

Palaeovegetation-model comparisons, climate change and tree succession in Scandinavia over the past 1500 years

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Abstract

1 We assess the robustness of a 1500-year palaeoclimate data base and forest gap model in simulating northern Scandinavian boreal forest succession since AD 500. We also evaluate trends in species abundance in a nemoral woodland in southern Scandinavia by comparing modelling results to palaeoecological data.

2 Simulated biomass trends for *Picea*, *Pinus* and *Betula* growing at Penningholmen (northern Sweden) are strikingly similar to those observed in the local pollen record, particularly in the replication of the early Little Ice Age (LIA) decline in *Betula* and the late-LIA dieback of *Picea* and *Pinus*.

3 LIA decreases in *Betula* may therefore be partly due to the effects of climate on its competitive interactions with *Pinus*, as well as the previously proposed effects of insect herbivory.

4 Simulations of Draved Forest (western Denmark), suggest that *Tilia* is under-represented in modern-day Scandinavian nemoral woodlands, and consequently that the present dominance of *Fagus* probably reflects strong human–plant interactions from as early as the beginning of the 17th century.

5 This study highlights the importance, despite general limitations associated with vegetation models, of model-data comparisons for understanding mechanisms and processes underlying past forest succession, and emphasizes the usefulness of forest models for reconstructing climate influences on past vegetation.

Key-words: forest succession, gap models, FORSKA2, tree dieback, late-Holocene, Little Ice Age, Medieval Warm Period, palaeoecology

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Introduction

Comparisons of palaeological data with model predictions have become a critical component of global change research (Bonan & Hayden 1990; Solomon & Bartlein 1992) because modelling experiments allow interacting biotic/abiotic components to be isolated and their relative influence to be evaluated in terms of trends observed in the palaeorecord. However, there are few examples of palaeodata-model comparisons conducted at the regional scale (Solomon & Shugart 1984; Davis & Botkin 1985; Campbell & McAndrews 1993), and even fewer at the stand-scale, although such comparisons can provide important insights into the

critical factors modifying local and landscape tree succession in response to changes in climate.

The accuracy and usefulness of such comparisons depend to a great degree on the quality of climate data. Previous simulations of past forest succession were based on either palaeoclimate reconstructed from pollen (and are thus subject to problems of circularity) (Solomon *et al.* 1981; Davis & Botkin 1985) or on static climatic parameters averaged over periods of several hundred years (Campbell & McAndrews 1993). To our knowledge, none have been based on available gap model simulations together with variable palaeoclimate reconstructions from tree-rings, which allow for much finer temporal resolution than other palaeotemperature proxies.

The objectives of our research were twofold. First, we wanted to evaluate the ability of gap FORSKA2 (Prentice *et al.* 1993) to simulate the past 1500 years of tree succession in a typical northern Scandinavian

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boreal forest. Although the ability of FORSKA2 to simulate forest dynamics when the climate is in equilibrium has previously been demonstrated (Prentice *et al.* 1993), it was necessary initially to assess its performance under variable climate, and also to evaluate the robustness of the palaeoclimate data base in capturing major successional trends in a region not influenced by human activity. We chose a northern Swedish site (Penningholmen) because human disturbance has probably been minimal for most of the past 1500 years (the last few decades being an exception), and any change in tree species abundance over time can thus be attributed primarily to changes in climate, in combination with other non-anthropogenic factors such as natural disturbances (i.e. fire and wind), herbivory and disease.

Our second objective was to conduct simulations of a semi-natural southern Scandinavian forest (Draved, western Denmark) to evaluate the relative importance of late-Holocene climate change in affecting the abundance of two important nemoral species, *Tilia cordata* and *Fagus sylvatica*. Our research was intended to provide new insights into the debate on the historical decline of lime (*Tilia*) and the origins of northern European beech woods (*Fagus*) (Turner 1962; Kuster 1997; Rackham 1997). For Scandinavia, historical documents dating to the 17th century are often cited in support of the common belief that beech forests are non-anthropogenic features of the southern Swedish landscape (Brunet 1995). Palaeoecological analyses of sediments in forest hollows across southern Scandinavia, however, indicate otherwise (Aaby 1983; Björkman & Bradshaw 1996; Björse & Bradshaw 1998; Bradshaw & Holmqvist 1999).

Methods

FOREST MODEL

FORSKA is a gap model which simulates the establishment, growth and mortality of trees in canopy gaps of approximately 0.1 hectare in size (Leemans & Prentice 1989; Prentice *et al.* 1993); it has been used to simulate forests in northern Europe (Prentice *et al.* 1991; Leemans 1992; Sykes & Prentice 1996), Canada (Price *et al.* 1993), and tropical Africa (Desanker & Prentice 1994). FORSKA2 (Prentice *et al.* 1993) differs from earlier gap models in that it offers more realistic mathematical representations of competition for light, and contains more explicit tree physiology-based parameters (Sykes & Prentice 1996).

