involves the study of seeds, fruits, leaves, wood, and charcoal (macrofossils) and of microscopic pollen grains, spores, cells (e.g., stomata), and charred particles (microfossils) preserved in lake, bog, alluvial, and other sediments where organic material can be preserved. Pollen analysis as a tool for vegetation reconstruction was invented in 1916 by the Swedish geologist Lennart von Post, and is still the dominant technique in the Quaternary period, especially the last 15,000 years of the late-Quaternary. Von Post had the idea of expressing fossil pollen assemblages as percentages of the sum of pollen grains counted, and of presenting these percentages as stratigraphical pollen diagrams with pollen assemblages plotted against their stratigraphical position through the sedimentary sequence (Fig. 1). He showed strong similarities in pollen diagrams from a small area, and striking differences between different areas. He was thus able to provide the dimension of time (vegetation’s fourth dimension) to the study of past vegetation and forests.1,2

Pollen analysis

There are ten basic principles of pollen analysis (see Box 1). The results of a pollen analysis are most commonly presented as a pollen diagram, showing how the percentages of different pollen types vary with depth, and hence age, in the sedimentary sequence (Fig. 1). When many sequences have been studied, their pollen data can be mapped for a particular time interval (e.g., 5,000 years ago) to produce so-called ‘isopollen’ maps for particular pollen types where the contours represent different pollen values (e.g., 2.5%, 5%, 10%) (Fig. 2). Alternatively when interest is centred on the directions and rates of tree spreading, so-called ‘isochrone’ maps can be constructed where the contours represent ages established by radiocarbon dating (e.g., 5,000, 6,000, 7,000 years ago). When the value of a particular pollen type exceeds a certain threshold value it can be interpreted as reflecting the first arrival of a taxon at different sites (Fig. 3). The first arrival of a taxon is more difficult to assess, because the absence of pollen or macrofossils may not mean a true absence of the taxon in the landscape. Interpretation of pollen-stratigraphical data in a qualitative manner in terms of major past vegetational changes is relatively straightforward. Quantitative interpretation of such data in terms of quantitative estimates of past plant abundances is less straightforward because of the differential production, dispersal, and hence representation of different pollen types. Approaches for quantitative interpretation are currently an area of active research within Europe and elsewhere (e.g., 5, 6).

Fig. 1: Summary pollen diagram from Loch Cill an Aonghais (Argyll), a small lake in south-west Scotland covering the last 12,000 radiocarbon years. The horizontal lines represent partitions of the pollen stratigraphy into pollen assemblage zones. The vertical axis is radiocarbon (14C) years before present (BP) based on eight radiocarbon dates. The small arrows by the Betula (birch), Quercus (oak), Alnus (alder), and Corylus/Myrica (hazel/bog myrtle) indicate when these trees or shrubs are inferred to have first expanded near this site. Cryo- spheric taxa are coloured red and stippled. These taxa become abundant again in the open conditions of the tundra phases where they are shown in plain red. Protocryoseric taxa are coloured black. Meso- cryoseric taxa are green, diacryoseric and taliocrassumin taxa are orange, and taxa associated with human activity and the tundra phases of the Holocene are shown in red. All the pollen and spores percentages are expressed as percentages of the total number of terrestrial pollen and spores counted (generally 500-600 per sample). Pollen analyses by Sylvia M. Peglar.

Fig. 2: ‘Isopollen’ maps of Quercus (oak) pollen percentages across Europe for 12,000, 10,000, 8,000, 6,000, 4,000, and 2,000 radiocarbon years before present (BP). Note the progressive northward spread into southern Scandinavia by 6,000 BP and the subsequent contraction at 2,000 BP in Norway. The percentage contours are percentages of total tree and shrub pollen. (Modified from Huntley and Birks.4)
Box 1: Principles of pollen analysis

i. Pollen grains and spores are produced in great abundance by plants

ii. A very small fraction of these fulfill their natural reproductive function of transferring the male gamete to the female ovary: the vast majority fail to the ground

iii. Pollen and spores decay more or less rapidly, unless the processes of biological decomposition are inhibited by a lack of oxygen, such as in bogs, lakes, and the ocean floor where pollen is preserved

iv. Before reaching the ground, pollen is well mixed by atmospheric turbulence, which results in a more or less uniform pollen rain within an area of similar vegetation and landform

v. The proportion of each pollen type depends on the number of parent plants and their pollen productivity and dispersal. Hence the pollen rain is a complex function of the composition of the vegetation. A sample of the pollen rain is thus an indirect record of the regional vegetation at that point in space and time

vi. Different pollen grains and spores can be identified to various taxonomic levels (e.g. species, genus, family)

vii. In vegetated areas pollen is ubiquitous in lake and bog sediments. Very high concentrations (usually around 100 000 grains/ml) in the sediment permit efficient analyses and statistically robust results (standard pollen counts are usually ca. 300-1000 grains per sample)

