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The history and present conditions of Suserup Skov – a nemoral, deciduous forest reserve in a cultural landscape

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Suserup Skov in central Zealand, Denmark represents one of the best examples of a semi-natural beech *Fagus sylvatica* dominated forest in northern Europe. The forest is developed on rather variable soils, including sandy and clayey glacial tills and lacustrine sediments formed in a final stage of the Weichsel Glaciation. The humus form is generally mull and the vegetation is in most parts dominated by early flowering perennial herbs, e.g. *Anemone* spp. and *Mercurialis perennis*. The flora of shrubs and trees is species-rich including ca 30 species typical of mull soils. The most important tree species apart from *Fagus sylvatica* are *Fraxinus excelsior*, *Quercus robur* and *Ulmus glabra.* The vegetation history of the forest has been studied by analysis of pollen and macrofossils in a sediment core obtained from a small hollow in the forest. The analysis shows that the forest has continuity of tree cover at least back to 4200 BC, indicating it to be a direct descendent of the primeval forests which invaded Denmark after the end of the Weichsel Glaciation, ca 12 000 yr ago. The forest composition and the prevailing disturbance regime have changed considerably over the last 6000 yr and the present beech-dominated forest has little in common with the primeval situation. Beech occurred for the first time in Suserup Skov ca 1700 BC and became dominant only ca 500 yr ago, together with oak. Before that the forest was a mixed deciduous forest with *Alnus*, *Betula*, *Corylus*, *Fraxinus*, *Quercus*, *Tilia*, *Ulmus* and even *Pinus sylvestris*. Forest fires were occasional until AD 800 and were probably a key in maintaining vital populations of light demanding tree species. The increase of beech seems to be closely related to human impact, especially the cessation of forest fires (natural and anthropogenic) and a shift in human use of the forest landscape from 600 BC to AD 900. Despite the historical impact from humans, Suserup Skov is now increasingly characterized by natural disturbance dynamics and is one of the best reference areas for naturalness in the nemoral part of northern Europe. This has attracted several research projects focussing on forest dynamics, ecology and biodiversity which are summarized in the paper or reported elsewhere in the current issue of Ecological Bulletins.

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Northwestern Europe has been influenced by humans for > 5000 yr, and no large natural areas have escaped cultural impact. The primeval forests, which once covered most landscapes, have vanished, and the persisting forests are fragmented and highly influenced by humans. During the last decades, the attempt to control natural processes in forest ecosystems seems to have reached a culmination, as it is recognized that forest biodiversity is seriously declining in the whole region, and it has been realized that traditional forestry is labour expensive and often results in ecologically unstable stands. Instead, increasing emphasis is paid to natural processes and dynamics in forest ecosystems. Nature-based forestry, mimicking natural disturbance regimes and regeneration principles, is increasingly appreciated as a relevant concept in a sustainable, multifunctional forestry which integrates timber production, conservation and an increasing demand for forests as a space for recreation.

With this change in focus, semi-natural forests have attracted considerable attention, based on the assumption that such forests provide a key for understanding natural forest processes and their potential in a silvicultural context. The natural processes of semi-natural forests in culturally influenced landscapes should however be viewed in the appropriate spatio-temporal context. It is especially important to recognize that present vegetation patterns, even in long-protected forest fragments, reflect the interaction between natural history and cultural influence at the stand as well as landscape scale.

Suserup Skov is situated in the central part of the Baltic beech forest region in northern Europe, in an area relatively rich in old beech forest remnants. Suserup Skov has been subject only to limited forest management during the last 150 yr and is one of the best examples of a semi-natural beech-dominated forest in northern Europe. The forest has attracted considerable scientific interest during the last decades, culminating in the research programme "SpyNatForce". The specific aim of the present paper is to provide updated background information about Suserup Skov, with special emphasis on forest history and its importance for the present forest composition and vegetation. This will provide a reference for researchers working in Suserup Skov, now and in the future, but will also emphasise for researchers working with forest structure and dynamics in general, that former human impact is just as important to consider as a natural disturbance regime if one wants to understand structures and dynamics of present day forests.

Site description

The general characteristics of Suserup Skov have been described in several papers. The status given below on landscape and soil development is mainly based on Vejre and Emborg (1996), while the overall vegetation patterns are described inspired by Christensen et al. (1993) and Emborg et al. (1996).

Setting and climate

Suserup Skov (19.3 ha) is situated in central Zealand in the eastern part of Denmark (55°22′N, 11°34′E)(Fig. 1). The climate of the area is cool-temperate and sub-oceanic with a mean annual temperature of 8.1°C, and a mean annual precipitation of 644 mm. The mean temperature of the coldest month (February) is 0.8°C, while that of the warmest month (August) is 16.7°C (Frich et al. 1997, Laursen et al. 1999). The forest is situated on the northern border of the lake Tystrup Sø, on undulating south-facing slopes (7–31 m above lake level). To the north and east, the forest borders farmland abandoned since 1993, on which tree growth is slowly expanding from the forest edges. To the west, the forest borders an abandoned, restored gravel pit (last digging in late 1960s), which is now a grazed wooded meadow with a fairly dense growth of 10–20 m tall trees. Further west, the wooded meadow joins with the forest Frederikskilde Skov (ca 15 ha), of which major parts have been declared as unmanaged forest since 2000. The plan for the wooded meadow is for it to remain grazed, with a minimum of human intervention. Within the next 10–20 yr, Suserup Skov will be surrounded by young forests on all sides, except for the southern border which bounds the lake. In the long run, it is planned to be part of a large natural forest area, amounting to ca 100 ha.