Tree establishment and growth depend on a favourable climate and the availability of photosynthetically active radiation (PAR), and are also strongly influenced by species-specific parameters such as shade-tolerance, establishment rate and sprouting potential. Tree mortality is modelled on the basis of two functions; an intrinsic mortality rate correlated with tree age and vigour (i.e. tree-growth efficiency) and random mortality resulting from disturbances such as wind and

fire. Disturbance is simulated by removal of tree cover in patches, and apart from random events, is also dependent on tree age. All physiologically based processes (establishment, photosynthesis and respiration) are subject to environmental constraints (i.e. growing-degree days, minimum and maximum temperatures, and soil drought index), which are calculated from mean monthly climate. As the robustness of FORSKA in predicting basic forest stand dynamics has been evaluated elsewhere (Leemans & Prentice 1987; Leemans & Prentice 1989; Leemans 1992), this paper will not address issues of model validation in detail.

SITE DESCRIPTIONS

Our northern site (Penningholmen, Sweden, Fig. 1) is a small (0.9 ha) and isolated island in Lake Uddjaure, and is dominated by *Betula pubescens*, *Picea abies* and *Pinus sylvestris*. Penningholmen is situated at a altitudinal (vertical) distance of approximately 300 m away from the forest-tundra ecotone and is close to the north-western range limits of *Picea abies* and *Pinus sylvestris*.

Our southern site (Draved Forest, western Jutland, Fig. 1) contains some of the least disturbed nemoral stands remaining in Denmark (Aaby 1983). It is approximately 200 ha in size and contains large populations of *Tilia cordata* on soils derived from glacial till, and *Fagus sylvatica* on partly drained soils derived from wind-blown sand. Part of the forest is a strict reserve where forest dynamics have been monitored since 1948 by the Geological Survey of Denmark and Greenland (P.F. Möller, personal communication, 1998).

CLIMATE

Over the past 1500 years, north-west Europe has experienced three important periods of changing climate: (i) a cold period preceding the start of the Middle Ages, sometimes referred to as the pre-Medieval Cold Period (MCP, AD 500–900), (ii) an interval of warmth during the Middle Ages termed the Medieval Warm Period (MWP, AD 900–1200), and (iii) a prolonged cold period called the Little Ice Age (LIA, AD 1200–1850) (Grove & Switsur 1994; Hughes & Diaz 1994; Keigwin 1996; Pfister *et al.* 1996).

Our 1500-year palaeoclimate data base was constructed by applying temperature and precipitation anomalies derived from palaeodata to modern-day climate parameters. Thirty-year mean monthly climate (1961–90; temperature, precipitation and percentage sunshine) was provided by an updated version (W. Cramer, personal communication) of Leemans & Cramer's (1991) interpolated global climate data base (summarized in Table 1).

Palaeotemperature anomalies were taken from Briffa *et al.*'s (1992) palaeoclimatic analysis of *Pinus* tree-ring chronologies in northern Fennoscandia, which is the only Scandinavian palaeotemperature data set longer than 500 years. The application of