viii. If a sample of the pollen rain is examined from a peat or lake-mud sample of known age (dated by annual layers or radiocarbon dating), the pollen assemblage is an indirect record of the regional and local vegetation surrounding the sampled site at a point of time in the past

ix. If pollen assemblages are obtained from several levels through a sediment sequence, they provide a record, admittedly an indirect one, of the regional and local vegetation and their development, as well as of the environmental conditions prevailing at the sampled site at various times through the time interval represented by the sedimentary record (Fig. 3)

x. If two or more series of pollen assemblage are obtained from several sites, it is possible to study changes in past pollen assemblages and hence in the regional and local vegetation through both time and space (Figs 2 and 3)

Europe’s forests prior to the Quaternary ice-ages

The Quaternary period with its multiple glacial stages with ice-sheets and intervening temperate interglacial stages lasted about 2.6 million years ago. What were European forests like prior to the Quaternary?

Knowledge of the Flora and vegetation of the Palaeoene and Neogene (‘Tertiary’ or ‘Eocene’) is not easy. Table 1 (Fig. 1) shows a partial geological time scale. Time is shown in million years with the youngest epoch at the top going down to older epochs at the bottom.

Table 1. Partial geological time scale. Time is shown in million years with the youngest epoch at the top going down to older epochs at the bottom.

<table>
<thead>
<tr>
<th>Epoch</th>
<th>Age (Million years)</th>
</tr>
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<tbody>
<tr>
<td>Eocene</td>
<td>53-23</td>
</tr>
<tr>
<td>Oligocene</td>
<td>23-13</td>
</tr>
<tr>
<td>Miocene</td>
<td>13-5.3</td>
</tr>
<tr>
<td>Pliocene</td>
<td>5.3-0.1</td>
</tr>
</tbody>
</table>

Period

Europe’s forests during Quaternary interglacial stages

Pollen analysis and macrofossil studies reveal that in north-western and central Europe there is strikingly similar vegetation development from the end of a glacial stage through the ensuing interglacial (about 10 000-15 000 years duration) and into the next glacial stage. Although the species and their relative abundances may vary from one interglacial to another, there are such strong ecological similarities that the Danish pollen analyst Johannes Verem recently in 1954 described an interglacial cycle consisting of four or five ecological phases (Figs 2 and 4)13,14. The cryocratic phase represents the cold and dry, often glacial, stage with sparse assemblages of pioneer, arctic-alpine, steppe, and ruderal herbs growing on skeletal mineral soils, frequently covered by wind-blown sand. Trees are absent, except in specialised refugia.

At the onset of an interglacial, temperature and moisture increase and the protoecological phases begin. Base-demanding shade-intolerant herbs, shrubs, and trees (e.g. Betula, Salix, Populus, Pinus, juniperus juniper), Sorbus aucuparia rowan) immigrate into formerly glacial areas and expand to form a mosaic of grassland, scrub, and open woodland growing on unleached, fertile soils rich in nitrogen and phosphorus and with a low humus content (Fig. 1). The mesocratic phase is characterised by the development of temperate deciduous forests of Quercus, Ulmus, Tilia lime, Corylus hazel, Fraxinus ash, and Alnus on fertile brown-earth soils (Fig. 1). Shade-intolerant herbs and shrubs are rare as a result of competition and habitat loss, except in openings caused by fire, wind-throw, and, possibly, grazing mega fauna15. The next phase, the oligocratic phase, comprises open conifer-dominated woods (Pinus, Picea, Abies), Ericaceae heaths, and bog vegetation but growing on intersitial (slowly drained (usually rich podsol) and feniferous acid soils. Climatic deterioration (temperature decreases, reduced moisture, etc.) occur in the final telocratic phase and, most especially, at the onset of the next glacial cryocratic phase as forests decline, frost action and cryoturbation destroy the leached and feniferous acid soils, and herbs expand on the newly exposed mineral soils. The telocratic forest vegetation is very similar to the oligocratic phase except that as the climate cools towards the end of the interglacial, deciduous trees and shrubs dominate the region and the seasonal range of the deciduous phase (Fig. 2).

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Europe’s forests in the Holocene (11 700 years ago–today)

The mesic phases in the Holocene interglacial stage was greatly modified about 5000–6000 years ago by the onset of forest clearance and prehistoric shifting cultivation and livestock farming (Fig. 1). This new phase, unique to the Holocene is called the Homo sapiens phase (see Box 2). There was a steep fall in Ulmus pollen values (Fig. 1), probably as a result of an interaction between prehistoric human activities and a tree pathogen, with elm pollen values halving within 5 years at a site in southern England, Italy, and Spain. Similarly, 5000-6000 years ago Abies disappeared from the Mediterranean and sub-Mediterranean lowlands of the Italian Peninsula, probably in response to excessive Neolithic disturbance and fire. Over the last 6000-7000 years, many forest pioneer and early successional species increased their presence in areas that had been cleared or cultivated areas, relaxation in grazing pressure, or over-exploitation of environmental resources.

