



ORIGINAL
ARTICLE



Soil phosphorus as a control of productivity and openness in temperate interglacial forest ecosystems

Petr Kuneš^{1*}, Bent Vad Odgaard¹ and Marie-José Gaillard²

¹Department of Geoscience, Aarhus University, Høegh-Guldbergs Gade 2, DK-8000 Århus C, Denmark, ²School of Pure and Applied Sciences, Linnaeus University, 39182 Kalmar, Sweden

ABSTRACT

Aim Observations of long chronosequences in forest ecosystems show that, after some millennia of build-up, biomass declines in relation to the slow depletion of soil phosphorus. Plants that dominate during this period of soil impoverishment have specialized strategies for P acquisition, including ectomycorrhiza or root clusters. We use quantitative, pollen-based reconstructions of regional vegetation in four Quaternary warm stages (Holocene, Eemian, Holsteinian, Harreskovian) to test whether inferred forest cover and productivity changes are consistent with long-term modification of soil nutrient pools.

Location Southern Scandinavia (Denmark, southern Sweden).

Methods The REVEALS model was used to estimate regional vegetation abundances of 25 pollen-type-equivalent taxa from pollen records of large sedimentary basins in southernmost Scandinavia. Based on the estimated regional vegetation, we then calculated time-series of Ellenberg indicator values for L (light), R (soil reaction) and N (a productivity proxy). We classified the vegetation records into distinct phases and compared these phases and the samples using hierarchical clustering and ordination.

Results All three interglacials developed coniferous or mixed forests. However, pure deciduous forests were never reached during the Holsteinian, while pure coniferous forests never developed in the Holocene. Above-ground productivity was inferred to be low initially, peaking in the first third of the warm stages and then slowly declining (except during the Holocene). Dominant trees of the post-peak phases all had ectomycorrhiza as a strategy for P acquisition, indicating that easily accessible P pools had become depleted. Increases in fire regimes may have amplified the inferred final drop in productivity. Mid/late Holocene productivity changes were much influenced by agricultural activities.

Main conclusions REVEALS vegetation estimates combined with Ellenberg indicator values suggest a consistent pattern in warm stages of initially rising productivity, followed by a long and slow decline. The P-acquisition strategies of dominant trees indicate that the decline reflects increasing P depletion of soils.

Keywords

Cromerian complex, Eemian, Ellenberg values, Harreskovian, Holocene, Holsteinian, pollen analysis, quantitative vegetation reconstruction, REVEALS, Scandinavia.

*Correspondence: Petr Kuneš, Department of Geoscience, University of Aarhus, Høegh-Guldbergs Gade 2, 8000 Århus C, Denmark. E-mail: petr@kunes.net

INTRODUCTION

Studies of natural forest ecosystems in long-term chronosequences indicate that, in the absence of disturbance, forest biomass will peak after a build-up phase of a few millennia,

and then decrease slowly (Wardle *et al.*, 2004). Along with the slow decrease in biomass, N : P ratios in soil humus increase, suggesting that P becomes limiting in later stages (Stevens & Walker, 1970; Wardle *et al.*, 2004). Striking examples of soil P limitations have been documented from Australia and South

Africa (Wardle *et al.*, 2004; Lambers *et al.*, 2008), where millions of years have passed since soil development initiated. However, long-term biomass declines have also been observed in younger landscapes that developed after glaciations 10,000–15,000 years ago, such as in Scandinavia (Wardle *et al.*, 2003).

Long-term changes in soil-P availability have been found to favour different plant nutrient-acquisition strategies (Lambers *et al.*, 2008). In the early stages of soil development, 'P-scavenging' strategies prevail, in which large volumes of soils are being searched for available inorganic P by rapidly growing roots and mycorrhizal fungi. In contrast, strategies in old soils tend to depend on 'P-mining' in which plants retrieve less accessible P-pools by exudation of carboxylates and phosphatase from root clusters or mycorrhizal symbionts (Lambers *et al.*, 2006, 2008). The scavenging strategy is morphologically and physiologically connected to plant–fungal symbiosis in the form of arbuscular mycorrhiza, while the mining strategy seems to be restricted to plants with ectomycorrhiza, ericoid mycorrhiza (Taylor *et al.*, 2009), or specialized 'cluster roots' (Lambers *et al.*, 2008). Such strategies may be relevant for understanding vegetation dynamics during the Quaternary period.

