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, 15000, 150000, 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 15000 years of the late-Quaternary. Von Post had the idea of expressing fossil pollen assemblages as percentages of the sum of pollen grains of the late-Quaternary. Swedish geologist Lennart von Post - was and still is the dominant technique in the Quaternary period, especially the last 15000 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 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. 5000 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. 5000, 6000, 7000 years ago). When the value of a particular pollen type exceeds a certain threshold value it can be interpreted as reflecting the first expansion of that taxon at different sites (Fig. 3). This 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.

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/Myrtonus (hazel/birk myrtle) indicate when these trees or shrubs are inferred to have first expanded near this site. Cryocratic taxa are coloured red and stippled. These taxa become abundant again in the open conditions of the Holocene phase where they are shown in plain red. Protoxeric trees are coloured black, mesoxeric trees are green, diacheiroxeric and halobatic taxa are orange, and taxa associated with human activity and the Holocene saproxylic 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.

![Image of pollen diagram](https://example.com/image1.png)

![Image of 'isopollen' maps](https://example.com/image2.png)

![Image of 'isochrone' maps](https://example.com/image3.png)
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 began about 2.6 million years ago. What were European forests like prior to the Quaternary?

Knowledge of the flora and vegetation of the Palaeoence and Neogene (‘Tertiary’ or early-middle Miocene) forests (Table 1) is based on studies of the pollen records (Figs. 2 and 3) for an outline of the relevant geological time scales) is very fragmentary due to the shortage of fossiliferous sedimentary sequences in Europe. Following the tropical and sub-tropical Palaeoence, Eocene (Eocene, Miocene, and Mioene epochs (166-5.3 million years ago) when plants (e.g. Alpina palma) found today 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, Abies fir) as well as genera growing today in eastern Asia and/or eastern North American (e.g. Pterocarya wing-nut, Liriodendron tulip-tree, Tsuga hemlock, Liquidambar sweetgum, Nyssa blackgum, Sequoia redwood, Taxodium cypress, Magnolia magnolia, Carya hickory, Clithera pepper-bush, Engelhardia, Aesculus chestnut). These trees belong to the so-called Arcto-Tertiary geoflora that in the Neogene existed widely in the Northern Hemisphere across North America, Europe, and Asia. This geoflora was first defined by J.S. Gardner and C. Ettinghausen in 1869. The successive loss of these taxa during the Pliocene epoch and the early Pleistocene of western Europe and America, Europe, and Asia is defined by the American botanist Asa Gray (1810-88). The cool phases of the early- or mid-Quaternary ice activities. Trees are absent, except in specialised refugia. As a result of the last glacial maximum (LGM) many of these taxa during the LGM, along with other coniferous and deciduous trees such as Pinus pine, and Picea spruce, have survived the last glacial maximum (LGM) in relatively narrow refugial elevational belts (ca. 500-800m) in the mountains of western Asia, Europe, and southern Europe (including the Caucasus) and possibly in parts of western Asia. These belts lay between lowland xeric, steppe-like vegetation too dry for tree growth and high-elevation tundra-like vegetation, or permanent snow or ice, too cold for tree growth. Such mid-elevation belts of trees can be seen today in the Andes, American Rockies, the Himalayas, the Tagus basin in Sichuan and Qinghai, in the Zagros mountains of Iran, and in parts of south-east Turkey, Tajikistan, Uzbekistan, and Kazakhstan.

At the onset of an interglacial, temperature and moisture rise and the proto-cryophytic phase begins. Basal-dominating shade-intolerant herbs, shrubs, and trees (e.g. Betula, Salix, Populus, Pinus, Juniperus, and Sorbus aucuparia) immigrate into formerly glaciated areas and form a mosaics of grassland, scrub, and open woodland growing on unglaciated areas, valley corridors in cold stages and to spread northward during temperate intervals. As a result of the west-eastern and the relatively cold stages in the late Pliocene and early Pleistocene, Europe lost many trees or their close relatives that today are found in the warm-temperate-subtropical ‘evergreen forest’ of south-eastern China. These were largely replaced by trees of the temperate ‘mixed mesophytic forest’. Many taxa had already disappeared at the beginning of the Quaternary (e.g. Liquidambar, Melosoma, Pseudolofira false larch, Stenwarl), while others survived longer (e.g. Liriodendron, Magnolia, Taxodium, Sequoia, Phellodendron cork tree, Tsuga, Caryya) to vanish finally from Europe during the course of the early- or mid-Quaternary.