In some areas of central and north-west Europe, forest clearance and prehistoric shifting cultivation and livestock farming (Fig. 1) were facilitated by the creation of abundant, large clearings within Tilia- or Quercus-dominated forests on well-drained soils. In some areas

The characteristic trees of the interglacial phases differ in their reproductive and as well as their biological and ecological and competitive tolerances. Protemocrotic trees have high reproductive rates, low competitive tolerances, high rates of population increase, and display ‘pioneer’ and ‘exploitation’ traits. Mesocrotic trees have low reproductive rates, high competitive tolerances, medium-low rates of population increase, arbuscular phosphorus-scavenging mycorrhiza, and late-successional, ‘competitive’, and ‘saturation’ traits. Oligocrotic and telocrotic trees have medium reproductive rates, high competitive tolerances, medium-low rates of population increase, ectomycorrhiza with a phosphorus-mining strategy, and ‘cold-stress tolerant’ and ‘avertisseur’ traits.

The mid interglacial stage marked by the rapid expansion of temperate deciduous forests and the reclamation of much of the steppe-like environments of the glacial stages. This corresponds to the protocrotic phase in central and northern Europe. At the onset of an interglacial, the corresponding to the protocrotic phase in central and north-west Europe, temperate taxa (e.g. deciduous Quercus, Ulmus, Ostrya, hornbeam, Carpinus) are present in forests together with evergreen broad-leaved trees (e.g. Quercus ilex, oak, Olea europea olive) and Mediterranean shrubs (e.g. Pistacia tschotschelian), while boreal and steppe vegetation declines (e.g. Betula, Juniperus, Artemisia wormwood). These changes commonly occurred after an extensive phase of human activity involving clearance and grazing followed by the abandonment of cleared and cultivated areas. This abandonment may have occurred as a result of local population collapse following, for example, climate change, emigration, or over-exploitation of environmental resources.

Other types of secondary woodland developed in areas beyond the natural geographical range of Fagus, for example woods of pure Fagus excelsior European ash, Quercus spp., Taxus baccata English yew, Betula spp., or Ilex aquifolium common holly became established on particular soil types following abandonment of cleared or cultivated areas, relaxation in grazing pressure, or reduction in fire frequency.

The westward, northward, and southward spread and expansion of Hippocastanum trees through Finland, Sweden, and Norway over the last 6000-7000 years may be a contemporaneous response to subtle step-wise climate change, a delayed migration unrelated to simple climate change, a response to forest disturbance creating gaps for colonisation, or a combination of these factors. However, whatever the causes, the invasion of Pinus into north and central Fennoscandia over the last 6000-7000 years resulted in major changes in forest composition and structure, and in soil conditions, with widespread accumulation of mor humus, soil leaching, and podsolisation and changes in the natural fire regime within the boreal forest.

Simulations of future vegetation dynamics at Lago di Massaciuccoli, a coastal lake in Tuscany (central Italy), with a dynamic vegetation model (LANDCLIM) for different climatic conditions (today vs. warming) and levels of disturbance (low vs. moderate). The mid- to late-Holocene sedimentary-pollen record of Lago di Massaciuccoli is used to validate the model, in particular LANDCLIM is able to simulate extinction vegetation types which were growing in the past at the site because anthropogenic disturbance became excessive. a) Present-day (1950-2000 AD) mean monthly temperature (°C) and average total monthly precipitation at Lago di Massaciuccoli close to Pisa (Tuscany).

Box 3: Palaeo-model comparison: past, present and future Mediterranean vegetation

b) Map of Italy and Switzerland with Lago di Massaciuccoli denoted by a black dot. c) Future (2071-2100 AD) mean monthly temperature and precipitation projected by a regional climate model (SMHI) for Lago di Massaciuccoli.

d) and e) Vegetation simulations at Lago di Massaciuccoli with LANDCLIM, a dynamic vegetation model with d) present climate and future climate e) All vegetation models were initialised with the same present-day climate scenario and moderate disturbance before 2010.

f) Holocene pollen percentages of upland trees and shrubs at Lago di Massaciuccoli.
and expansion of more permanent land-use practices (e.g. animal tree combinations in the different interglacial stages have resulted in a continuous dynamic of tree survival in refugia 27, 37)

These palaeoecological questions suggest that it is inadequate to project future ecosystem conditions solely on the basis of present- environmental changes that led to the development of the system and the palaeoecological record, when the time window extends to 10 000-15 000 due to major changes in the Earth's climate in the past 10 500 years raises critical questions about appropriate targets and management of emerging novel ecosystems to ensure high biodiversity.