During the last 900,000 years, temperate and northern latitude ecosystems have been exposed to repeated cycles of long cold stages and shorter warm stages, as described by the classical model of the glacial/interglacial cycle by Iversen (1957). This model was modified by Andersen (1969, 1994) and Birks & Birks (2004), who incorporated nutrient dynamics. For a warm stage, the model predicts an initial rise in plant biomass to a maximum with peak N availability and sufficient P access followed by a biomass decline as soil P becomes limiting. While this model was originally formulated to explain patterns in traditional pollen records (Andersen, 1969; Birks, 1986), the interpretation of these records has so far been constrained by the inherent biases of classical pollen analysis, including differential pollen production and transport. However, recent developments in modelling pollen–vegetation relationships (REVEALS; Sugita, 2007a) have opened the way for a direct estimation of regional vegetation using fossil pollen records, permitting a more objective re-evaluation of the soil nutrient model for glacial/interglacial cycles.

While the glacial/interglacial model does not include disturbances such as herbivory, the role of grazing by megaherbivores in pristine forest ecosystems has recently achieved considerable interest as a potentially important factor controlling openness (Vera, 2000; Svenning, 2002; Mitchell, 2005). According to Vera's (2000) model, landscapes that would otherwise be densely forested are kept in a continuous degeneration/regeneration cycle ('wood pasture'; Kirby, 2004) by intensive herbivory, in some cases reaching savanna-like stages. This model predicts that the interglacial landscapes of central Europe would have been generally rather open, including during periods with productive soils otherwise capable of supporting dense forest.

This study was motivated by the following question: Can a consistent pattern of initially rising productivity followed by a

long and slow decline be inferred for warm stages in spite of possible differences between the stages in terms of soil conditions, disturbance [including grazing, as implied by Vera's (2000) hypothesis of herbivory-maintained openness], interspecific interactions and climate? To answer this question we discuss the possible controls of openness and productivity on the basis of REVEALS reconstructions and Ellenberg ecological values (Ellenberg *et al.*, 1992; Thompson *et al.*, 1993; Hill *et al.*, 1999). We compare the P-acquisition strategies (scavenging or mining) of dominant tree taxa across temporal series to test the hypothesis that the mining-type strategy dominates in the later stages of terrestrial ecosystems. The results are expected to further our understanding of long-term nutrient dynamics of temperate terrestrial ecosystems.

MATERIALS AND METHODS

Pollen records

Regional land cover was estimated based on pollen records from four southern Scandinavian sites with warm stage (i.e. interglacial or Holocene) lacustrine sequences: Krageholmssjön (Holocene; 220 ha), Hollerup (Eemian; > 70 ha), Vejlby (Holsteinian; > 125 ha), and Harreskov (Harreskovian; > 70 ha) (Fig. 1). All interglacial pollen counts were made by Andersen (1965), while Gaillard (1984) produced the Holocene pollen data. The Hollerup site (see Appendix S1a in Supporting Information) is well correlated palynologically with other Eemian (Marine Isotope Stage, MIS, 5e) sites in northern Europe (Müller, 1974a; Zagwijn, 1975; Cleveringa *et al.*, 2000; Granoszewski, 2003). Based on annually laminated sediments, the duration of the Eemian interglacial has been estimated at 10,000–11,000 years (Müller, 1974a), ending with a major cooling around 115 ka (Shackleton *et al.*, 2002). The Vejlby site (Appendix S1b) can be palynologically correlated with the Holsteinian/Mazovian interglacial (Müller, 1974b; Urban, 1995; Mamakowa, 2003). The correlation between the Holsteinian and the marine isotope stages is currently debated (e.g. Geyh & Müller, 2005; Nitychoruk *et al.*, 2006; Koutso-dendris *et al.*, 2010), but most studies [including land–sea data correlation (Desprat *et al.*, 2005)] argue for MIS 11. The duration of the Holsteinian has been estimated to be around 15,000 years (Kühl & Litt, 2007). Palynostratigraphically, the Harreskov site (Appendix S1c) can be safely correlated with the Hunteburg site in Germany and the Ferdinandówian sites of Poland (Hahne, 1996; Krzyszkowski *et al.*, 1996; Rzechowski, 1996). A palaeomagnetic reversal at the base of the Hunteburg site (Hahne, 1996) has been used as evidence of the Brunhes/Matuyama transition, implying that the Hunteburg series belongs to MIS 19 (Fromm, 1994). There are no varve-based estimates for the duration of the Harreskovian, but it seems reasonable to assume that it lasted 10,000 years or more. Further discussion on these correlations can be found in Ber (2005, 2006) and Zagwijn (1996).

