Past forests of Europe

H. J. B. Birks, W. Tinner

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 types vary with depth, and hence age, in the sedimentary sequence. 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. 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 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 the true absence of a 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 fitchii, Quercus (oak), Alnus (alder), and Corylus/Myrica (hazel/bog myrtle) indicate where 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 sapropel phase where they are shown in plain red. Protocryatic taxa are coloured blue, and mesocratic taxa are green. Diagenetic and lithocryatic taxa are orange, and taxa associated with human activity and the Holocene sapropel 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 4.3)
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. 300-1 000 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 in time in the past.

ix. 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).

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 spanned about 2.6 million years. What were European forests like prior to the Quaternary?

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Knowledge of the Flora and vegetation of the Palaeoaege and Neogene (‘Tertiary’) period is generally limited (see Table 1 for a list of the relevant geological time scales) as it is very fragmentary due to the destruction of fossiliferous sedimentary sequences in Europe. Following the tropical and sub-tropical Palaeoaege, Eocene, Oligocene, and Miocene epochs (165-5.3 million years ago) when plants (e.g. Alpe palma) found today in the tropical lowlands of the Indomalaya region occurred in northwest 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 northern America (e.g. Picea spruce, Liriodendron tulip-poplar, Tsuga hemlock, Liquidambar sweetgum, Nyssa blackgum, Sequoia redwood, Taxodium cypress, Magnolia magnolia, Carya hickory, Clethra 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. Gardiner and C. Ettingshausen in 1869. The successive loss of this flora during the Pliocene (about 5 million years ago) caused the Quaternary and their restriction today to two almost opposite areas of the globe (eastern Asia and eastern North America) is explained by the hypothesis explicitly presented in the 1850s by the American botanist Asa Gray (1818-1888). The cool phase within the late Pliocene epoch and the subsequent Pleistocene continental glaciations, combined with the changes of glacialized mountains (e.g. Pyrenees, Alps, Carpathians, Caucasus mountains) and the Mediterranean Sea provided barriers to the southward and northward retreat of the Arcto-Tertiary geoflora resulting in their progressive extinction in Europe. In contrast, the mountain chains and valleys of south-eastern Asia (e.g. Yunnan) and North America (e.g. Appalachian, Rocky Mountains) run north-west to south-east or north to south reaching low latitudes without sea barriers, thereby permitting temperate and warm temperate trees to spread southward along unglaciated areas or valley corridors in cold stages and to spread northward during temperate intervals. As a result of the west-east barriers and the relatively cold climates in the last 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, Melissosma, Pseudolarix false larch, Stenoba), while others survived longer (e.g. Liriodendron, Magnolia, Taxodium, Sequoia, Phellodendron cork tree, Tsuga, Coryl) 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 and environmental change (Fig. 3).

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 around the sun. 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 anthroposphere) 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 cooler 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, an obvious question is 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, Asian Rockies, the Himalayas, the west of the Sino-Himalayan region, and the Tien Shan in Kazakhstan. Trees may also have occurred scattered in moist sites (water seepages, ravines), so-called ‘cryptic’ or ‘micro’ refugia in the Mediterranean (e.g. Pinus pine, Larix larch) and in the Zagros mountains of Iran, and in parts of south-east Turkey, Tadjikistan, Uzbekistan, and Kazakhstan. There is increasing evidence from macrofossils and charcoal remains in central, eastern, and north-eastern Europe that conifer trees such as Pinus pine, Larch may have grown locally in such microrefugia during the LGM, along with Betula birch, Salix willow, and possibly Alnus alder, Populus aspen, and Ulmus elm. As the climate improved, the northern limits of the northernmost ice-sheet in Russia at 60° N (14, 22), but see (23) 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 stage. The pattern of vegetation change may vary from one interglacial to another, there are such strong ecological similarities that the Danish pollen analyst Johannsen recognised in 1958 an interglacial cycle consisting of four or five ecological phases (Iversen 2002 and Fig. 4D). The cryocratic phase represents the cold and dry, often glacial stage, with sparse组装es of pioneer, arctic-alpine, steppe, and ruderal herbs growing on skeletal mineral soils, frequently disturbed by ground-activity and bioturbation. Plants are absent, except in specialised refugia. At the onset of an interglacial, temperature and moisture rise and the proteophagic phase begins. Base-demanding shade-intolerant herbs, shrubs, and trees (e.g. Betula, Salix, Populus, Pinus, Juniperus juniperus, Sorbus aucuparia) invagrate into formerly glacial and acid areas 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 fauna. The next phase, the oligocratic phase, comprises open conifer-dominated woods (Pinus pine, Picea spruce), Ericaericous heaths, and bog vegetation on intermittently wet mires with phosphorus-rich podsol soils and peats. 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 fertile podsol soils and peats, 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, mountain and maritime trees grow on open mountain tops (e.g. Larix larch, Pinus pine, Abies fir, Juniperus juniperus, Betula birch, Alnus alder). Such mid-elevation belts of trees can be seen today in the Andes, Asian Rockies, the Himalayas, the west of the Sino-Himalayan region, and the Tien Shan in Kazakhstan.
Europe's forests in the Holocene (11 700 years ago–today)

The mesic 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 step 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 central England.