Europe’s forests during the 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 relative abundances of the taxa may vary from one interglacial to another, there are such strong ecological similarities that the Danish pollen analyst Johannes Værnæs recognised in 1958 an interglacial cycle consisting of four or five ecological phases (Fig. 2 and Fig. 4) and the cryophytic 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 snow or ground-ice activities. These are absent, except in specialised refugia. The onset of an interglacial, temperature and moisture rise and the proto-cryophytic phase begins. Base-dominating shade-intolerant herbs, shrubs, and trees (e.g. Betula, Salix, Populus, Pinus, Juniperus juniper, Sorbus aucuparo) immigrate into formerly glaciated areas and form a mosaics of grassland, scrub, and open woodland growing on unglaciated areas, valley corridors in cold stages and to spread northward during temperate intervals. As a result of the west-eastern and the relatively cold stages in the late Pliocene and early Pleistocene, Europe lost many trees or their close relatives that today are found in the warm-temperate-subtropical ‘evergreen forest’ of south-eastern China. These were largely replaced by trees of the temperate ‘mixed mesophytic forest’. Many taxa had already disappeared at the beginning of the Quaternary (e.g. Liquidambar, Melosoma, Pseudolofira false larch, Stenwarl), while others survived longer (e.g. Liriodendron, Magnolia, Taxodium, Sequoia, Phellodendron cork tree, Tsuga, Caryya) to vanish finally from Europe during the course of the early- or mid-Quaternary.

Europe’s forests in the Quaternary period

The Quaternary period (last 2.6 million years) witnessed very marked and widespread climatic and environmental changes. Large terrestrial ice-sheets started to form in the Northern Hemisphere about 2.75 million years ago, resulting in multiple (at least 50) glacial-interglacial cycles driven by secular variations in insolation as a result of periodic fluctuations in the Earth's orbit. Glacial-stage conditions account for 80% of the Quaternary whereas the remaining 20% consists of shorter interglacial stages during which conditions were similar to, or slightly warmer than, the present day. During the glacial stages, environmental conditions were very different from the present interglacial (Holocene or post-glacial plus the recent anthropocene) in which we live today. Much of the region north of 40° N was covered by large terrestrial ice-sheets and widespread permafrost with temperatures possibly 10-25 ° C lower than present. High aridity and temperature 2-5 ° C lower than today were features of low-latitude areas. Global atmospheric CO2 concentrations were as low as 180 ppm during glacial stages, rising to pre-industrial levels of 280 ppm in interglacial stages. Given these extreme conditions in the glacial stages that cover 80% of the last 2.6 million years, it is an obvious question how did European forest trees survive these repeated long glacial-stage conditions and where did they grow in the glacial stages? The evidence we have suggests that many European trees survived the last glacial maximum (LGM) in relatively narrow refugial elevational belts (ca. 500-800m) in the mountains of southern Europe (including the Caucasus) and possibly in parts of western Asia. These belts lay between lowland xeric, steppe-like vegetation too dry for tree growth and high-elevation tundra-like vegetation, or permanent snow or ice, too cold for tree growth. Such mid-elevation belts of trees can be seen today in the Andes, American Rockies, the Himalayas, the Tagus basin in Sichuan and Qinghai, in the Zagros mountains of Iran, and in parts of south-east Turkey, Tajikistan, Uzbekistan, and Kazakhstan.