Suserup Skov is privately owned by the Foundation of Sorø Academy, while the surrounding meadows, forests and farmland are owned by the state.

Landscape and soils

Suserup Skov is situated in a landscape shaped under the last part of the Weichsel Glaciation (10 000–12 000 BC). At that time, Tystrup Sø was part of a melt-water valley draining most of south Zealand. The overall waterflow was northerly where the recipient water body of Kattegat was more or less ice free. At a later stage, the direction of the waterflow in Tystrup Sø reversed due to ice retreat at the southern border of the reservoir, and the water level of the lake gradually declined. The water flow was now southerly and has remained so ever since. The different stages in the ice retreat and the variable water table heights in the late glacial Tystrup Sø have resulted in the formation of several terraces in the present lake valley, and locally occurring glaciolacustrine sediments are higher than the present water level in the lake (Andersen 1931).

The complex late-glacial history of the area is also reflected in the soil properties within Suserup Skov, with a clear delimitation between undulating upland soils and more flat lowland areas in the central part (Fig. 2), as de-

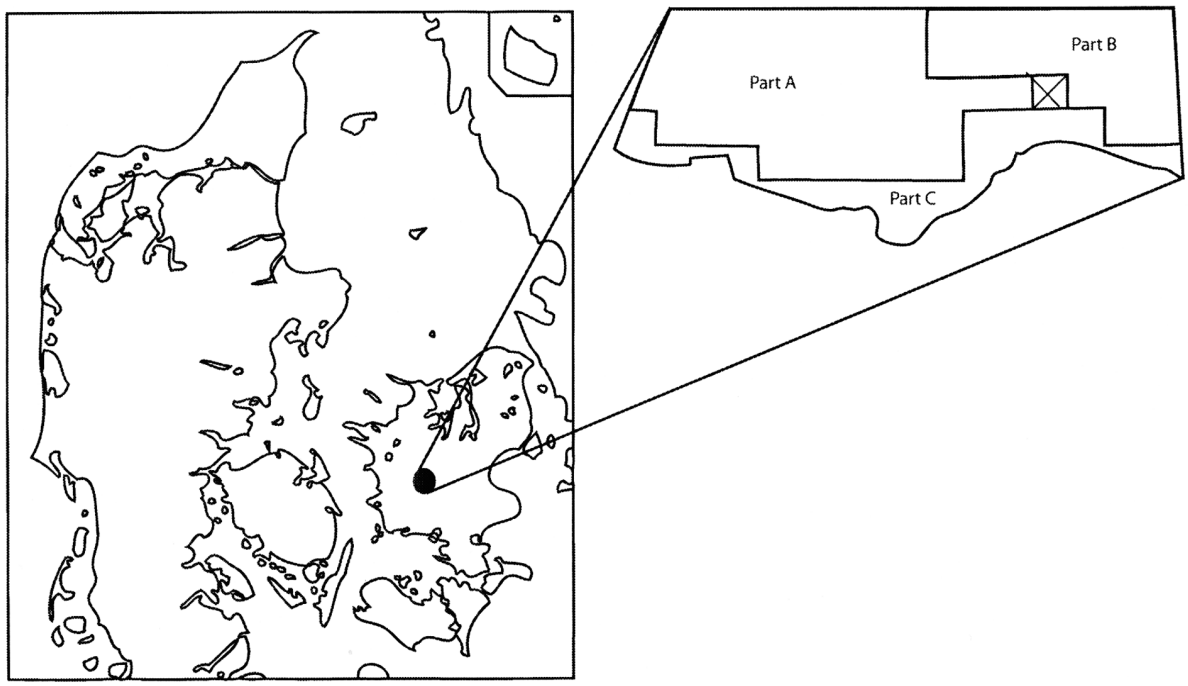

Fig. 1. The location of Suserup Skov in Denmark, and its division into part A, B and C.

scribed in more detail by Vejre and Emborg (1996). The lowland is dominated by homogenous and almost stone free lacustrine sediments and can be subdivided in two distinct land units: a slightly elevated plateau consisting of heavy clay soils and a slightly lower area with sandy soils. The elevated clay plateau can be interpreted as the bottom of a small glaciolacustrine lake, created in the terminal phase of the Weichsel Glaciation when the valley was partly filled with ice (Vejre and Emborg 1996). Following this interpretation, the sandy lacustrine deposits are slightly younger and were formed in a larger lake, probably the young Tystrup Sø, created after the ice barriers defining the glaciolacustrine lake melted away.

The uplands consist of various types of glacial tills intermixed with patches of glaciofluvial sediments (mostly gravel). Clayey and loamy tills dominate the central part while sandy tills dominate the eastern part. In the central and eastern part, several small gravel pits (diam. < 10 m) show that the glaciofluvial deposits have been exploited to some degree in former times.

The highland and lowland parts are more or less clearly separated by a ca 10 m high slope, which was probably formed by erosion in the late glacial Tystrup Sø. In the eastern and western part of the forest, where lacustrine deposits have a limited extension, the slope continues directly to the present shores of Tystrup Sø. Springs occur scattered along the slope, and in several places meter-thick travertine deposits have formed, adding to the heterogeneity of soil types within the forest.

The soil development varies considerably between the upland and lowland soils. The well drained tills of the upland have permitted a deep to very deep soil development (in places to a depth of ca 1.5 m), with extensive leaching of base cations (e.g. Ca and Mg), while the relative contents of Al has increased over time. The dominant humus form however, is mull, with pH in the range of 4–5 ($CaCl_2$) (Vejre and Emborg 1996).