The REVEALS approach (Sugita, 2007b) implies that the pollen loading on a lake surface is dominated by pollen

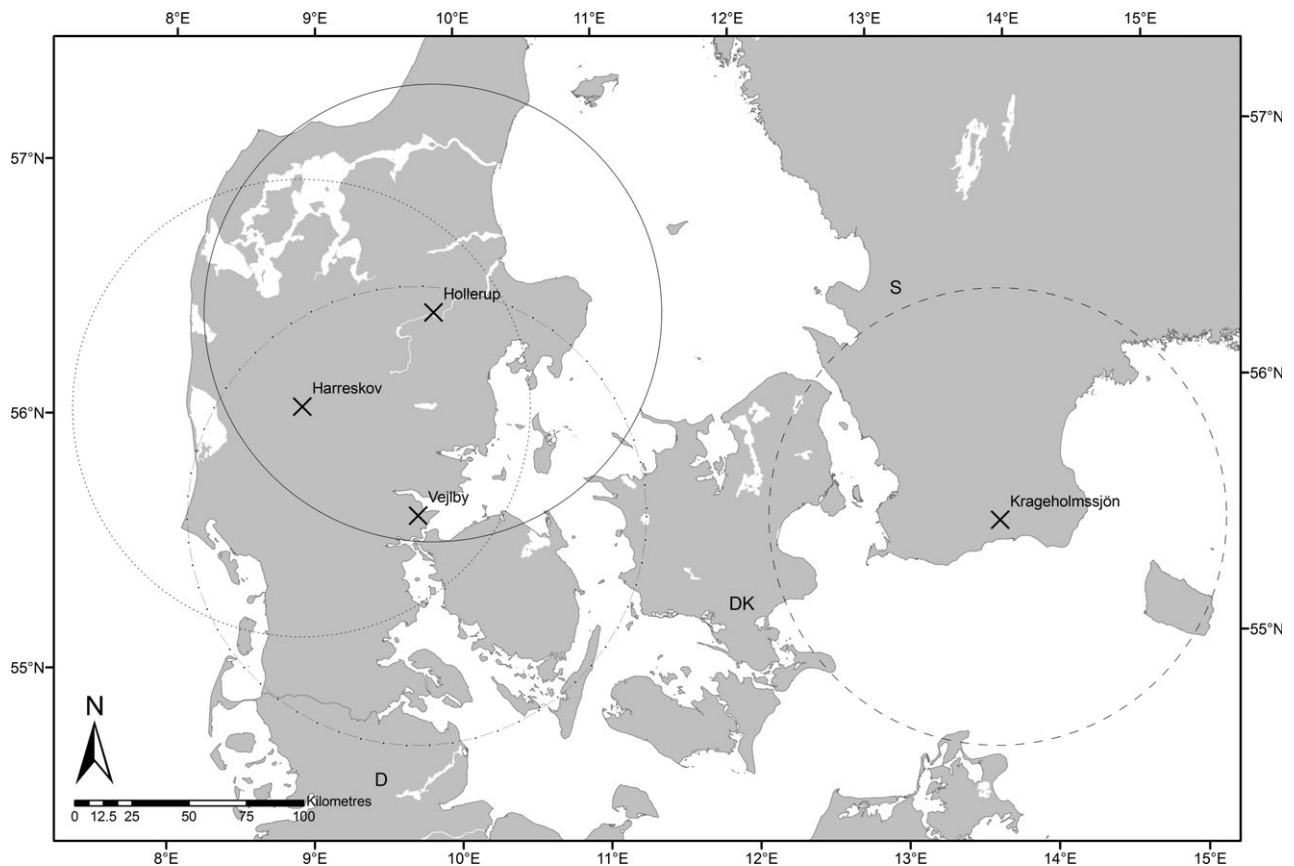


Figure 1 Map of southern Scandinavia indicating localities used in the study. Circles around each locality represent a 100 km radius.

originating from a large source area (i.e. 'background' pollen). The pollen data used should therefore be from large lakes of c. 100 ha or more (Sugita, 2007b). Unfortunately, the exact basin size may be difficult to identify for interglacial deposits because often only a few cores or sections are available. According to geological prospecting (Andersen, 1965, 1967; Björck *et al.*, 2000), all the interglacial sites selected for this study have basin diameters larger than 300–400 m, and all pollen records are assumed to represent regional vegetation (see below). No complete Holocene pollen record from a large lake exists in Denmark, so we use a record from the large lake Krageholmssjön in Scania, southern Sweden, for comparison with the Danish interglacials. The Krageholmssjön region is comparable to Denmark in terms of climate, geology, geomorphology and soils (Berglund, 1991). Also, the Holocene vegetation history is almost identical to that of fertile soils in Denmark (Odgaard & Rasmussen, 2000; Fritzboøger & Odgaard, 2010). Data on geology and inferred soils at each site are given in Appendix S2.

