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 5000 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, 5000, 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 - invented in 1916 by the Swedish geologist Lennart von Post - was and still is 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 sediment 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.

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 appearance of that 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.

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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 British (BP), Quercus (oak), Alnus (alder), and Corylus/Martynia (hazel/bog myrtle) indicate where these trees or shrubs are inferred to have first expanded north or south. Cryo-Atlantic taxa are coloured red and stippled. These taxa become abundant again in the open conditions of the Ilanmo steppes phase where they are shown in plain red. Protonotrocal trees are coloured blue, meso-Atlantic trees are green, diagnostically Early Glacial taxa are orange, and taxa associated with human activity and the Ilanmo steppes phase of the Holocene are shown in red. All the pollen and spore 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

1. Pollen grains and spores are produced in great abundance by plants.
2. A very small fraction of these fulfil their natural reproductive function of transferring the male gamete to the female ovary: the vast majority fail to the ground.
3. 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.
4. 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.
5. 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.
6. Different pollen grains and spores can be identified to various taxonomic levels (e.g. species, genus, family).
7. In vegetated areas pollen is ubiquitous in lake and bog sediments. Very high concentrations (usually around 100,000-1,000,000/μm³) in the sediment permit efficient analysis and statistically robust results (standard pollen counts are usually ca. 300-1,000 grains per sample).
8. 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 sampled at the site at a point in time in the past.
9. If pollen assemblages are obtained from several levels through a sediment sequence, they provide a record, admittedly an indirect record, of the regional and local vegetation and their development near the sampled site at various times through the time interval represented by the sedimentary record (Fig. 1).
10. If two or more layers 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).

Knowledge of the flora and vegetation of the Palaeogene and Neogene (‘Tertiary’ and ‘Quaternary’) forests of Europe (Fig. 3) is critical for understanding the development of the current vegetation. The Quaternary period is the last 2.6 million years and is divided into two epochs: the Pleistocene (1.8 million years ago to 11,700 years ago) and the Holocene (11,700 years ago to the present day). During the Pleistocene, the Earth experienced several ice ages, with ice sheets covering parts of the northern hemisphere. The interglacial periods were warmer, allowing forests to spread southwards into regions that are now covered by ice sheets.

Europe’s forests in the Quaternary ice-ages

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

<table>
<thead>
<tr>
<th>Period</th>
<th>Epoch</th>
<th>Age (million years)</th>
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<tbody>
<tr>
<td>Quaternary</td>
<td>Pleistocene</td>
<td>1.8</td>
</tr>
<tr>
<td></td>
<td>Holocene</td>
<td>11,700</td>
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In other words, the distribution of forest vegetation during the Quaternary is complex and varied, with forests spreading and contracting in response to changes in climate. The presence of these forests is documented through pollen analysis, which provides a record of the vegetation that was present at the time the pollen was produced. This record can be used to infer past climates and environmental changes, which is crucial for understanding the development of the current vegetation.
The characteristic trees of the interglacial phases differ in their reproductive and asocial biology and ecological and competitive tolerances. Protopratic trees have high reproduction rates, low competitive tolerances, high rates of population increase, and display 'pioneer' and 'exploitation' traits. Mesopratic trees have low reproduction rates, high competitive tolerances, medium-low rates of population increase, arbuscular phosphorus-scavenging mycorrhiza, and 'late-successional', 'competitive', and 'saturation' traits. Oligopratic and telopratic trees are of medium reproductive rates, high competitive tolerances, medium-low rates of population increase, ectomycorrhiza with a phosphorus-mining strategy, and 'cold-stress tolerant' and 'adversity' traits.

Within these three broad groups of protopratic, mesopratic, and oligopratic and telopratic plants, the actual floristic and forest composition varies from interglacial to interglacial in north-western and central Europe. Factors such as location of refugia in the cryopratic phase, rates of spreading, distances over which spread occurred, competition, predation, genotypic variation, and chance as it affects survival, dispersal, and establishment may all have contributed to the observed differences in interglacial forest patterns. Similar cycles occurred in southern Europe, yet with substantial differences in comparison to central and north-western Europe. Due to warmer conditions, European tree species persisted locally, although strongly reduced, in the steppe-like environments of the glacial stages. This corresponds to the cryopratic phase in central and northern Europe. At the onset of an interglacial, corresponding to the protopratic phase in central and north-western Europe, temperate taxa (e.g. deciduous Quercus, Ulmus, Ostrya, hop-hornbeam, Carpinus) form open forests together with evergreen broad-leaved trees (e.g. Quercus ilex, holm oak, Olea europea, pistacia), and Mediterranean shrubs (e.g. Pistacia, pistacia), while boreal and steppe vegetation declines (e.g. Betula, Juniperus, Artemisia, wormwood, Chenopodiaceae goosefoot). In the following phase during the mid-interglacial, corresponding to the mesopratic phase in central and north-western Europe, warm-temperate and Mediterranean conifers (e.g. Abies, Pinus) expand into the broad-leaved deciduous and broad-leaved evergreen forests and arborescent cover increases, probably in response to rising moisture availability. Towards the end of the interglacial, corresponding to the oligopratic phase in north-western and central Europe, moisture-loving taxa such as Fagus, Alnus, and Abies gradually replace Mediterranean evergreen broad-leaved trees, while broad-leaved deciduous trees remain important. Finally, forest cover declines and steppe-like environments expand during the climatic deterioration at the transition from the interglacial to the next glacial (temperature decreases, reduced moisture), corresponding to the telopratic phase. There is an apparent order within interglacial forest patterns when viewed at the broad scale of the interglacial cycle of 100 000-15 000 years, whereas within each phase of an interglacial (ca. 5 000 years) there is often great variation between interglacials, hence the ability of pollen stratigraphy to differentiate between many of the different interglacials.