In the lowland soils, a high water table and restricted drainage has prevented a deep soil development. In the lowest and wettest sandy parts, accumulation of weakly decomposed organic matter has occurred and locally regular peat layers have formed. In the more elevated part, especially in the slightly elevated clayey plateau, soil organic matter is by contrast low, and the contents of exchangeable Ca, K and Mg high. The humus form here is a rich mull with a pH close to 6 ($CaCl_2$), and high rates of biological activity are indicated by a rapid litter decomposition rate (Vejre and Emborg 1996). In addition, the lower lakeside slopes with their springs and travertine deposits are characterized by rich mull soils and a high content of base cations. Topsoil pH values exceeding 7 have been measured in this zone (Feilberg 1993, Møller 1997).

Vegetation

Today Suserup Skov is a mixed deciduous forest dominated by ash *Fraxinus excelsior*, beech *Fagus sylvatica*, wych elm

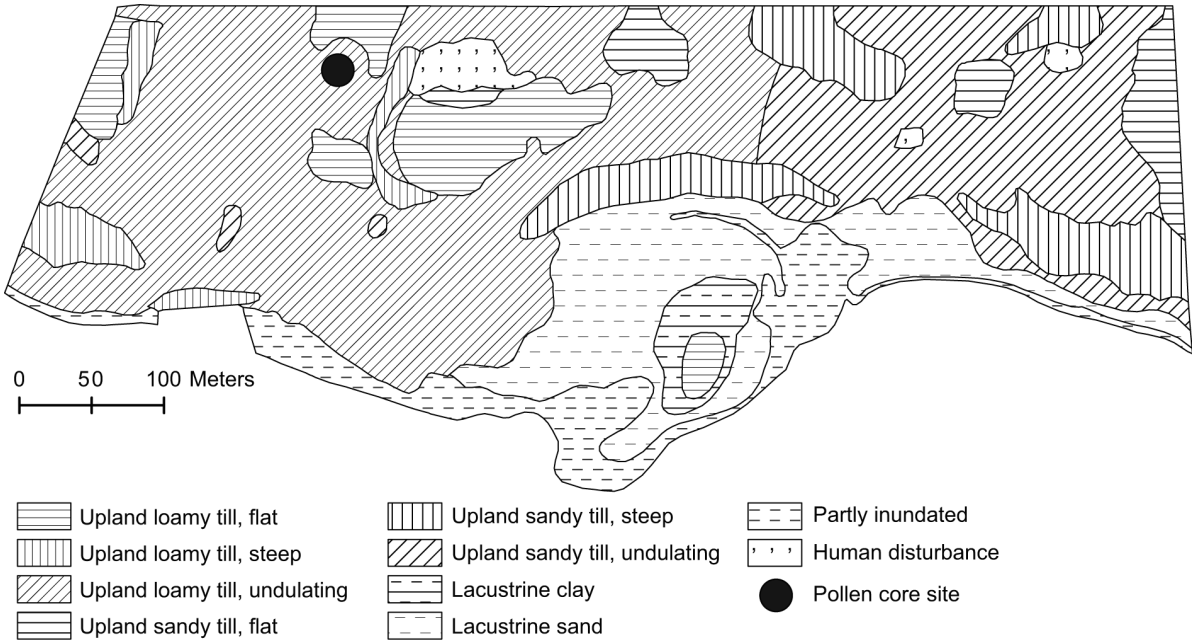

Fig. 2. Distribution of main deposit types in Suserup Skov, revised from Vejre and Emborg (1996), with indication of the pollen/macrofossil core site reported in Hannon et al. (2000).

Ulmus glabra and pedunculate oak *Quercus robur*, with a rich occurrence of alder *Alnus glutinosa* along the lake border (Emborg and Heilmann-Clausen 2007). Oak is mostly present as old specimens and contributes significantly to the standing volume even though the stem number is limited. By contrast, elm occurs only as young specimens and contributes significantly to the stem numbers, while the contribution to the standing volume is negligible (Emborg and Heilmann-Clausen 2007). Of the subdominant tree species, large-leaved lime *Tilia platyphyllos* and sycamore maple *Acer pseudoplatanus* occur regularly in some parts of the forest, while wild cherry *Prunus avium*, crab apple *Malus sylvestris*, rowan *Sorbus aucuparia*, horse chestnut *Aesculus hippocastaneum*, Norway maple *Acer platanoides* and willows *Salix caprea* and *S. fragilis* are scattered throughout. Horse chestnut, sycamore maple and *Salix fragilis* are exotic species and rather recent additions to the tree flora of Suserup Skov. Large-leaved lime is also probably planted, although the species occurred naturally in the forest 5000 yr ago (Hannon et al. 2000).

The shrub-layer is dominated by elder *Sambucus nigra*, hazel *Corylus avellana* and hawthorn *Crataegus* spp. with scattered occurrences of spindle *Euonymus europaeus*, gooseberry *Ribes uva-crispa*, wild currant *Ribes nigrum*, *R. rubrum*, wild roses *Rosa* spp. and dogwood *Cornus sanguinea.* Bramble *Rubus fructicosus* agg. and raspberry *Rubus idaeus* occur regularly in gaps created after tree death, while dewberry *Rubus caesius* is common along the lake shore. The various sallow species (*Salix cinerea*, *S. viminalis*) also occur along the lake shore.

The ground vegetation is dominated by early flowering perennial herbs, typical of mull soils. Dominant and subdominant species include *Anemone nemorosa*, *A. ranunculoides*, *Circaea lutetiana*, *Corydalis bulbosa*, *Galium odoratum*, *Lamiastrum galeobdolon* and *Mercurialis perennis.* Of the graminoids the most common species are *Carex sylvatica*, *Hordelymus europaeus* and *Melica uniflora.* For more details on the ground vegetation see Thomsen et al. (2005), Hahn and Thomsen (2007).