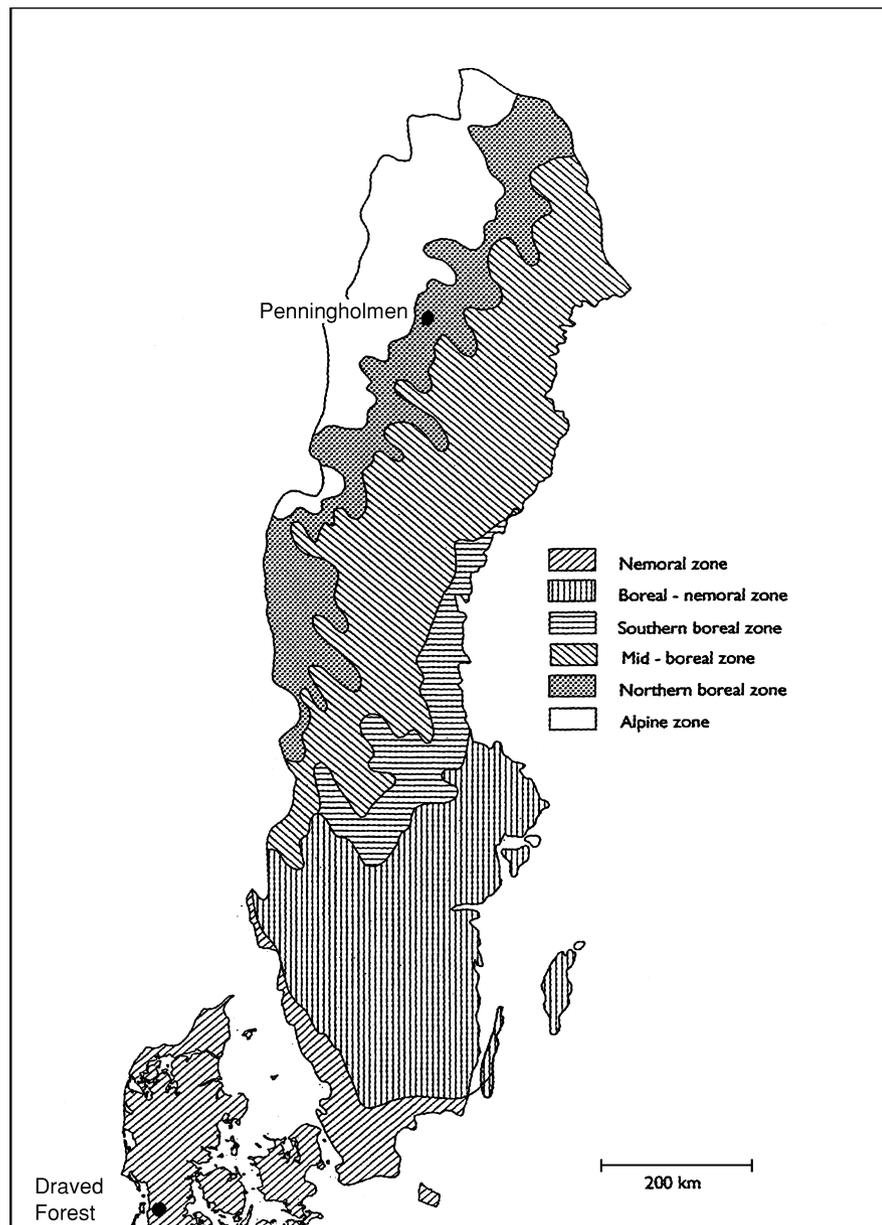


Fig. 1 Location of simulated forest sites in northern Sweden (Penningholmen) and western Denmark (Draved Forest).

Table 1 Mean temperature of the coldest and warmest months of the year ($^{\circ}\text{C}$), precipitation (mm year^{-1}) and sunshine (percentage of total) for the period 1961–1990 at Penningholmen and Draved

Parameter	Penningholmen	Draved
Maximum temperature	11.1	15.2
Minimum temperature	-13.2	-0.1
Precipitation	521	882
Sunshine	28	36

northern data to southern Scandinavia is supported by the observation that major northern temperature anomalies are duplicated in shorter data sets from further south (Kalela-Brundin 1999). Because species

parameters prescribed in FORSKA2 are based on 30-year mean values, we employed successive, independent 30-year means for simulations, although some studies have indicated the importance of climatic extremes for plant establishment and growth (Porter & Gawith 1999).

Mean temperatures during the MWP were up to 0.5°C greater than today, with a general warming trend beginning by AD 900 and ending by AD 1200 (Fig. 2a). The LIA is a long period of cooling (AD 1200–1850), punctuated by one major warming interlude starting at AD 1400. LIA temperatures reached a maximum cooling around AD 1600 with a mean anomaly of up to 0.8°C decrease relative to today (Fig. 2a).

Palaeoprecipitation anomalies were prescribed from Lamb's (1967) semi-quantitative analysis of long-term precipitation trends in England. Lamb (1967)

