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 million 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 - 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 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.
Box 1: Principles of pollen analysis

- pollen grains and spores are produced in great abundance by plants
- 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
- 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
- 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
- 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
- different pollen grains and spores can be identified to various taxonomic levels (e.g. species, genus, family)
- in vegetated areas pollen is ubiquitous in lake and bog sediments. Very high concentrations (usually around 100,000 grains/m²) in the sediment permit efficient analyses and statistically robust results (standard pollen counts are usually ca. 300-1,000 grains per sample)
- 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
- 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, with the sampled site at various times through the time interval represented by the sedimentary record
- if two or more series of pollen assemblages are obtained from several sites, it is possible to study changes in past pollen assemblages and hence in the regional and local vegetation between both time space (Figs. 2 and 3)

European forests to the Quaternary ice-ages

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

<table>
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<tr>
<th>Period</th>
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<th>Age (million years)</th>
</tr>
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<tbody>
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</tr>
<tr>
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<td>Eocene</td>
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</tr>
<tr>
<td>Palaeocene</td>
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Knowledge of the Flora and vegetation of the Palaeogene and Neogene (‘Tertiary’) has been intensively studied (Table 1 for an outline of the relevant geological time scales) is very fragmented due to the shortage of fossiliferous sedimentary sequences in Europe. Following the tropical and sub-tropical Palaeocene, Eocene (Oligocene, and Miocene epochs 46-5.3 million years ago when plants (e.g. Alpinia palma) found it possible in the tropical lowlands of the Indo-Malaya region occurred in north-west Europe, the European tree flora of the Pliocene epoch (5.3-2.6 million years ago) contained many genera characteristic of modern European forests (e.g. Quercus oak, Carpinus hornbeam, Fagus beech, Pinus pine, Picea spruce, Alnus willow) in some regions of south-east Turkey, Tajikistan, Uzbekistan, and Kazakhstan. There is an increase in evidence from macrofossils and charcoal remains in central, eastern, and northern Europe that cypress trees such as Pinus, Picea, and L. larch may have grown locally in such microforests during the LGM, along with Betula birch, Salix willow, and possibly Alnus alder, Populus aspen, and Ulmus elm, which are typical of the northern European temperate ice-sheet in Russia at 60°N (12, 44), but see (30) for a contrasting view.

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 phase, which their relative abundances may vary from one interglacial to another, there are such strong ecological similarities that the Danish pollen analyst Johann Vermeersen recognised in 1958 an interglacial cycle defined by four or five ecological phases (Fig. 2 and 4F, 14). The cryophilous phase represents the cold and dry, often glacial, stage with sparse assemblages of pioneer, arctic-alpine, steppe, and eucalyptus herbs growing on arid, nutrient-poor mineral soils, frequently disturbed and wind-ice activities. Trees are absent, except in specialised refuges.

At the onset of an interglacial, temperature and moisture rise and the protoecosystem begins. Base-demand shade-intolerant herbs, shrubs, and trees (e.g. Betula, Salix, Populus, Pinus, Juniperus juniper, Sorbus aucuparia) invaginate into formerly glacially opened areas and expand to form a mosaic of grassland, scrub, and open woodland growing on unsealed, fertile soils rich in nitrogen and phosphorus and with a low humus content (Fig. 1). The mesophytic 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, e.g. in openings caused by fire, wind-throw, and, possibly, grazing megaherbivores. The next phase of the oligocryophyte, comprises open conifer-dominated woods (Pinus, Picea, Abies), Ericaceous heaths, and bog vegetation growing on gently sloping, well-drained, nutrient-rich podsol and peatlands. Climatic deterioration (temperature decreases, reduced moisture, etc.) occur in the final telediocryophyte phase and, most especially, at the onset of the next glacial cryophyte phase as forests decline, fire action and snowdrift destroy the tundra and eucalyptus herb communities, and herb species expand on the newly exposed mineral soils. The telediocryophyte forest is very similar to the oligocryophyte phase except that as the climate cools toward the end of the interglacial, old-growth, deciduous, herb-rich forests become more common and the broadleaved deciduous and coniferous tree species, e.g. Betula, Alnus, and Fagus decline. These ecological phases within an interglacial are not synchronous between sites because the onset of a phase such as the oligocryophyte phase may depend on local site features such as bedrock geology, topography, climate, and land-use.
Europe's forests in the Holocene (11 700 years ago–today)

The mesophytic forest 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 2i). 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 disturbance and the transition from the interglacial to the next glacial (temperature decreases, reduced moisture availability). Towards the end of the interglacials, forest cover declines and steppe-like environments expand. This corresponds to the protocyclopean phase in central and northern Europe. At the onset of an interglacial, corresponding to the protocyclopean phase in central and northern 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 europaea olive) and Mediterranean shrubs (e.g. Pistacia pitaush). While boreal and steppe vegetation declines (e.g. Betula, Juniperus, Artemisia wormwood), Chenopodiaceae goosefoot appears in this phase during the mid-interglacial, corresponding to the mesocyclopean phase in central and northern-west Europe, warm-temperate and Mediterranean conifers (e.g. Abies, Pinus) expand into the boreal-decidual deciduous and broad-leaved evergreen forests and arboreal cover increases, probably in response to rising moisture availability. Towards the end of the interglacials, corresponding to the oligocyclopean 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 telocyclopean phase. There is an apparent order within interglacial forest patterns when viewed at the broad scale of an entire interglacial cycle of 10000-15000 years, whereas within each phase of an interglacial (ca. 5000 years) there is often great variation between interglacials, hence the ability of pollen stratigraphy to differentiate between many of the different interglacials.

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In general, disturbance-sensitive taxa such as Tilio, Ulmus, Ficusus, Acer maple, Abies, and Hedera ivy declined while disturbance-resistant taxa such as Quercus, Ostrya, Corylus, Betula, Alnus, Salix, Fagus (re-sprouters), and Picea (non-palatable) expanded. Quercus, Fagus, and Picea were also favoured by humans for their valuable acorns or timber, ultimately forming manocropic successions. Continued forest clearances and agriculture, interspersed by periods of abandonment and reforestation, have resulted in a continuous dynamic of tree survival in refugia that are so characteristic of the Quaternary (Pleistocene, Holocene).

Why is European forest history important to us? Why is it important to understand the past? What lessons ‘from the past’ can be learnt from the ever-changing composition, structure, and extent of forests in Europe? We see that European forests have been changing since the Palaeogene, with progressive extinction from Europe of trees of the so-called Arot-Tertiary geoflora in the Pliocene and early Pleistocene. The repeated glacial-interglacial cycles, that are so characteristic of the Quaternary, have resulted in a continuous dynamic of tree survival in refugia that are so characteristic of the Quaternary (Pleistocene, Holocene). Forests have become abundant and dominant at specific areas under particular environmental conditions.

And how have ecological processes during the past millions of years changed, and are these changes relevant to our current and future research? Dynamic questions of these kind require us to produce palaeo-validated scenarios of future vegetation dynamics under global change conditions.

References

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Fig. 5: Dense evergreen oak forest (Quercus ilex) south of Gorgo Basso. This vegetation type is representative of natural conditions in coastal Sicily prior to human-induced creation of maquis vegetation (Fig. 4). Forest vegetation survival on rocky calcareous slopes less suited for agriculture...

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