The distribution of tree and plant species is not uniform throughout the forest and Emborg et al. (1996) distinguished between three rather different forest parts (Fig. 1). The western part of the upland soils (Part A, 10.7 ha) is dominated by beech intermixed with ash and oak. Elm occurs abundantly in the understorey. Most large trees have straight boles except for a few very old (250–500 yr) oak trees, indicating a former period of more open conditions. The shrub-layer is poorly developed, except in gaps, and the flora is dominated by early flowering perennial herbs. The northeastern part B (4.9 ha) is characterized by large oaks of which many have short boles and wide crowns, intermixed with fast growing, straight boled individuals of ash, sycamore maple and beech. The shrub-layer is well developed, with large individuals of hawthorn, hazel and crab apple pointing to a more recent period of semi-open conditions. The western part bordering part A stands apart, due to occurrence of many tall, straight-boled oaks, which were most likely planted in an open forest part, early in the 19th century. The differentiation of parts A and B probably reflect differences in the past management re-

gime interacting with differences in the soil characteristics. The two parts are separated by a distinct earthen bank, which probably divided the forest into separate land use units before 1793 (Fritzbøger and Emborg 1996). Grazing was most likely pronounced in part B, which is characterized by sandy soils and a richness of thorny shrubs and low-boled oak trees. The area may have been a wooded meadow before it was fenced. Part A, characterized by more clayey soils, may have been used for feeding pigs on the beech mast and probably has longer continuity as a closed forest.

The forest facing the lake-border, part C (3.7 ha), is characterized by alder stands with a rich shrub-layer, but ash also occurs abundantly intermixed with beech in the higher parts. Two areas along the lake were grazed until ca 1925 and are now covered by rather young forest. The light, south-facing forest edges have a rich flora, containing a mixture of forest, meadow and reed-swamp plants.

Forest history

The history of Suserup Skov has up to now been investigated following two different approaches. Hannon et al. (2000) analysed the forest development over the last 6000 yr based on pollen, charcoal and macrofossils extracted from a small wet hollow within the forest (Fig. 2), while Fritzbøger and Emborg (1996) surveyed the recent landscape history of the forest based on a wide range of historical, published and unpublished sources. The two papers are summarised in the present section.

Suserup Skov as a mixed primeval forest

The invasion of forest trees in the Suserup area after the end of the Weichsel Glaciation is not documented by local pollen or macrofossil sources, but it is most likely that the major vegetation development has been rather similar to that described from other sites in eastern Denmark (Iversen 1967). Thus, the first postglacial forests, which grew 10 000 BC, were probably dominated by birch *Betula pubescens*, later also *B. pendula* and Scots pine *Pinus sylvestris* with some aspen *Populus tremula*, willows *Salix* spp. and junipers *Juniperus communis*. Plausibly this pioneer forest was gradually invaded by shade tolerant tree-species, first hazel *Corylus avellanus* and somewhat later also elm (mostly *Ulmus glabra*) and lime *Tilia cordata*, *T. platyphylla*, which became dominants between 6000 and 7000 BC. The light demanding species alder *Alnus glutinosa* and oak *Quercus robur* and *Q. petraea* also invaded during this period, showing that the forest still had room for species with pioneer attributes.

The oldest part of the Suserup Skov sediment core, dated to ca 4200 BC and analysed by Hannon et al. (2000) gives a very good impression of the local composition of the rich mixed forests of this period (Fig. 3). The pollen composition shows that hazel, lime, pine, oak and alder were the most abundant tree species adjacent to the core site, with some presence of ash, birch, elm and willow. In addition, macrofossil records show that maples *Acer campestre* and *A. platanoides* were also present locally. The presence of *Quercus petraea* macrofossils is noteworthy as this species is not considered native to Zealand today (Ødum 1968).

Macroscopic charcoal remains and charred wood are regular in the period from 4200 to 3200 BC indicating that local forest fires occurred with intervals of 100–300 yr. A similar fire history has been documented from the nearby forest at Næsbyholm (Andersen 1989) suggesting that the fire history of Suserup Skov is not untypical for the region in this period. It is uncertain whether forest fires originated from lightning ignition or represents anthropogenic activity, but there are no unequivocal indicators of human activity in Suserup Skov in the period. The occasional fires helped to maintain local populations of the light demanding species birch and pine, and were most likely also beneficial to oak. There is no evidence that the forest fires were extensive, resulting in large open areas, and tree pollen percentages are constantly high throughout the period (85–90% of total pollen numbers). Such values suggest closed forest conditions, at least in the vicinity of the hollow, although pollen data alone can underestimate the extent of openness (Sugita et al. 1999). Plant macrofossils are very precise indicators of local forest structure and they indicate open, wet conditions at least near the sampling site during this period.

Humans move closer

About 3200 BC a distinct change occurs in the pollen composition. The concentration of elm pollen decreases rather abruptly, and somewhat later the same occurs for pine pollen. Oak and ash pollen show an increasing trend, while hazel and lime pollen percentages show highly fluctuating patterns. The shift in pollen composition agrees with the timing of the "elm decline" in other parts of northern Europe and points to a distinct shift in the disturbance regime, which could be imposed in part by an outbreak of the Dutch elm decease. Anthropogenic indicators, as described by Andersen (1989), are not common in Suserup Skov in this period, but the presence of *Rumex* pollen suggests human use of the forest to be likely, possibly in the form of limited cattle grazing. Forest grazing would be consistent with the lack of charcoal residues pointing to absence of forest fires in the period, and with the increase in the importance of oak, which is favoured by open conditions (Vedel 1969, Van Hees et al. 1996).