Vegetation reconstructions

The REVEALS model describes the relationship between regional vegetation and pollen deposition on the surface of large basins. The model assumes that pollen transport and deposition can be estimated using a dispersal function based

on Sutton's equations (Tauber, 1965). Model parameters include pollen productivity for each species, terminal fall speed for each pollen type, and wind speed.

The assumptions underlying REVEALS include: (1) pollen is transported by wind above the vegetation; (2) wind transport is uniform from all directions; (3) sedimentary basins are circular; (4) basins are large enough to be dominated by background pollen; (5) most of the pollen derive from within the chosen size of the region (Z_{\max}); and (6) pollen productivity can be estimated from modern vegetation and is constant through time and space. For further details on the REVEALS model and its validation, see Sugita (2007b) and Hellman *et al.* (2008a).

REVEALS v. 4.1.9 (Sugita, 2007b) was used on all sites separately using all available pollen assemblages. Following Hellman *et al.* (2008a), the radius of the regional area (Z_{\max}) was set to 100 km. Wind speed was set to 3 m s^{-1} in accordance with previous studies (Prentice, 1985; Sugita *et al.*, 1999; Hellman *et al.*, 2008a,b). Pollen productivity estimates (PPEs, Appendix S3) were determined relative to Poaceae using data from southern Sweden (Sugita *et al.*, 1999; Broström *et al.*, 2004), which is the largest PPE dataset in Scandinavia and comes from an area with a flora similar to Denmark's (Mossberg & Stenberg, 2005). Because no PPE for *Carpinus* was available from Sweden, the Danish value from Andersen (1970) was used. In the absence of a published PPE

for *Taxus*, we used the PPE of *Juniperus*, assuming it to be comparable. Fall speed of pollen (vg) was obtained from Eisenhut (1961) and Gregory (1973) for trees, and from Broström *et al.* (2004) for herbs. Altogether 25 pollen taxa were used in the model runs (Appendix S3), which excluded non-terrestrial or local pollen types. It is difficult to know whether members of the Cyperaceae were a part of the regional vegetation or merely represented local wetland stands. However, because none of the sites experienced terrestrialization (Andersen, 1965; Gaillard, 1984) Cyperaceae was included as a terrestrial component. The locally extinct genera *Pterocarya* (in the late Holsteinian) and *Celtis* (in the mid-Harreskovian) were excluded from the analysis as no PPE is available for *Celtis* and PPE for *Pterocarya* indicate that it is strongly over-represented palynologically (Filipova-Marinova *et al.*, 2010). Considering that these taxa are represented by pollen percentages < 1, they are assumed to have been minor elements in the vegetation.

Testing the REVEALS model in southern Sweden shows that it performs very well in estimating the cover of larger plant groups such as herbs, conifers, deciduous trees, and total trees. REVEALS also provides reasonable estimates for individual taxa (Hellman *et al.*, 2008a). Moreover, Soepboer *et al.* (2010) concluded that REVEALS estimates of modern land cover inferred from pollen data were more similar to the Swiss CORINE vegetation-cover data than pollen percentages.

Estimation of Ellenberg indices

Ellenberg indicator values (Ellenberg *et al.*, 1992; Thompson *et al.*, 1993; Hill *et al.*, 1999) for nitrogen (N), soil reaction (R) and light (L) were calculated for each sample based on vegetation composition reconstructed by REVEALS and weighted by taxon abundance (ter Braak & Barendregt, 1986; ter Braak, 1995; Diekman, 2003). Ellenberg indicator values are expressions on a 9-graded scale of realized plant-species niches in relation to one-dimensional resource availabilities (Ellenberg *et al.*, 1992).

Because the pollen morphology of Poaceae and Cyperaceae does not generally allow identification to genus or species level, these two taxa were not included in the Ellenberg indicator value calculations. For the rest of the terrestrial taxa, a median indicator value was calculated for each pollen type using relevant plant taxa of current south Scandinavian distribution (see Appendix S4). We used the modified British values (Hill *et al.*, 1999) in calculations.

Zonation

REVEALS vegetation estimates (as proportions) were plotted using C2 software v. 1.6.7 (Juggins, 2003). Pollen proportions were added to the diagram for comparison.