There is increasing evidence from macrofossils and charcoal remains in central, eastern, and north-eastern Europe that coniferous trees such as Pinus pine, and Picea spruce have grown locally in such microrefugia during the LGM, along with Betula birch, Salix willow, and possibly Alnus alder, Populus aspen, and Ulmus elm, and may have formed the northern edge of the largest ice-sheet in Russia at 60° N (42, but see 44 for a contrasting view).
The characteristic trees of the interglacial phases differ in their reproductive and asymptotic biology and ecological and competitive tolerances. Protocytic trees have high reproductive rates, low competitive tolerances, high rates of population increase, and display ‘pioneer’ and ‘exploitation’ traits. Mesocytic 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. Oligocytic and telocytic trees are 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 protocytic, mesocytic, and oligocytic and telocytic 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 cryptic 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 environment of the glacial stages. This corresponds to the cryptocytic phase in central and northern Europe. At the onset of an interglacial, corresponding to the protocytic phase in central and north-western Europe, temperate taxa (e.g. deciduous Quercus, Ulmus, Ostrya hornbeam, Carpinus) form open forests together with evergreen broad-leaved trees (e.g. Quercus ilex, holm oak, Olea europeae olive) and Mediterranean shrubs (e.g. Pistacia palaestina), while boreal and steppe vegetation declines (e.g. Betula, Juniperus, Artemisia wormwood, Chenopodaceae goosefoot) in the following phase during the mid-interglacial, corresponding to the mesocytic 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 arboreal cover increases, probably in response to rising moisture availability. Towards the end of the interglacial, corresponding to the oligocytic 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 telocytic phase. There is an apparent order within interglacial forest patterns when viewed at the broad scale of an entire interglacial cycle of 10 000-15 000 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 mesocytic phase in the Holocene interglacial stage was greatly modified about 5 000-6 000 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 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, 5 000-6 000 years ago Abies disappeared from the Mediterranean and sub-Mediterranean lowlands of the Italian Peninsula, probably in response to excessive Neolithic disturbance by fire and by browsing. 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 Italian Switzerland, respectively. In some areas of central and north-west Europe, forest clearance and reforestation of cleared lands may have facilitated local colonisation and expansion of new immigrants such as Fagus sylvatica European beech, Picea abies Norway spruce, and possibly Carpinus betulus European hornbeam. While the establishment of Fagus sylvatica 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 4 000-5 000 years may have only been facilitated by the creation of abundant, large clearings within Tilia- or 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 Tilia- or Fagus-dominated 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 oakfium 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 6 000-7 000 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 Picea into northern and central Fennoscandia over the last 6 000-7 000 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.
In general, disturbance-sensitive taxa such as Tilia, Ulmus, Fraxinus, Acer maple, Abies, and Hedera ivy declined while disturbance-resistant taxa such as Quercus, Ostrya, Corylus, Betula, Alnus, Salign, Fagus (ex-sprouters), and Picea (non-palatable) expanded. Quercus, Fagus, and Picea were also favoured by humans for their valuable acorns or timber, ultimately forming monospecific forests. Few major forest areas existed in the past and by reconstructing the environmental conditions under which these systems were initiated and developed. A narrow time window (e.g. 200-500 years) underestimates the range of variation within which a forest system is sustainable, and this underestimates the risk of major disruption of the system by environmental change.5,6 Longer time periods (e.g. 1,000-2,000 years) inevitably increase the inherent range of natural variation in the earth system.5 Many systems disappear, as shown by the palaeoecological record, when the time window extends to 10,000-15,000 due to major changes in the Earth’s climate system due to orbital forcing.5 The palaeoecological record can pinpoint the time of origin of particular forest systems (e.g. 5,6,10) and can, by inference in some cases, indicate the specific environmental changes that led to the development of the system and the range of environmental variation under which the system maintained itself in the past. Such information, only obtainable from the palaeoecological record, can thus help to identify critical environmental thresholds beyond which specific modern forest systems can no longer be sustained.5

The palaeoecological record for European forests provides several additional insights and important lessons from the past.5 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) that had a completely different composition, structure, plant-functional traits, and ecosystem properties.5,6 Second, similar forest ecosystems, as defined by their dominant species have developed in different places and at different times. These systems had 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 climatic shifts that led to widespread synchronous transformations of ecosystems. This pattern is not, however, universal but rapid regime-shifts in the earth system may be accompanied by widespread ecosystem changes in diverse regions.5,4,5,45 Fifth, forest ecosystems of today have no long history even in the time span of the Holocene and the many forest compositions in modern counterparts are ‘analogues’.5,6,44 Examples include the former abundance of Corylus avellana in the early Holocene across much of north-west Europe,44 and the importance of Abies alba in southern Europe in the mid-’Arctic’ (see Box 3).5,18

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-the last 11,700 years since the last glacial stage. A critical question is thus are today’s ecosystems and climate representative of tree and ecosystem-climate relationships under past or future climate change? Are they robust to climate changes beyond modern states? Are species ranges in equilibrium with environmental factors such as climate5 or have the realised environmental niches of species been significantly altered by climate-change driven by human activities? These palaeoecological questions suggest that it is inadequate to project future ecosystem conditions solely on the basis of present-day observations.5,45 A promising novel approach is to combine dynamic eco-physiological models with palaeoecological evidence to produce palaeo-ecological reconstructions of future vegetation dynamics under global-change conditions.4,5,18,19

The dynamic nature and the often non-analogue character of European forest systems is also seen in the palaeoecological record. Even the last 5,000 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.5,18,20,45,46 and have shown that secular climate change has kept many forests moving at centennial to millennial time scales.5,18,45,46 Ongoing rapid environmental changes may almost certainly ensure that many historical restoration targets will be unsustainable in the coming decades.5,45 Restoration efforts should aim to conserve or restore historical patterns, but more flexible, plastic design and management of forest ecosystems is likely to produce globally novel ecosystems to ensure high biodiversity and a supply of ecosystem goods and services in the future.45

The palaeoecological record of European forest and tree species has a rich and largely untapped record of ecological dynamics over a wide range of timescales. As Karl Flies and Steve Jackson discuss, this record is a long-term ecological observation where historical forest vegetation and the ecological legacies of societal activities can be deciphered, quantified, and used as a key to ‘understanding the biotic effects of future environmental change’.5,45 There is very much still to be learnt about past European vegetation by using the vast amount of palaeoecological data available in Europe.5,45,11,28,29,30,31,32,33,34,35,36,37,38,39,40,41,42,43,44,45,46

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