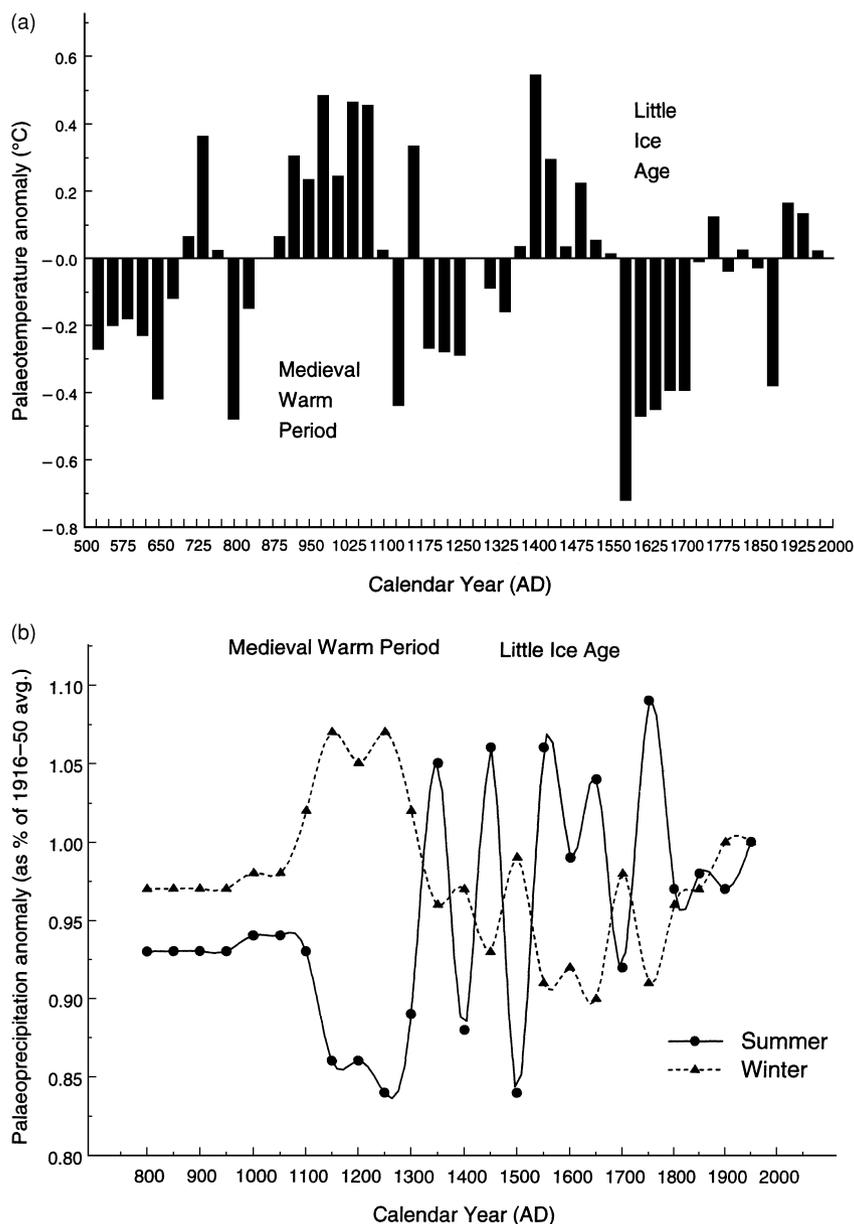


Fig. 2 1500-year (AD 500–2000) trends in (a) palaeotemperature anomalies reconstructed from *Pinus* tree-rings in northern Fennoscandia (Briffa *et al.* 1992) (presented here as 30-year means), and (b) winter and summer palaeoprecipitation anomalies reconstructed from historical and meteorological records in England (Lamb 1967).

incorporated data from historical, botanical and meteorological records to estimate summer and winter precipitation anomalies (percentage of 1916–50 average) from the beginning of the 10th century onward. The MWP generally experienced wetter winters (7%) and drier summers (17%) relative to 1916–50 averages (Fig. 2b). In contrast, LIA winters were drier (5–10%) and summers were variable, but tending towards wetter (Fig. 2b).

Quantitative palaeoprecipitation data for southern Scandinavia are completely lacking. With just two palaeoprecipitation reconstructions available to us, we felt that the more maritime English data base was more appropriate for our simulations than reconstructions from central European data. We encourage more research on the development of quantitative proxies for

palaeoprecipitation reconstructions because temperature and precipitation are equally important influences on tree growth.

Our experimental approach offers two key methodological refinements over previous palaeoforest simulations. First, modern advances in palaeoclimate analysis have resulted in reconstructed palaeotemperature anomalies with increasingly fine temporal resolution. Earlier research by Campbell & McAndrews (1993) incorporated only a steady 2 °C cooling from AD 1200–1850 for LIA modelling experiments, but our study includes fifty 30-year mean temperature variations over a 1500-year period. Second, because we incorporate palaeoclimate anomaly reconstructions from tree-rings, we avoid circularity issues, which can be a problem with

methodologies where pollen is used both to determine climate and to perform data-model comparisons.

SIMULATIONS

Trends in above-ground biomass (Mg ha^{-1}) were simulated for both the northern (Penningholmen) and southern (Draved) Scandinavian sites. All data represent an average of 300 patch simulations, which is greater than the estimated minimum number of simulations (150–200) required to match average species-specific parameters (Bugmann *et al.* 1996). Simulations were conducted with a soil water holding capacity of 150 mm. Disturbance return interval (defined as the average time between successive disturbance events) was prescribed at 300- and 150-years for Draved and Penningholmen, respectively; values which are supported by research on reconstructed disturbance histories in northern Scandinavia (Zackrisson 1977) and Denmark (P.F. Möller, personal communication).

Our forest model was modified to incorporate a user-defined parameter that allowed species to 'migrate' into or become 'extinct' from an area at a specified time during the simulation. In FORSKA2, natural processes of migration are not as yet explicitly modelled, instead the presence or absence of a species is forced based on whether or not propagules of a species are available for establishment.

PALAEODATA-MODEL COMPARISONS

Palaeoecological data are presented as percentage tree pollen (i.e. percentage of total arboreal pollen) and model data as percentage forest biomass. Pollen counts were not transformed by representation factors. To facilitate direct comparisons, pollen and forest biomass data at Penningholmen are plotted as 50-year averages. Pollen is scored into a 50-year time-step and then averaged for that time-step. If pollen data were unavailable for a particular 50-year period, then the average of the preceding and subsequent time-steps was used. Fewer samples were ^{14}C -dated for the Draved site, and only time-steps which correspond to a dated pollen horizon were plotted on the figure. Pollen data for Draved and Penningholmen were obtained from stand-scale studies by Bradshaw & Zackrisson (1990) and Aaby (1983), respectively.