Zonation was performed to identify phases of relatively stable vegetation. This was done by identifying stages that were significantly different from those of the preceding period following the procedure applied by Bradshaw *et al.* (2005). The

oldest sample was compared sequentially to the following samples using squared chord distance (SCD; Prentice, 1980) as a dissimilarity measure. The level at which dissimilarity increased above a selected cut-off level was accepted as the transition to a new vegetation phase. The oldest sample of the new phase was then used as the template against which all later samples were compared, and so on. The analysis continued until the uppermost sample was reached. Davis (1995) suggested a cut-off level of 0.15 for SCD; we used 0.14 to achieve a slightly more detailed zonation.

Ordinations and cluster analysis

Principal components analysis (PCA) was applied to the REVEALS vegetation estimates in order to summarize vegetation changes and facilitate comparison of the warm stages. Detrended correspondence analysis (DCA) was also used, to check gradient length. All levels with REVEALS estimates from all sites were analysed simultaneously in CANOCO v. 4.5 (ter Braak & Šmilauer, 2002) on a covariance matrix, using logarithmic transformation of the percentage data and centering by samples and species. This is equivalent to the log-ratio transformation suggested by Aitchison (1986) to circumvent the problem of closure in percentage data.

Mean vegetation proportions were calculated for each zone and subsequently subjected to cluster analysis for comparison of all sites. We used hierarchical clustering with Ward's method of linkage and *R*-squared distances to measure differences between joined clusters (Johnson, 1967). Calculations were carried out using SYSTAT v. 9 (Wilkinson, 1998).

RESULTS

Eight vegetation phases were identified at Harreskov (Fig. 2), nine at Vejlbj (Fig. 3), six at Hollerup (Fig. 4), and seven at Krageholmssjön (Fig. 5). Two phases at Harreskov (Ha-1, Ha-8) and two phases at Vejlbj (Ve-1, Ve-3) have only one sample. Other phases contain at least three samples each.

Ellenberg's N (productivity, see Discussion) and R (soil reaction) show an initial increase followed by a significant decrease from the early warm-stage phases towards the end of all three interglacials. The largest drop is observed during coniferous vegetation phases. Early- to mid-Holocene records of productivity and soil reaction are similar to those of the interglacials, but there is little, if any, long-term decline during the late Holocene. Interglacial light (Ellenberg's L) values are initially high, but the lowest values (reflecting shady, closed forest stands) appear during the vegetation phases of the early-middle part of the interglacial, followed by a slow and steady increase. The early- to mid-Holocene exhibits a very similar development, but shows an increase in the reconstructed L index at 4000 ¹⁴C yr BP.

Among trees, those dependent entirely or partly on arbuscular mycorrhiza (Table 1) are most frequent during earlier phases of the interglacials, while those dependent on ectomycorrhiza dominate during their later stages (Fig. 6). Trees with