The deposits dating from 3200 to 2700 BC are extraordinarily rich in well-preserved macrofossils. All tree species

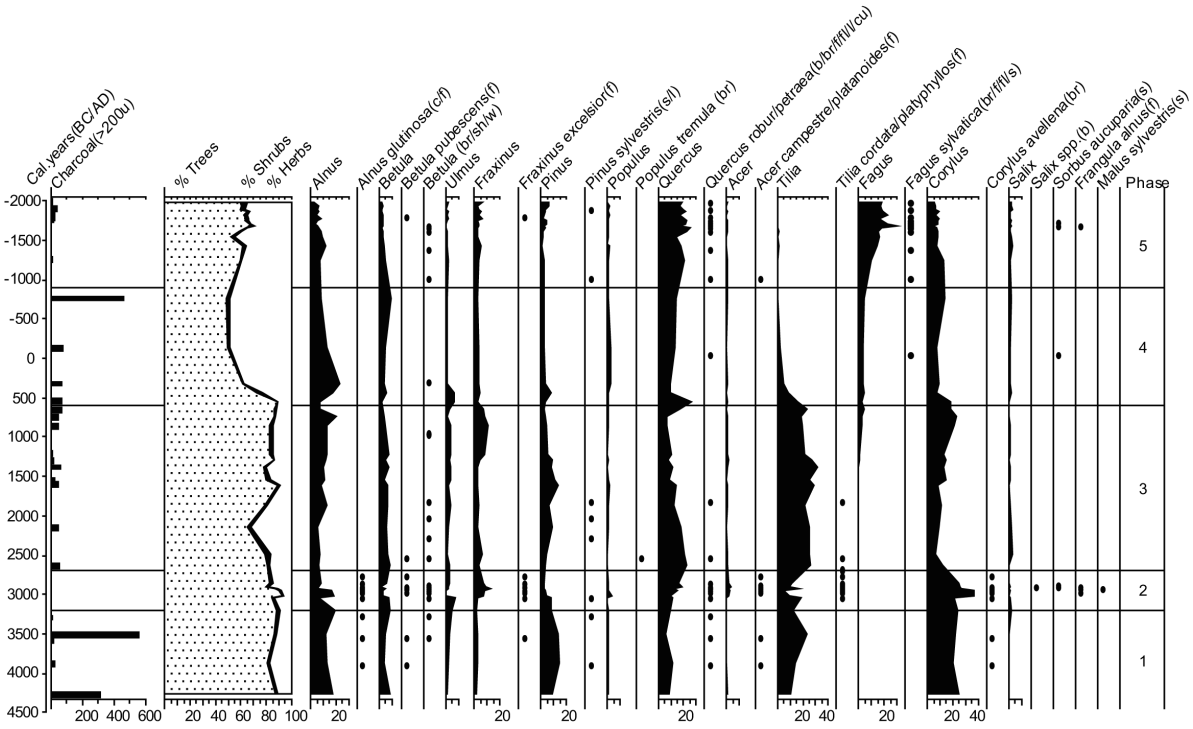

Fig. 3. Diagram of the charcoal concentration, percentage sums for trees, shrubs and herbaceous taxa, selected percentages of tree and shrub pollen (silhouettes) and plant macrofossil occurrence (dots), against calibrated calendar years and sediment depth for Core A, Suserup Skov. Abbreviations: b = bud, br = catkin or bud bract, c = cone, cu = cupule, f = fruit, fruitlet or fruitstone, fl = flower, l = leaf, n = needle, s = seed, sh = shoot, w = wood.

represented by pollen are present, but in addition rowan *Sorbus aucuparia*, wild apple *Malus sylvestris* and bird cherry *Frangula alnus* are represented. The macrofossils show that both small-leaved and large-leaved limes were present, the former apparently with the highest frequency. The presence of large-leaved lime in Denmark during mid to late Holocene has been disputed (Ødum 1968), and the records from Suserup Skov are the first unmistakable proof that the species was indeed present.

About 2700 BC a new shift in the forest composition is evident from the pollen deposits. Charcoal residues are again regular and pine pollen percentages increase, while hazel pollen decreases. Oak and lime retain a high and relatively stable occurrence for ca 2000 yr. Thus the forest composition and the disturbance regime seem to be rather similar to the situation before the elm decline. About 2000 BC, cereal and *Plantago lanceolata* pollen replace *Rumex* pollen suggesting that forest grazing ceased, while arable farming was initiated in the vicinity. Around 1700 BC beech *Fagus sylvatica* pollen occurs for the first time in the deposits, but with low frequency. The intensity of anthropogenic activity is uncertain, but the combination of charcoal residues and cereal pollen indicate that some agriculture may have been practised within the present forest.

Beech takes over

Around 600 BC dramatic changes occur in Suserup Skov. The percentage of tree pollen in the deposits decreases rapidly to ca 50–60% of the total pollen sum, while pollen of Poaceae, cereals and *P. lanceolata* increase. The decline in tree pollen percentages is especially evident for lime, while oak and birch show a weakly increasing trend. These shifts indicate that more extensive clearance for agriculture occurred around, but also within the present day Suserup Skov. It seems most likely that the local landscape in this period was a spatio-temporal dynamic mosaic of arable fields, shrubland and more or less open forest. Possible remains of Bronze Age field borders, in the form of long stony banks, are still visible in the higher parts of Suserup Skov, and suggest that agriculture might have been restricted to these forest parts.