Results

PENNINGHOLMEN

Simulated biomass trends for *Pinus*, *Picea* and *Betula* closely follow those observed in the pollen record for most of the past 1500 years (Fig. 3). *Pinus* experiences two periods of lower abundance and declines, around AD 1050 (i.e. MWP) and AD 1650 (i.e. late-LIA), which are also generally observed in pollen data. There are minor discrepancies in the timing of decreased abundance, for

instance in the LIA, when FORSKA2 simulates biomass reductions for *Pinus* starting AD 1250, but the pollen record indicates a starting date of AD 1450. Such discrepancies may be related in part to empirical errors associated with ^{14}C -dating of humus samples, and to modelling errors associated with the simulation of the development of forest from bare soil.

Betula populations at Penningholmen experience only one major period of decreased abundance, during the early part of the LIA, which is reflected in both model and pollen diagrams (Fig. 3). Once again, the timing of tree dieback differs somewhat between model and pollen data, with FORSKA2 simulating low *Betula* biomass at AD 1600 and the pollen record indicating lowest birch pollen abundance around AD 1450. During the MWP, *Betula* biomass is simulated to increase slightly, with a maximum abundance occurring at AD 1100; a trend that is not so easily detected in the pollen record.

FORSKA2 is, as yet, unable to simulate propagule dispersal, instead migrational effects were forced by switching availability of propagules 'on' and 'off'. When *Picea* propagules are switched on, it takes less than 250 years to reach maximum biomass, with an equally rapid establishment observed in the pollen record (Fig. 3). *Picea* is sensitive to maximum LIA cooling (i.e. AD 1600–AD 1800); as revealed by low simulated biomass and low pollen abundance. *Picea* appears much later in the Penningholmen pollen record than for most of northern Sweden sites because of its island location and its proximity to the distributional limits for this species.

DRAVED

Trends in predicted abundance of *Tilia* and *Fagus* are closely similar to those observed in the pollen data prior to AD 1600, but major discrepancies occur thereafter and remain significant until the present (Fig. 4). Both modelling and pollen data indicate a rise in *Tilia* abundance during the MWP, a decrease into the start of the LIA and then a small rise in abundance coinciding with the slight warming event observed during the mid-part of the LIA. However, FORSKA2 predicts that although *Tilia* declines in abundance during the latter part of the LIA, its populations then recover up to the present day, whereas pollen data show a dramatic drop in *Tilia* abundance around AD 1600, approaching zero by modern times.

Simulation and pollen data for *Fagus* again show similar population trends prior to the early 17th century (Fig. 4). However, whereas FORSKA2 simulates a decrease in *Fagus* abundance during the latter part of the LIA (with small population recovery to present), the palaeorecord indicates a dramatic rise in *Fagus* starting AD 1600 and lasting until the present. Interestingly, *Fagus* pollen data show a small dip in populations around the late 1800 s, which may be associated with the final cooling trend associated with the termination of the LIA.