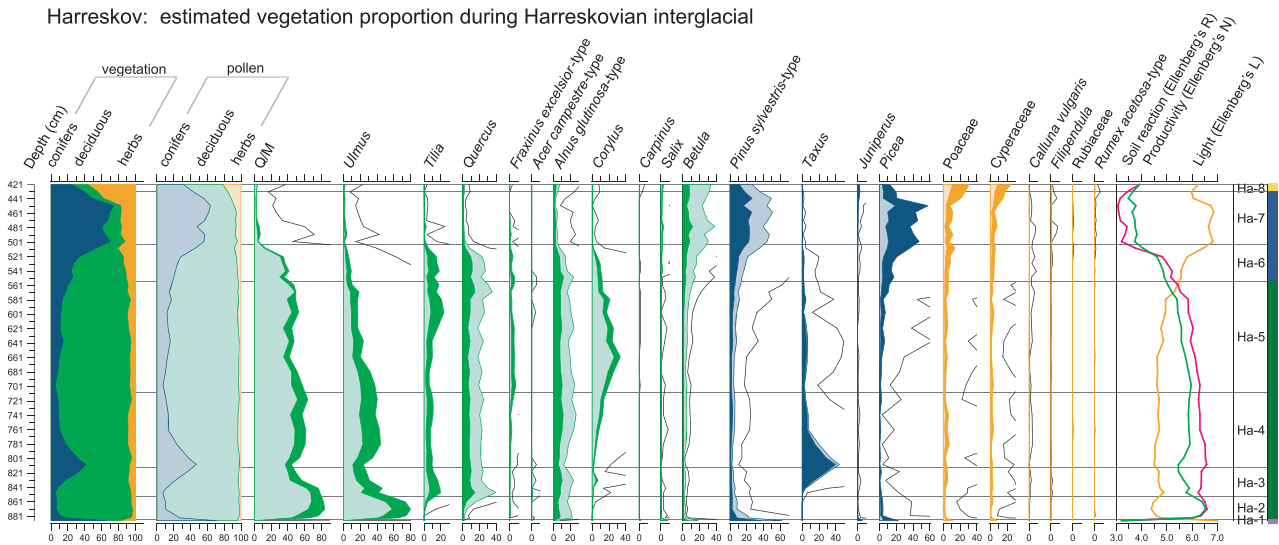


Figure 2 Diagram of REVEALS-estimated vegetation abundance compared with pollen proportions for the Harreskovian-aged locality Harreskov. Estimated vegetation proportions are displayed in darker colours, pollen proportions in lighter colours. Black solid lines over each curve represent 10× exaggeration of vegetation values. The colours of the sums on the left correspond to colours of individual taxa (conifers = blue, deciduous = green, herbs = yellow). Ellenberg ecological factors represent: N, productivity value; R, soil reaction; L, light. Colours in the column to the right refer to the classification by cluster analysis (Fig. 8).

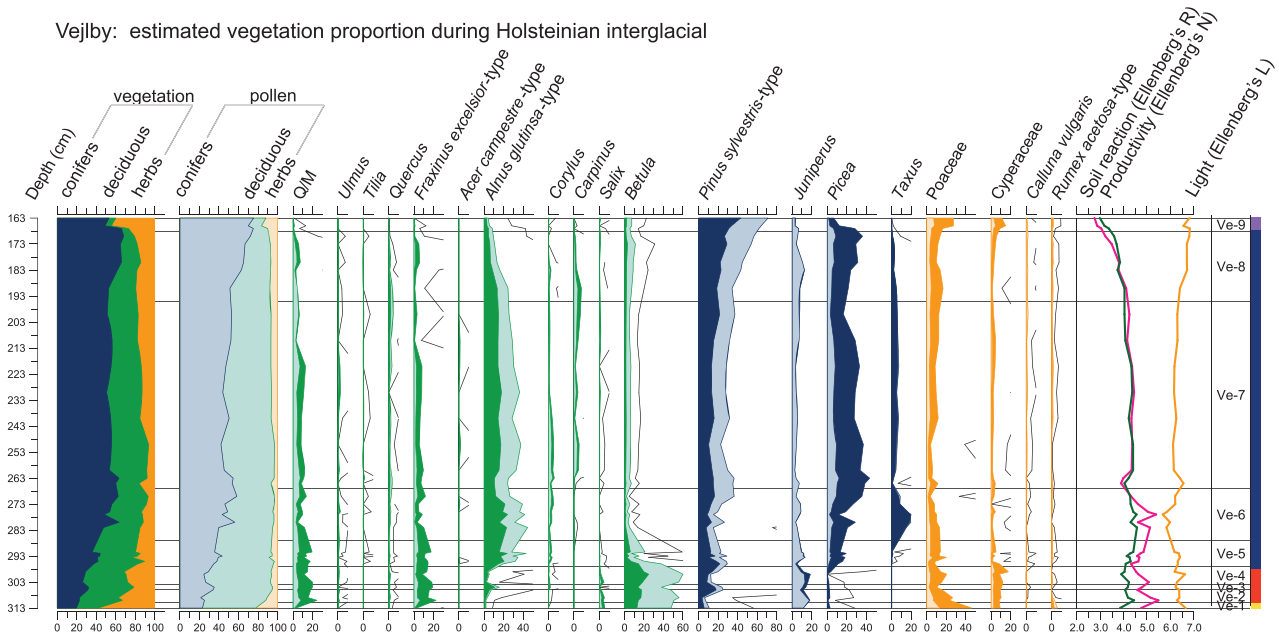


Figure 3 Diagram of REVEALS-estimated vegetation abundance compared with pollen proportions for the Holsteinian-aged locality Vejlbj (see Fig. 2 for symbol explanations).

arbuscular mycorrhiza also achieved maximum abundance during the early and middle Holocene.