Similarly, 5000–6000 years ago Abies disappeared from the Mediterranean and sub-Mediterranean lowlands of the Italian Peninsula, probably in response to excessive anthropogenic disturbance creating gaps in forest cover. Abies had been a dominant species of Mediterranean forests in the early interglacial stage (c. 5000 years) and was often associated with other species such as Quercus ilex and Pistacia lentiscus (Box 2). Whatever its cause, the invasion of Pinus into northern and central Fenno-Scandia over the last 6000–7000 years resulted in major changes in forest composition and structure in central and northwestern Europe.

Box 2: Glacial-interglacial phases in north-west Europe

The glacial-interglacial cycle showing the broad changes in biomass, soil, and temperature that take place during a glacial (cyclopic) stage and associated interglacial stage. The phases of the interglacial (protocric, mesocric, oligocric, and telocric) are shown along with the dominant soil features.

Cryocric:
- glacial stage
- aspen, balsam poplar, birch, spruce, and larch
- skeletal mineral soils

Protocric:
- early interglacial stage
- rich assemblages of herbs, shrubs, and trees (birch, pine, willow)
- unashed fertile soils

Mesocric:
- mid interglacial stage
- temperate deciduous forests
- fertile brown-earth soils

Oligocric & Telocric:
- late interglacial stage
- open conifer (spruce, pine), encarcaceous heaths, bogs
- infertile, humus-rich podsol and peats

Unique to the Holocene

Homo sapiens:
- mid late Holocene (6000 years ago–present)
- forest clearance, agriculture
- range of soil types, often fertilised

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

Simulation 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 extinct vegetation types which were growing in the past at the site before anthropogenic disturbance became excessive.

a) Present-day (1950–2000 AD) mean monthly temperature (+1 standard deviation) and average total monthly precipitation at Lago di Massaciuccoli close to Pisa (Tuscany).

b) Map of Italy and Switzerland with Lago di Massaciuccoli denoted by a black star, red star shows position of Gorgo Basso in southern Sicily (Fig 4).

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 simulated at Lago di Massaciuccoli with LANDCLIM, a dynamic vegetation model with d) present climate and future climate e) All vegetation models were initialized 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.

Simulations of today’s vegetation under low disturbance shows Abies abies co-dominates with Quercus ilex (see right image) in the Mediterranean forest. This vegetation type disappeared during the late Holocene most likely in response to extreme anthropogenic burning and land use. In agreement, simulations show the disappearance of this vegetation type under current climate with moderate land use. Future climate and vegetation conditions at Lago di Massaciuccoli are comparable to present climate and vegetation conditions at Gorgo Basso, southern Sicily (Fig 5). With low land use, evergreen oak forest will prevail, while under moderate land use forests will be reduced and maquis (low biomass) will expand.

In some areas of central and north-west Europe, forest clearance and the use of covering clearings may have facilitated local colonisation and expansion of new immigrants such as Fagus sylvatica, Abies alba, Picea abies, Pinus sylvestris, and, possibly Carpinus betulus European hornbeam. While the establishment of Fagus is strongly linked to warming 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 Ulmus or Quercus-dominated forests on well-drained soils. In some areas
or abruptly when the dominant trees are replaced by other trees, usually in response to extrinsic environmental change44 or major disturbances (e.g. forest pathogens, fire, human activity)45. Few major forestal systems have existed for more than 10 000 years and most are considerably younger: some developing only after the last few centuries. These forestal systems are thus inevitably uncertain and historically contingent. Given the richness of forest-tree responses during the Quaternary with all its climatic and environmental fluctuations, outcomes, and ecological surprises are certainly possible.46

Assessing whether current forest systems are sustainable in the face of future global change is aided by considering the range of environmental variation in the time-trees of the past. Such information, only obtainable from the palaeoecological record, can thus help to identify critical environmental thresholds below which specific modern forest systems can no longer be sustained.47

The palaeoecological record for European forests provides several additional insights and important lessons from the past.48

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 formed composition, structure, plant-functional traits, and ecosystem properties.49, 50. Second, similar forest ecosystems, as defined by their dominant species have developed in different places and at different times. Even forest systems had different antecedents in different places. Thus apparently similar systems may have different properties owing to different histories and to legacies effects of different antecedents.40, 51. 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.41

This pattern is not, however, universal but rapid regime-shifts in the earth system may be accompanied by widespread ecosystem changes in diverse regions.42, 52. Fifth, forest ecosystems of today have no long history even in the time span of the Holocene and thus little forest system-ecosystem-climate-rural counterparts (‘analogues’)43. Examples include the former abundance of Corylus avellana in the early Holocene across much of north-west Europe44 and the importance of Abies alba in southern Europe in the mid-Holocene (see Fig. 3a).45

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.46 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 stage. A critical question is thus 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 climate47 or have the realised environmental niches of species been significantly altered by human activities?48

These palaeoecological questions suggest that it is inadequate to project future ecosystem conditions solely on the basis of present-day observations49. A promising novel approach is to combine dynamic eco-physiological models with palaeoecological evidence to produce palaeoecological models of future vegetation dynamics under global-change conditions.46

The dynamic nature and the often non-analogue character of European forests over the last 5000 years also raises critical questions about appropriate targets (‘baselines’) for restoration efforts. Palaeoecological studies have revealed major human impacts on many, if not all, systems in Europe50 and have shown that secular climate change has kept many trees moving at centennial to millennial time scale.51, 52. Ongoing rapid environmental changes may almost certainly ensure that many historical restoration targets will be unsustainable in the coming decades.53 Restoration efforts should aim to conserve or restore historical floristic composition, but move towards an ecosystem design and management that can cope with the changes that are inevitable.54

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