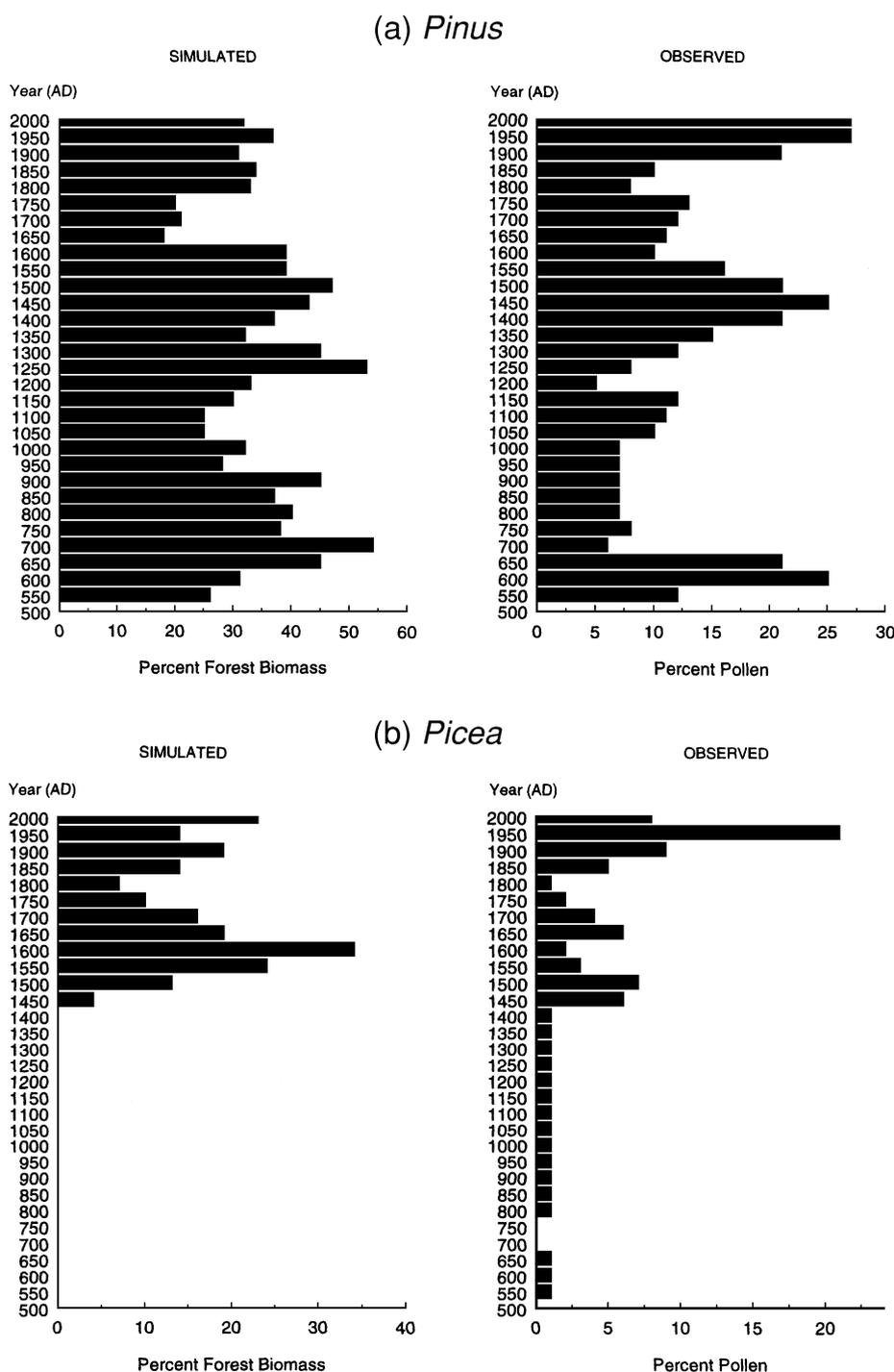


Fig. 3 Palaeoforest data-model comparisons for (a) *Pinus*, (b) *Picea* and (c) *Betula* abundances at Penningholmen, northern Sweden. Simulated tree abundance data (on left) is presented as percentage forest biomass, which is defined as the percentage of species biomass relative to total forest biomass (Mg ha^{-1}). Observed tree species abundance data (on right) is presented as percentage pollen (expressed as a percentage of a sum of all woody taxa), with pollen data graphed as 50-year averages to match scales used for presenting biomass data.

Discussion

CONSEQUENCES OF LATE-HOLOCENE
CLIMATE FOR NORTHERN TREE ABUNDANCES

Explanations for the increased presence of *Betula* and decreased *Pinus* biomass observed and simulated at

Penningholmen during the Medieval Warm Period (MWP) remain somewhat uncertain. Briffa *et al.*'s (1992) *Pinus* tree-ring data indicate that this species should have increased biomass during the MWP, yet an observable increase in *Pinus* pollen percent at Penningholmen (Fig. 3) is very weak, if at all. The low *Pinus* biomass during the MWP is also simulated by FORSKA2

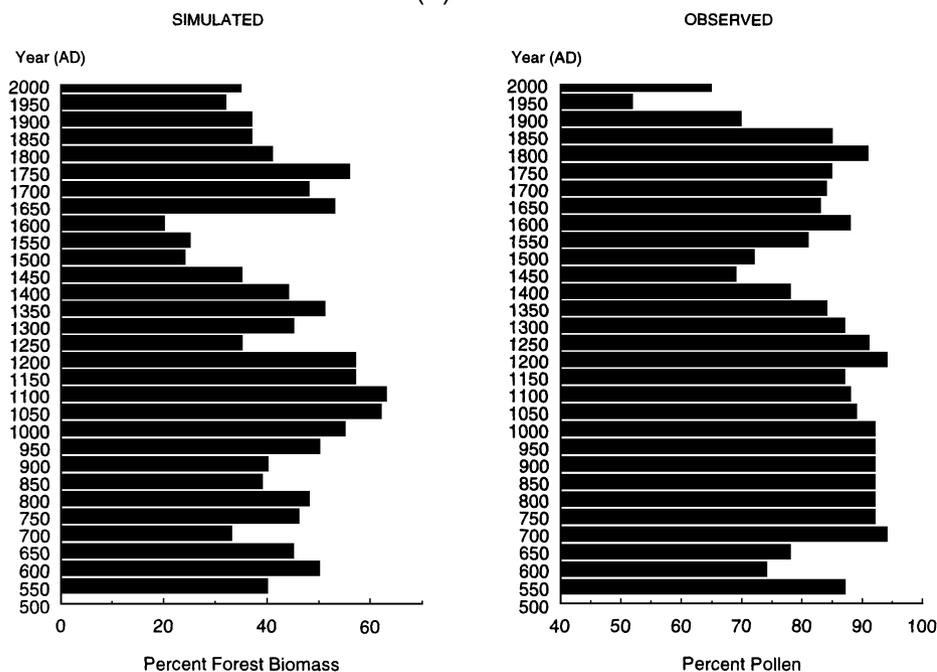
(c) *Betula*

Fig. 3 Continued.