DCA shows a first axis gradient-length of 1.75 standard deviations, indicating that linear ordination techniques are appropriate. The first two axes of the PCA result explain 53.8% of the total variance (axis 1 explains 33.7%; Fig. 7). The ordination summarizes the vegetation development followed during each stage and also reveals some differences between

stages. Axis 1 (Fig. 7e) gives conifers and species found on poor soils positive scores, while deciduous trees demanding better soils are given negative scores. Hence this axis may represent a soil nutrient gradient. Alternatively, axis 1 could be interpreted as a temperature gradient, but occurrence of scattered palynological indicators of high winter or summer temperatures (*Hedera*, *Ilex*, *Buxus* and *Viscum*) in deciduous as well as coniferous stages (see Appendix S1) would appear to

Hollerup: estimated vegetation proportion during Eemian interglacial

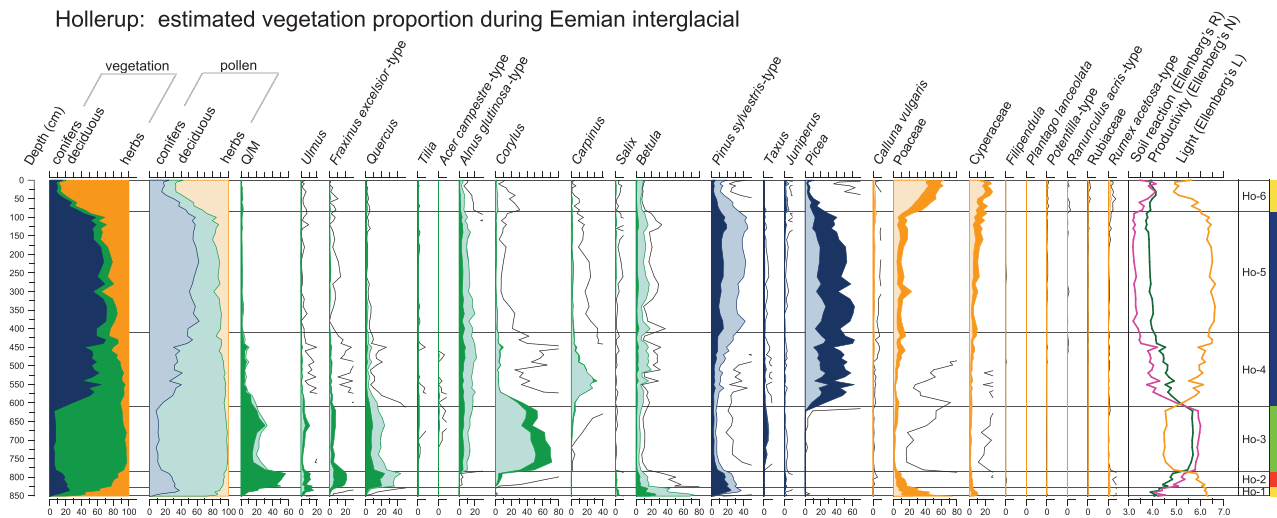


Figure 4 Diagram of REVEALS-estimated vegetation abundance compared with pollen proportions for the Eemian-aged locality Hollerup (see Fig. 2 for symbol explanations).

Krageholmssjön: estimated vegetation proportion during the Holocene

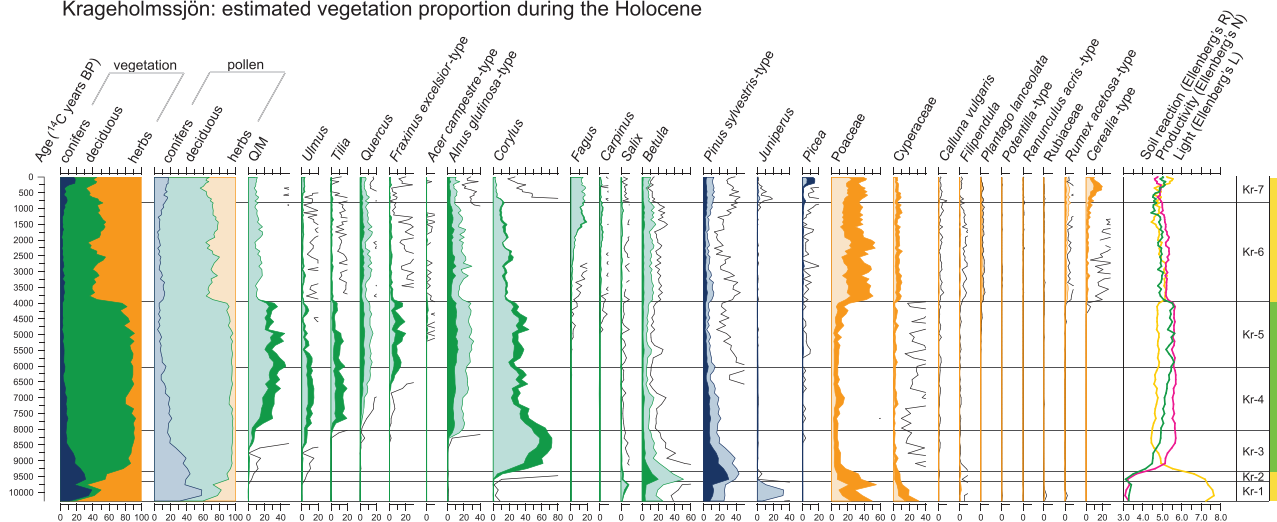


Figure 5 Diagram of REVEALS-estimated vegetation abundance compared with pollen proportions for the Holocene-aged locality Krageholmssjön. The time scale is given in uncalibrated radiocarbon years (^{14}C yr BP). See Fig. 2 for symbol explanations.