After AD 900, tree pollen increases again in importance pointing to a release in the intensity of human use and a regrowth of forest. The new forest however, differed from the forest which grew before local human cultivation, in several respects. It was still a mixed forest, with a diversity of deciduous tree species, but hazel, elm, lime and maple were far less important trees than before and at least small-leaved lime and pine became locally extinct. Another ma-

jor change is indicated by the absence of charcoal. Fire ceased to be a disturbance factor in the forest after at least 5000 yr of irregular burning. Beech is a particularly fire-sensitive species and it responds to this altered disturbance regime by increasing in abundance to local dominance. Beech was probably restricted by fire for at least the previous 1000 yr. The local disappearance of pine is also a likely result of the cessation of fire. The previous fire regime was probably largely under anthropogenic control, so the cessation of fire most likely reflects a change in human land-use. Beech shows a steadily increasing trend and becomes dominant, together with oak, ca AD 1500. The tree pollen percentages in the period is stable, ca 60–70% and is thus considerably higher than in the previous open period, but lower than the 80–90% characteristic of the lime period. The hollow from which the pollen core is taken is close to the present forest border, and the long constant ratio between tree and non-tree pollen after AD 900 could indicate that the northern forest margin has been rather stable since that time.

Suserup Skov in the medieval

The first written records of Suserup date back to the period between AD 1202 and 1214 (Fritzbøger and Emborg 1996), at which time a man named Bjørn settled in Suserupøster (East Suserup). He "cut down a great part of the wood and grubbed new land for fertile fields, and he resided there himself and his descendants for a long time" (Liber Donationum of the Cistercian Convent in Sorø; here cited from Fritzbøger and Emborg (1996)). The actual forest clearings have most likely been east of the present Suserup Skov as the pollen deposits show no signs of intensive cuttings in the period. Slightly later records in Liber Donationum state the presence of three separate settlements: Suserup, Suserupøster and Ny Suserup (New Suserup) as well as of Suserup Skov, called Pukizeberg ("silva Susorpe dicta Pukizebiergh"). The precise location of the medieval settlements Suserup, Suserupøster and Ny Suserup are not known with certainty, but all may have been situated within the present day village of Suserup, adjacent to the old mill stream Lynge Bæk, northeast of Suserup Skov.

The oldest detailed maps of the area, dating back to about 1770, show Suserup village to be more or less surrounded by forest, and Suserup Skov is coherent with extensive forest tracts to the west. A slightly younger and more detailed map, drawn upon request of the Royal Road Commission in 1799, shows Suserup Skov bordering the village of Suserup and its farmland to the north and northeast, while the western limit is less clear. Suserup Skov was in these times not clearly separated from open arable lands. Suserup village was a forest settlement and its fields were partly covered with trees, some with cereal crops and some which were partially used for grazing. Even parts of the present day forest may have been cultivated from time to time during the period from the medieval to 1800, but the permanent high tree pollen percentages indicate that the extend of such activities within the forest was limited.

Suserup Skov as a managed forest

At ca 1800, Suserup Skov got its present delimitation due to land reforms which significantly changed the land use and ownership patterns in Denmark. Remaining forest, including Suserup Skov, were fenced and protected for timber production. At the same time, the remaining forest and shrub areas outside protected forests were cleared to provide timber and increase arable land. Suserup Skov thus became an isolated forest surrounded by farmland. One of the first steps taken after the conversion of Suserup Skov from multiple use forestry to modern tree production was to record both the stock of trees as well as the fellings. The first stock records from 1791 indicate oak was dominant at Suserup Skov with only a low abundance of beech, but it is not until 1815 that relatively reliable data are preserved giving a more detailed impression of the standing timber volume. Oak still appears to be the most important tree species, but beech volumes are only slightly smaller. Other tree species were present, but only to a very limited extent (Fig. 4). In the next decades, beech volumes increased at the expense of oak, even though the annual felling and thinning records show that approximately equal volumes of oak and beech were removed from the forest (Fig. 5). In 1833, a management plan states that Suserup Skov "contains a considerable stock of old forest, even though it is hardly dense anywhere. An extraordinary regeneration, among which lots of ash and elm trees, have sprouted up" (Fritzbøger and Emborg 1996). About 20 yr later, the botanist C.T. Vaupell visited the forest and describes that "the young trees have had the opportunity to try their strength against the old". As usual the oak has given no regeneration while there is plenty of elm and especially, beech (Vaupell 1863). In the 1885 management plan most of Suserup Skov is described as "a scattered stand of huge and tall beech trees with broad canopies mixed with generally sound oak trees and ash and elm trees in different ages". Taken together, these reports give a clear picture of a forest growing gradually denser and darker, due to a vigorous regeneration of beech, ash and elm under an open canopy of old oaks. This undoubtedly reflects the cessation of forest grazing after the forest was fenced.

The forest management plans give only few details about silvicultural activities in the period, but there is rather clear evidence that a limited number of beech, oak and lime trees were planted in the 19th century (Fritzbøger and Emborg 1996, Emborg et al. 1996). Volumes of felled trees were modest and written sources from the 1850s onwards describe the forest as a minimal intervention ornamental forest park (Fritzbøger and Emborg 1996). As a testimony from this time, most of the oldest beech trees in

