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 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 5,000, 10,000, 15,000, 100,000, 15 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 (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 expansion 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.
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 fulfil 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/cm³) 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 one, 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. 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 intermediate temperate interglacial stages spanned about 2.6 million years ago. What were European forests like prior to the Quaternary?

Knowledge of the flora and vegetation of the Palaeogene and Neogene (‘Tertiary’) in Europe (Table 1) is limited to an estimated 2.6 million years before present (2.6 My) or 0.8 million years before present (0.8 My) in western and central Europe. In the region east of the Urals, and the craton of Asia, the record is fragmentary (Figs. 2 and 3), as the Siho-Minhalay region, and the Tien Shan in Kazakhstan have been covered by large terrestrial ice-sheets and widespread permafrost with temperatures possibly 15-20 °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 forests survive these repeated long glacial-stage conditions and where did they grow in the ice ages?

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 Asia11. 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 and the Hailuogou National Park of Sichuan and Qinghai, in the Zagros mountains of Iran, and in parts of south-east Turkey, Tajikistan, Uzbekistan, and Kazakhstan12. There is increasing evidence from macrofossils and charcoal remains in central, eastern, and north-eastern Europe that conifer trees such as Pinus, Picea, and 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, which together with the northern alder genus Alnus linden may extend as far north as the north-eastern edge of the present day forest-ice-sheet in Russia at 60° N13, but see 14 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 (Table 2). Of course the environmental conditions may vary from one interglacial to another, there are such strong ecological similarities that the Danish pollen analyst Johannes Iversen recognised in 1958 an interglacial cycle consisting of four or five ecological phases (Iversen 1958a, 1958b)47. The cold 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, frequent fire and disturbed ground-ice activities. Trees are absent, except in specialised refugia.

At the onset of an interglacial, temperature and moisture rise and the protoecophase begins. Base-demand shade-intolerant herbs, shrubs, and trees (e.g. Betula, Salix, Populus, Pinus, Juniperus, and Quercus) immigrate into formerly glaciated areas and form a mosaic of grassland, scrub, and open woodland growing on unbleached, fertile soils rich in nitrogen and phosphorus and with a low humus content (Fig. 1). The mesoecophase 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-herds37. The next phase, the ooligocryptophase, comprises open conifer-dominated woods (Pinus, Picea, Abies), ericaceous heaths, and bog vegetation. The forest is expressed in 1958b as dominated by spruces and fir at the northernmost limit of Pinus, Picea, Abies dominated woods (Fig. 3). The cold phase or ooligocryptophase is characterised by the development of temperate deciduous forests of Quercus, Ulmus, Tilia, 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-herds37. The next phase, the ooligocryptophase, comprises open conifer-dominated woods (Pinus, Picea, Abies), ericaceous heaths, and bog vegetation. The forest is expressed in 1958b as dominated by spruces and fir at the northernmost limit of Pinus, Picea, Abies dominated woods (Fig. 3).
The characteristic trees of the interglacial phases differ in their reproductive and assodual biology and ecological and competitive tolerances. Proctoecic trees have high reproduction rates, low competitive tolerances, high rates of population increase, and display pioneer and ‘exploitation’ traits. Mesocratic trees have low reproduction rates, high competitive tolerances, low-medium rates of population increase, arbuscular mycorrhizal mycorrhiza, and ‘late-successional’, ‘competitive’, and ‘saturation’ traits. Oligocritic and telocratic trees have medium reproduction rates, high competitive tolerances, low-medium rates of population increase, ectomycorrhizal with a phosphorus-mining strategy, and ‘cold-stress tolerant’ and ‘adversity’ traits.

Within these three broad groups of protocotic, mesocratic, and oligocritic and telocratic plants, the actual floristic and forest composition varies from interglacial to interglacial in north-western and central Europe. Factors such as location of refuge in the cryocritic 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 cryocritic phase in central and northern Europe. At the onset of an interglacial, corresponding to the protocritic 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 europaea olive) and Mediterranean shrubs (e.g. Pistacia pista pistachio), 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 mesocratic 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 oligocritic 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 stage (temperatures decreased, reduced moisture), corresponding to the telocritic phase. There is an apparent order within interglacial forest patterns when viewed at the broad scale, i.e. the mid-interglacial to the next glacial 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 mesocratic 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. Whatever its cause, the invasion of Picea 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.

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 (cryocritic) stage and associated interglacial stage. The phases of the interglacial (protocritic, mesocratic, oligocritic, and telocritic) are shown along with the dominant soil features.

Cryocritic:
- glacial stage
- sparse assemblages of pioneer, arctic-alpine, steppe, and nyalard plants
- skeletal mineral soils

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

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

Oligocritic & Telocratic:
- late interglacial stage
- open conifer (spruce, pine), encasuces heaths, bogs
- infertile, rushy-rich podsol soils and peats

Unique to the Holocene

Home 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

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 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) Present climate (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 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.

Simulations of today's vegetation under low disturbance shows Abies abies co-dominant with Quercus ilex (see right image) in the Mediterranean forest. This vegetation type disappeared during the late Holocene from north to central Europe. 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.
and have shown that secular climate change has kept many resources moving at centennial to millennial time-scales. 109, 110 Ongoing rapid environmental changes may almost certainly ensure that many historical restoration targets will be unsustainable in the coming decades. 111 Restoration efforts should aim to conserve or restore historical patterns, but more often design and manage emerging novel ecosystems to ensure high biodiversity and a supply of ecosystem goods and services in the future. 112

The palaeoecological record of European forest and tree history is a rich and largely untapped record of ecological dynamics over a wide range of time-scales. As Karl Fließa and Steve Jackson 47, 48 discuss, this record is a long-term ecological observatory where historical changes 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. 113 There is very much still to be learnt about past European forests, judging the vast amount of palaeoecological data available in Europe. 114

Acknowledgement:
We are very grateful to Cathy, Jenks for preparing this text and figures in a very short time and for her meticulous editing.