(Fig. 3), perhaps because simulation of a disturbance event coincides with a time of climate warming.

Betula is not surprisingly unaffected by falling temperatures during the coldest part of the LIA. *Betula* populations are both simulated and observed to remain high from the period starting AD 1650, through to AD 1800 (Fig. 3). The Scandinavian tree-line contains a mix of *Picea*, *Pinus* and *Betula*, with mountain birch being the northernmost woodland species. Although maximum cooling during the LIA may have caused northern tree-line retreat (Kullman & Engelmark 1990), Penningholmen lies a vertical distance of approximately 300 m away from the Scandinavian forest-tundra ecotone, and *Betula* abundance was therefore unlikely to have been significantly altered.

Penningholmen, however, lies quite close to the north-western range limits of *Picea abies* and *Pinus sylvestris*. Simulated and observed declines in *Pinus* and *Picea* during the coldest period of the LIA (Fig. 3) therefore, may be related to an eastward contraction of the *Pinus-Picea* species limit. Kullman (1987, 1988) reports a 30 m altitudinal recession of *Pinus* at its northerly limit in the central Scandes mountains over a period spanning AD 1200 to AD 1700. Inadequate conifer reproduction due to cold LIA summer temperatures and episodes of severe winter cold were cited as possible causes for the premature dieback of conifers at high elevations (Kullman 1987).

The unusual dieback of *Betula* observed during the first half of the LIA was postulated by Bradshaw & Zackrisson (1990) to be related to insect herbivory because peak values of chitinous fragments in sediments were found to match with temporary collapses in *Betula* populations. FORSKA2, however, also simu-

lates a dieback (Fig. 3), suggesting that the effects of LIA climate on northern woodland succession (particularly on the competitive interactions between *Pinus* and *Betula*) may contribute to the latter's decline.

The striking similarity between successional trends simulated by FORSKA2 and those observed in the Penningholmen pollen record (Fig. 3) leads to the conclusion that the use of forest succession models in connection with pollen records can be extremely useful in separating the confounding influences of anthropogenic and non-anthropogenic (i.e. climate and disturbance) factors on vegetation dynamics, particularly when their effects are in the same direction (i.e. increasing or decreasing tree abundances).

DECLINE OF *TILIA* AND RISE OF *FAGUS*
IN THE SOUTH

Much debate focuses on the origins of beech forests in northern Europe, primarily owing to the current dominance by this species of forest stands across large areas, but also because beech forests are valued historical landscapes in many countries (Rackham 1980, 1997; Brunet 1995; Kuster 1997; Peters 1997). A widely held opinion in north-west Europe is that beech forests are 'natural' components of the landscape, a notion reinforced by papers citing historical documents describing the existence of beech forests 300–400 years ago (Brunet 1995; Björkman 1997).

On the continental-scale, *Fagus sylvatica* is arguably in equilibrium with climate (Huntley *et al.* 1989), and thus is an expected component of modern southern Scandinavian forests. Palaeoecological investigation of sediments in small forest hollows in southern Sweden

