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, 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 of the late-Quaternary. European forests have varied in their composition, structure, and extent to the forests of Europe today?

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. 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 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/ml) in the sediment permit efficient analyses and statistically robust results (standard pollen counts are usually ca. 300-1000 grains per sample)

viii. If two or more series of pollen assemblages are obtained from a peat or lake sample, a sedimentological analysis of the sediments sampled to create 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

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. 3)

Knowledge of the Flora and vegetation of the Palaeogene and Neogene (‘Tertiary’ Pangaea) is based on the Quaternary (Box 2 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 Palaeoaeocene, Eocene (Gondwana, and Miocene epochs (16-5.3 million years ago) when plants (e.g. Alpia palma) found today in the tropical lowlands of the Indomalaya 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. Picea white-pine, Liriodendron tulip-tree, Tsuga hemlock, Liquidambor sweetgum, Nyssa blackgum, Sequoia redwood, Taxodium cypress, Magnolia magnolia, Carya hickory, Clethra pepper-bush, Engelhordia, Aesculus chestnut). These trees belong to the so-called Arco-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. Edingerham in 1869. The successive loss of this flora during the Pleistocene climatic phases and the retention of the Palaeogene and 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 (1818-88). The cold phase represents the cool and dry, often glacial, stage with sparse vegetation of deciduous forests and their relative abundance and distribution may vary from one interglacial to another, there are such strong ecological similarities that the Danish pollen analyst Johann Albersbo observed in 1959 an interglacial cycle consisting of four or five ecological phases (Iversen recognised in 1958). The cyclophase represents the cold and dry, often glacial, stage with sparse assemblages of pioneer, arctic-alpine, steppe, and ruderal herbs growing on mineral or skeletal mineral soils, frequently disturbed by wind and sound activities. Trees are absent, except in specialised refugia.

At the onset of an interglacial, temperature and moisture increase and the proto-vegetation phase begins. Base-demand shade-tolerant herbs, shrubs, and trees (e.g. Betula, Salix, Populus, Pinus, juniperus juniperus, Sorbus aucuparia) innanve into formerly glacially formed areas and expand to form a mosaic of grassland, scrub, and open woodland growing on unbleached, fertile soils rich in nitrogen and phosphorous and with a low humus content (Fig. 1). The mesoecotide 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, and/or, and possibly, grazing major taxa. The next phase, the oligoecotide, comprises open conifer-dominated woods (Pinus, Picea, Abies), evergreen heaths, and bog vegetation dominated by mosses on phosphorous-rich podsol soils and peats. Climatic deterioration (temperature decreases, reduced moisture, etc.) occur in the final telocretic phase and, most especially, at the onset of the next glacial cyclophase as forests decline, fire action and overgrowth destroy the leaching of hardwood and fertile acid soils, and herbs expand on the newly exposed mineral soils. The teleocretic forest vegetation is very similar to the oligoecotide phase except that as the climate cools towards the end of the interglacial, deciduous forests of Alnus, Tilia lime, Betula, Salix, and Populus得以生存, and the herbaceous flora of open heathlands such as Erica, Chamaenerion, and Ledum decline. These ecological phases within an interglacial are not synchronous between sites because of the onset of a phase such as the oligoecotide phase may depend on local site features such as bedrock geology, topography, climate, and land-use.