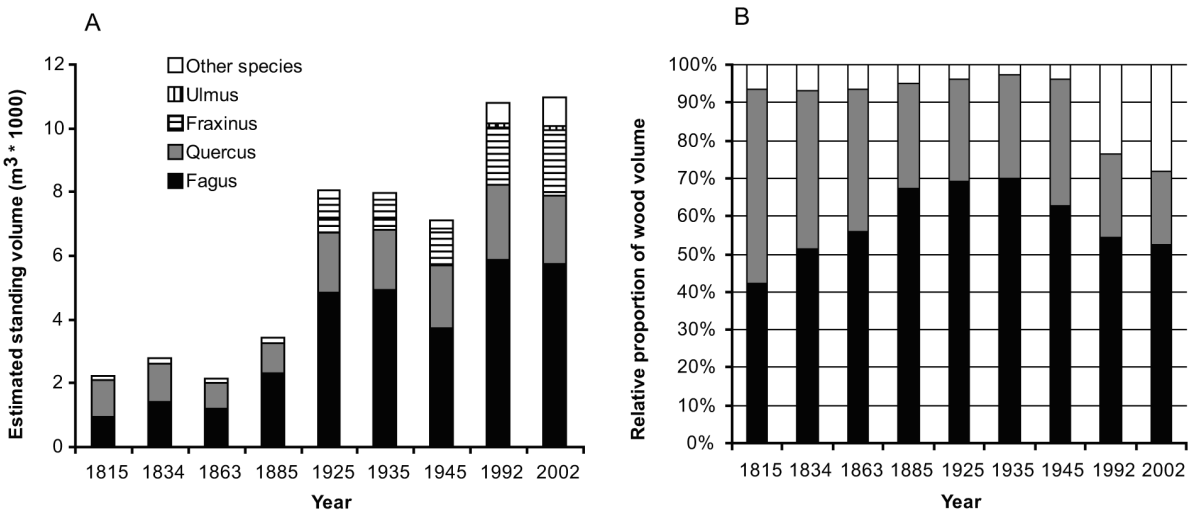

Fig. 4. The development in the estimated total standing wood volume in Suserup Skov since 1815, including trees with DBH exceeding ca 30 cm. A shows the development in absolute wood volume, while B illustrates the relative importance of the most important tree species. In B "other species" is inclusive of *Ulmus* and *Fraxinus*. All pre-1885 measurement were made using the "Ocular Method" involving a considerable element of subjectivity. From 1885 and onwards measurements were made using a Vernier gauge implying a higher level of certainty. Finally, the estimates from 1992 and 2002 are based on DBH measurements of all trees in the forest. For further details on estimates before 1992 see Fritzbøger and Emborg (1996).

Suserup Skov are marked with capital Z's for "Zir" = ornamental, not to be felled. Suserup Skov became an increasingly popular destination for the Sunday picnics of Sorø residents and a goal for botanic and drawing excursions from the renowned college at the Sorø Academy. The forest guard cottage "Sarauwsminde" functioned as a sort of tea garden for visitors and public footpaths were established in the forest.

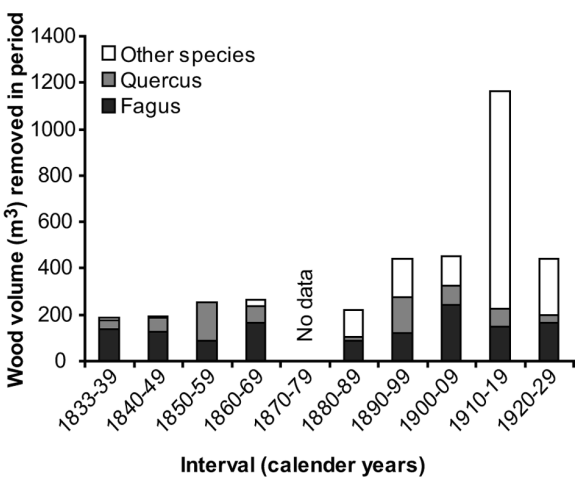

Fig. 5. The annual fellings in Suserup Skov 1833–1929 simplified from Fritzbøger and Emborg (1996). For further details see that paper.

Suserup Skov as a forest reserve

The standing timber volume of Suserup Skov more than doubled in the period from 1885 to 1925 according to contemporary stock recordings (Fig. 4). This is remarkable as there are no records of a decreasing felling rate (Fritzbøger and Emborg 1996). In particular, during World War I, considerable wood volumes were removed from the forest due to compulsory fellings. Most of the old beech and oak trees were however saved throughout the period and younger ash and elm trees apparently delivered most of the volume removed during the war (Fig. 5). It seems most likely that fellings were undertaken carefully with the aim of preserving a rather open forest landscape, and the increase in standing volume in the period was probably mainly due to growth of retained large beech and oak trees forming the canopy.

In 1925, Suserup Skov was conserved formally for biological and recreation reasons. Ostenfeld (1926) provides a detailed description of the recently protected forest, which "has been treated with big caution as especially the large trees have not been cut. Only occasionally, single individuals have been removed, because they were declining, dead or because they stood in the way for the free development of particularly beautiful neighbouring trees". The aim of the protection was not to protect Suserup Skov as a strict non-intervention forest, but rather to secure a continuation of the past careful management, as described by Ostenfeld (1926): "The aim of the protection is to conserve the present appearance of the forest, in particular the magnificent old trees. These are in the western part mainly

beech, in the eastern part mostly ash, elm and oak. Special attention will be taken to secure that oak and ash can remain to be the most important tree species, and to ascertain that the dominance of beech is restricted to the western part. Likewise, caution will be taken to secure that the very vigorous regeneration of elm not grow so dense that ash and oak, and the natural understorey occurring beneath these tree species, is disturbed". Suserup Skov was considered a historical monument of natural beauty, rather than a dynamic, semi-natural forest. The ideal was the romantic, picturesque, open forest, which was so often depicted on paintings from the late 18th and early 19th century.