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

The mesopratic phase 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. Similarly, 5000-6000 years ago Abies disappeared from the Mediterranean and sub-Mediterranean lowlands of the Italian Peninsula, probably in response to excessive Neolithic deforestation by fire and by burning. As with Ulmus in England, Abies collapses were rapid, with pollen values of Abies halving within 13 and 22 years at sites in Italy and Swissland, respectively. In some areas of central and north-west Europe, forest clearance and the deposition of terracettes may have facilitated local colonisation and expansion of new immigrants such as Fagus sylvatica, beech, Picea abies Norway spruce, and possibly Carpinus betulus European hop-hornbeam. While the establishment of Fagus sylvatica and Carpinus betulus European hop-hornbeam during Mesolithic times followed climate change (cooling and a moisture increase) in southern and southern-central Europe, it is possible that the rapid spread of Fagus across central Europe in the last 4000-5000 years may have only been facilitated by the creation of abundant, large clearings within Quercus-dominated forests on well-drained soils. In some areas mixed Fagus–lex holly–Quercus forests developed whereas in other areas there was a rapid change from Filaro–Quercus–dominance to Fagus–dominance. 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 Fraxinus 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 Picea abies 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. Whatever its causes, the invasion of Pinus into northern 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.
and or abruptly when the dominant trees are replaced by other trees, usually in response to extrinsic environmental change or major disturbances (e.g. forest pathoses, fire, human activity). Nevertheless, few major forested ecosystems have persisted for more than 10,000 years and most are considerably younger, some developing only during the last phases of the last ice age. These forest systems are thus inevitably uncertain and historically contingent. Given the richness of forest-tree responses during the Quaternary with all its climatic fluctuations, extreme weather events, forest fires, land-use, outcomes, and ecological surprises are certainly possible. Assessing whether current forest systems are sustainable in the face of future global change is aided by considering the range of environmental variation over the time spans of the last 10,000 years. Such information, only recently directly inferred from the palaeoecological record, can thus help to identify critical environmental thresholds below which specific modern forest systems can no longer be sustained. The palaeoecological record for European forests provides several additional insights and important lessons from the past.

First, all existing forest systems have a finite time limit to growing in the places where they occur and all have been preceded by ecosystems (not necessarily forest systems) through which the process of composition, structure, plant-functional traits, and ecosystem properties have evolved. Second, similar forest ecosystems, as defined by their dominant species have developed in different places and within different environmental settings, which may have different antecedents in different places. Thus apparently similar systems may have different properties owing to different histories and to legacy effects of different antecedents. Fourth, different systems arose at approximately the same time in different places, presumably in response to regional- or global-scale shifts in atmospheric circulation involving climate shifts that led to widespread synchronous transformations of ecosystems. Their pattern is not, however, universal but rapid regime-shifts in the earth system may be accompanied by widespread ecosystem changes in diverse regions. Fifth, forest ecosystems of today have no long history even in the time span of the Holocene and many forest systems in the modern counterpart (‘analogues’). Examples include the former abundance of Corylus avellana in the early Holocene across much of north-west Europe, and the importance of Alnus in southern Europe in the mid-Holocene (see Box 3A).

Palaeoecologists look to the past whereas global-change ecologists look to the future, but both rely solely on their understanding of modern ecosystems and ecological processes as a basis for past reconstructions or future predictions. Palaeoecologists apply the concept that “the present is the key to the past” whereas global-change ecologists project this forward and use “the present is the key to the future”. But the present is only one-slice in the last 11,700 years since the last glacial age. A critical question is thus: how are today’s ecosystems and climate representative of tree and ecosystem-climate relationships under past or future climate change? Are they robust to climate conditions beyond modern states? Are species ranges in equilibrium with environmental factors such as climate or have the realised environmental niches of species been significantly affected by climatic and human activities? These palaeoecological questions suggest that it is inadequate to project future ecosystem conditions solely on the basis of present-day observations. A promising novel approach is to combine dynamic eco-physiological models with palaeoecological evidence to produce projections of future ecosystem dynamics under global-change conditions.

The dynamic nature and the often non-analogue character of European ecosystems means that it is unlikely that any present-day analysis or study could reasonably provide a complete list of possible future trajectories. However, the last 500 years raises critical questions about appropriate targets (‘baselines’) for restoration efforts. Palaeoecological studies have revealed major human impacts on many, if not all, systems in Europe and have shown that secular climate change has kept many forests moving at centennial to millennial time-scales. Ongoing rapid environmental changes may almost certainly ensure that many historical restoration targets will be unsustainable in the coming decades. Restoration efforts should aim to conserve or restore historical biodiversity, but more fundamentally to design and manage emerging novel ecosystems to ensure high biodiversity and a supply of ecosystem goods and services in the future.

The palaeoecological record of European forest and tree-fossil history is a rich and largely untapped record of ecological dynamics over a wide range of time-scales. As Karl Flinsche and Steve Jackson discuss, this record is a long-term ecological observatory where historical shifts in climate and the ecological legacy of societal activities can be deciphered, quantified, and used as a key to ‘understanding the biotic effects of future environmental change’. There is very much still to be learnt about past European forests using the vast amount of palaeoecological data available in Europe.

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