**Europe’s forests in the Quaternary period**

The Quaternary period (last 2.6 million years) witnessed vast climatic and environmental changes throughout the Northern Hemisphere, corresponding to the large terrestrial ice-sheets that 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. The 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 2-4 °C lower than today were also restricted to 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 no 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 valleys (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 today too far from growth for 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, Alaskan, Rockies, the Himalayas, the north-west of the Sino-Himalayan region, and the Tian Shan in Kazakhstan. Trees may also have occurred scattered in locally moist sites (water seepages, ravines), so-called ‘cryptic’ or ‘micro’ refugia in the LGM. Pollen evidence from the LGM sites in Sichuan and Qinghai, in the Zagros mountains of Iran, and in parts of south-east Turkey, Tajikistan, Uzbekistan, and Kazakhstan is increasing. There is increasing evidence from macrofossils and charcoal remains in central, eastern, and north-eastern Europe that temperate trees such as Pinus, Picea, and Loniche 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 have been found in the northern part of Europe. The LGM ice-sheet in Russia at 60°N, but see for a contrasting view. Introduction | European Atlas of Forest Tree Species
The characteristic trees of the interglacial phases differ in their reproductive and as well as physiology and ecological and competitive tolerances. Protoprotocentric trees have high reproductive rates, low competitive tolerances, high rates of population increase, and display pioneer and exploitation traits. Mesocratic trees have lower reproductive rates, high competitive tolerances, medium-low rates of population increase, arbuscular phosphorus-scavenging mycorrhiza, and late-successional, competitive, and saturation traits. Oligocentric and telocentric trees have 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 protocentric, mesocentric, and oligocentric and telocentric 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 cryotopic 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 epochs of the glacial stages. This corresponds to the cryotopic phase in central and northern Europe. At the onset of an interglacial, corresponding to the protocentric phase in central and north-western Europe, temperate taxa (e.g. deciduous Quercus, Ulmus, Ostrya) form open forests together with evergreen broad-leaved trees (e.g. Quercus ilex, holm oak, Olea europaea olive) and Mediterranean shrubs (e.g. Pistacia palaestina), while boreal and steppe vegetation declines (e.g. Betula, Juniperus, Artemisia wormwood). Chrysopogonaeae grasses dominate in this 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 oligocentric 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 telocentric phase. There is an apparent order within interglacial forest patterns when viewed at the broad scale of an interglacial cycle of 100,000–15,000 years, whereas within each phase of an interglacial (ca. 50,000 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 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 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 over-exploitation of environmental resources such as forags sylvaticos European beech, Pinus abies Norway spruce, and possibly Carpinus betulus European hornbeam. While the establishment of Fagus during the following 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 Tilia- or Quercus-dominated forests on well-drained soils. In some areas mixed Fagus-Ilex-Ilex-Quercus forests developed whereas in other areas there was a rapid change from Fagus-Ilex-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., Taxis bocconii English yew, Betula spp., or Ilex aquosum 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 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 (cryotopic) stage and associated interglacial stage. The phases of the interglacial (protoprotocentric, mesocratic, oligotropic, and telotropic) are shown along with the dominant soil features. Cryotopic:
- glacial stage
- sparse assemblages of pioneer, arctic-alpine, steppe, and nival plants
- skeletal mineral soils
Prototropic:
- early interglacial stage
- rich assemblages of herbs, shrubs, and trees (bark, pine, willow)
- unleached fertile soils
Mesocratic:
- mid interglacial stage
- temperate deciduous forests
- fertile brown-earth soils
Oligotropic & Telocratic:
- late interglacial stage
- open forest (spruce, pine), encarcous heaths, bogs
- infertile, humus-rich podsolis 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

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 distinct 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 (°C) 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 simulations 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 beo da dominion with Quercus ilex (see right image) in the Mediterranean forest. This vegetation type disappeared during the late Holocene most likely in response to excessive 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, whereas under moderate land use forests will be reduced and maquis (low biomass) will expand.
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, Sais, 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 manocrop systems. Continued forest clearances and agriculture, interspersed by periods of abandonment and secondary regeneration, occurred as the result of the development and expansion of more permanent land-use practices (e.g. animal husbandry, ploughing, crop cultivation, woodland management) during the late Neolithic, Bronze Age, Iron Age, Roman, Viking, Medieval, and recent times. Forests initially became more open, and expansion of more permanent land-use practices (e.g. animal husbandry) and rapid regime shifts in atmospheric circulation involving climate 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. Fifth, forest ecosystems of today have no long history even in the time span of the Holocene and represent widespread new ecosystems in modern counterparts ([analogue]es). Examples include the former abundance of Corylus avellana in the early Holocene across much of North-West Europe, and the importance of Abies alba in southern Europe in the mid-Holocene (see Fig. 3b). 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 time-slice in the last 11 700 years since the last glacial stage. A critical question is thus: are today’s ecosystems and climate representative of the 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 climate or have they realised environmental niches of species been significantly expanded or contracted by 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 palaeo-environmental reconstructions of future vegetation dynamics under global-change conditions.

The dynamic nature and the often non-analogue character of European forest ecosystems is made more complex by the last 5 000 years which 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 industries 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 states, but more than 5 000 years of design, creation and managing novel ecosystems to ensure high biodiversity and the supply of ecosystem goods and services in the future. The palaeoecological record of European forest and tree ecosystems is a rich and largely untapped record of ecological dynamics over a wide range of timescales. As Karl Fliese and Steve Jackson discuss, this record is a long-term ecological observatory where historical legacies 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 and the vast amount of palaeoecological data available in Europe.