A committee was set up to secure that the protective guidelines were followed, and the correspondence between this committee and the forest managers gives good insight in the practical management initiatives. It is clear that elm was selectively cut, and attempts were made to eradicate the species from the forest. As late as 1960, it was even discussed if chemical herbicides should be used to achieve this goal. We do not know if herbicides were ever used in Suserup Skov, but the attempt to eradicate elm was only partly successful. In an inventory carried out in 1992 only two elms with a diameter in breast height (DBH) exceeding 50 cm were recorded (Christensen and Heilmann-Clausen unpubl.), but the recruitment of young individuals was massive (Christensen et al. 1993). Ash and beech were also cut if they stood in the way for older trees. During World War II, even a few young oak trees were cut. Stumps of 38 large beech and oak trees were still visible in the forest in 1992 (Christensen et al. 1993).

Despite the attempts to conserve the "present conditions", Suserup Skov has changed slowly. Most notably the forest grew denser to the detriment of oak. In 1834, 530 living oak trees were recorded in the forest. In 1945 this figure had decreased to 199, of which 159 remained in 2002. In 1961, the protection status was changed and all cutting of trees ceased, except for fallen trees lying across foot paths. In 1968, the buildings of Sarauwsminde burned, and a few large oak trees were cut to make space for fire engines. The effort could not save the buildings, which were later demolished. Since then the forest has invaded the old garden and lawns of Sarauwsminde (ca 0.5 ha).

Suserup Skov as a research environment

In 1917, a field station was built at the margin of Suserup Skov, close to the lake shore, under the auspices of Prof. C. Wesenberg-Lund of the Univ. of Copenhagen. The field station was for several decades a highly important institution for research in freshwater biology and parasitology, culminating in the publication of "Biological studies on the River Susaa" (Berg 1948). This publication was, in its time, the most detailed account on the biology of running waters published worldwide. The official use of the laboratory for field courses and research ceased in 1969, due to the bad stage of the buildings, and an increasing demand for space for students and equipment.

No research in forest biology was published in the time of the Suserup Laboratory, so even though the forest was protected as a scientific reserve, its first scientific era was dedicated to the nearby lakes and river. In the late 1960s the forest was increasingly used in the education in forest ecology at the Royal Veterinary and Agricultural Univ. and a research programme was initiated by Prof. Helge Wedel and Lise Rastad focusing on forest vegetation and regeneration patterns. Unfortunately the results of the efforts have not been published. A third research era was initiated in 1992 by two research projects: an all forest inventory and a Ph.D. project focussing on forest dynamics. The projects were at first uncoordinated, but soon contact was established in the field between the respective research teams, and a fruitful collaboration was established bottom up. In the first project (Christensen et al. 1993) a 50×50 m grid was marked throughout the forest and all living trees with DBH exceeding 3 cm were measured. In addition trees, living and dead, with DBH of 29 cm or more were mapped, for the drawing of a stem position map. The Ph.D. project involved detailed studies on forest structure and regeneration (Emborg et al. 1996, 2000, Emborg 1998), forest history (Fritzbøger and Emborg 1996, Hannon et al. 2000) and the interaction between soil and vegetation (Vejre and Emborg 1996).

The research projects established Suserup Skov as one of the best conserved and well described semi-natural deciduous forests of the northwestern European lowlands, and stimulated a fourth wave of research. The present issue of Ecological Bulletins is the culmination of these efforts, summarizing results from extensive research in forest ecology carried out in Suserup Skov since 1999.

Apart from research in forest history, structure and dynamics, several studies have evaluated the importance of Suserup Skov for biodiversity. Møller (1997) coordinated a multi-disciplinary research project in which species richness of higher plants, bryophytes, fungi, lichens, saproxylic clickbeetles, crane flies, oribatid mites, gastropods, birds and bats were investigated in a number of natural/managed forest pairs. The study confirmed Suserup Skov to be of crucial importance for biodiversity, especially to saproxylic organisms, and two mite species new to science were recorded from crumbling beech snags. The flora and wood-inhabiting fungi have been subject to more detailed studies (Feilberg 1993, Graae and Heskjær 1997, Heilmann-Clausen 2001, Heilmann-Clausen and Christensen 2003). For the latter group, the locality is considered to be of European importance in a conservation perspective (Christensen et al. 2005). Finally the structure and diversity of the nematode fauna has been studied in some detail; see Bjørnlund et al. (2002).

Perspectives – the value of Suserup Skov as a natural reference

The development of Suserup Skov during the last 2500 yr has been closely linked with human activity in and around the forest. The increase in beech to become a dominant tree species is especially the result of human use of the landscape and the forest. The same seems to be true for most beech forests in southern Scandinavia (Bradshaw and Lindbladh 2004). If there had never been any human activity in and around Suserup Skov, the forest would probably still be dominated by lime and maybe even be affected by forest fires now and then. From a palaeoecological perspective the forest is therefore not very natural in its present composition. However, most of the processes and structures that characterize the present forest are natural and not results of human activity. In this respect the forest is highly natural and presents a relevant reference for silviculture, nature management and the general understanding of forest ecosystems. This reference value is even enhanced by the fact that the shift from lime dominated mixed deciduous forests to beech dominated stands has been very extensive in the northwestern European lowlands. Beech dominated stands thus dominate managed deciduous forests in Denmark and are even of major conservation interest, because the forest type has been in the region long enough to be crucial for forest biodiversity. In other words, the development of Suserup Skov during the last 6000 yr is deeply imbedded in the overall landscape history. Even though this development has been influenced strongly by humans, we find it relevant to perceive Suserup Skov as one of the most important references for natural forest dynamics, structures and composition in the modern landscape of northwest Europe.

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