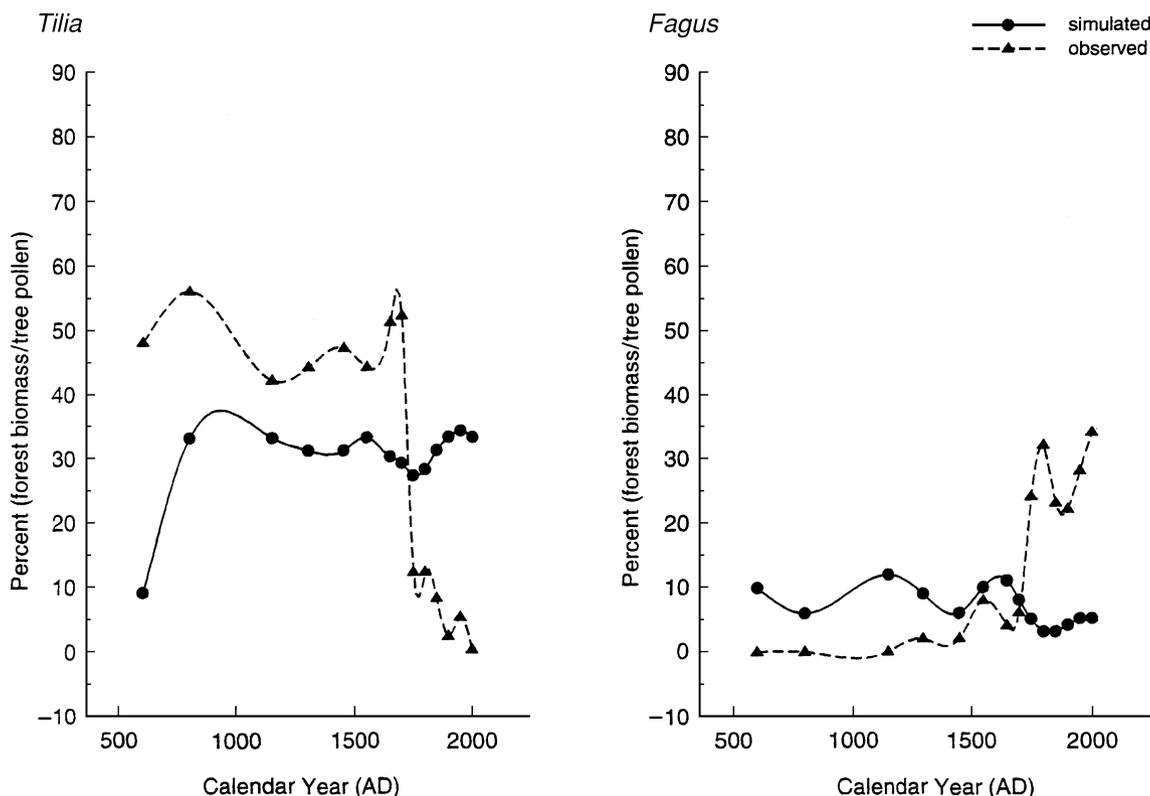


Fig. 4 Palaeoforest data-model comparisons for *Fagus* and *Tilia* at Draved Forest, western Denmark. Conventions as in Fig. 3.

(Björkman & Bradshaw 1996; Björse & Bradshaw 1998), however, indicate that from a palaeoecological perspective (i.e. over time-scales of millennia), *Fagus* should not be a dominant of contemporary nemoral forest. Furthermore, small forest hollows in present-day *Fagus* stands show signs of anthropogenic interference prior to the rise of *Fagus* dominance (Hannon *et al.* 2000). Controversy therefore concerns not so much whether *Fagus* should be present on a continental-scale, but rather at the stand-level, and whether its overwhelming abundance in southern Sweden and Denmark has a non-anthropogenic origin (Chambers 1993; Kuster 1997; Bradshaw & Holmqvist 1999). If modern *Fagus* stands are not in equilibrium with climate, then monospecific *Fagus* woodlands across north Europe are a distinctly anthropogenic feature.

Our simulations do not support the hypothesis that historical changes in climate were favourable for stand-scale dominance of beech, and indicate that following cooling during the LIA, *Tilia* tree populations should have rapidly re-established their dominance in nemoral woodlands (Fig. 4). *Fagus* and *Tilia* are physiologically similar in the sense that they are resource competitors in these woodlands (Peters 1997). *Fagus* is however, more cold-sensitive, because the much greater sprouting potential of *Tilia* allows it to reproduce vegetatively and thus persist on sites despite the colder climate (Prentice & Helmisaari 1991). Examples where *Tilia* individuals have remained in areas with unfavourable climate for up to several centuries have been noted for northern Europe (Pigott & Huntley 1981).

Seed production in *Fagus*, however, is strongly affected by climate (Peters 1997), with cooling-induced decreases in *Fagus* abundance being well represented in this and other forest modelling experiments (Campbell & McAndrews 1993). Simulations of hardwood forest succession in southern Ontario (Canada) by Campbell & McAndrews (1993), for example, indicate a decline in *Fagus grandifolia* beginning at AD 1400, with replacement first by *Quercus* and then by *Pinus*. This feature of the pollen record was originally attributed to native forest clearing but is now linked to LIA climate.

Based on the results of our simulations, *Fagus* should not dominate modern-day nemoral woodlands, whereas *Tilia* should be present in significantly higher than the observed quantities (Fig. 4). The weak presence of *Tilia* has been a long-standing characteristic of forests in north-west Europe (Iversen 1958; Turner 1962; Berglund 1969) and FORSKA2 simulations support the theory that factors other than LIA cooling must be responsible for its near disappearance in southern Scandinavia.

Anthropogenic factors such as large-scale forest clearance for agriculture, introduction of domesticated grazing animals, and selective cutting may have affected *Tilia* and, although selective cutting seems unlikely in light of its historical importance as a fodder species (Behre 1988), timber, furniture construction and fibre production may have favoured its selective removal. Large-scale forest clearance for agriculture would likely have enhanced *Tilia*'s establishment potential because of its ability to proliferate by stump

sprouting (Aaby 1983). Herbivore–plant interactions may also have played a significant role in shaping the Scandinavian landscape during the late-Holocene (Bradshaw & Mitchell 1999). Field studies show that *Tilia* is preferentially selected by deer, elk and domesticated livestock, while *Fagus* is least preferred, prompting Nilsson (1997) to conclude that grazing animals (both native and domesticated) have played a more important role than climate in altering Swedish boreo-nemoral forest succession in the late-Holocene. If most herbivore pressure in the past was due to domesticated rather than native herbivores, then *Tilia*'s decline may have been a consequence of changing human land-use patterns and/or increasing human populations. FORSKA2 simulation data (Fig. 4), however, indicate that *Tilia* was already starting to decline as a result of LIA cooling when human disturbance began to intensify, thus it is possible that LIA cooling weakened existing *Tilia* populations, making them more susceptible to anthropogenic pressures.

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