contradict such a conclusion. Axis 2 (Fig. 7e) separates light-demanding taxa such as herbs and pioneer trees (positive scores) from shade-tolerant woody plants (negative scores). The results of the ordination for Vejlbj (Fig. 7b) are especially influenced by conifers. The Hollerup record (Fig. 7c), in which *Picea* is especially abundant, shows major variations in vegetation along both axes 1 and 2, the Vejlbj record exhibits only some variation along axis 1 and, in contrast, the Harreskov record (Fig. 7a) is characterized by very little variation along axis 2. The Krageholmssjön record (Fig. 7d) shows variation between light-demanding taxa and deciduous trees, the variation being highest along axis 1.

Results of hierarchical clustering of mean vegetation proportions per zone are shown in Fig. 8. At R -squared distances higher than 2.5, three clusters can be identified: coniferous or mixed forest, open vegetation, and deciduous

forest. Each of the 3 major clusters can be subdivided into two subclusters: coniferous/mixed forest splits into spruce (*Picea*)- and pine (*Pinus*)-dominated forest types; open vegetation into very open and semi-open; and the deciduous forest into elm (*Ulmus*) and hazel (*Corylus*)/oak (*Quercus*) types.

Vegetation dynamics

An *open vegetation* type (Figs 7 & 8, 20–50% forest cover) developed during the early stages of all warm stages except the Harreskovian. The lack of a fully open stage at Harreskov probably reflects a sedimentary hiatus at this site, because late-glacial pollen records are known from other continuous Harreskovian sites in Jutland (B.V. Odgaard, unpublished). During the open phase at the three other sites, tree cover was less than 70% and comprised a mixture of conifers (*Pinus*,

Table 1 Mycorrhiza types in dominant south Scandinavian warm stage trees according to Harley & Harley (1987). Less common types are bracketed. Data on root clusters are from Lambers *et al.* (2006, 2008).

	Arbuscular mycorrhiza	Ectomycorrhiza	Cluster roots
<i>Taxus baccata</i>	x		
<i>Ulmus glabra</i>	x		
<i>Acer campestre/platanoides</i>	x	(x)	
<i>Fraxinus excelsior</i>	x	(x)	
<i>Juniperus communis</i>	x	x	
<i>Populus tremula</i>	x	x	
<i>Salix spp.</i>	x	x	
<i>Alnus glutinosa</i>	x	x	x
<i>Tilia cordata/platyphyllos</i>	(x)	x	
<i>Betula pendula/verrucosa</i>		x	
<i>Carpinus betulus</i>		x	
<i>Corylus avellana</i>		x	
<i>Fagus sylvestris</i>		x	
<i>Picea abies</i>		x	
<i>Pinus sylvestris</i>		x	
<i>Quercus robur/petraea</i>		x	

some *Juniperus*) and pioneer deciduous trees (*Betula*, *Salix*). A similar vegetation type occurred during the latest phases of the interglacials, marking the transition to the subsequent cold stages at Harreskov and Hollerup. The final stages at Krageholmssjön, from 4000 yr BP onwards, are also classified as open vegetation types, almost certainly as a result of farming practices (Gaillard, 1984).

The vegetation type *open vegetation with mixed forest* (60–80% forest cover) developed as a successor to open vegetation at Vejlbj and Hollerup. A striking feature is the abundance of *Fraxinus* (ash) in this phase, which may indicate the existence of glacial refugia of ash trees not far to the south during the preceding cold stages.

Deciduous forest with elm (Ulmus) and Tilia as co-dominants (90–97% forest cover) developed after the early phase at Harreskov (Fig. 2). It is characterized by shade-tolerant species that require relatively fertile soils, by intense competition and by dense forest cover. Although playing a minor role, the appearance of *Celtis* (see Appendix S1c) is noteworthy. In Europe today *Celtis australis* L. has a widespread Mediterranean distribution and prefers deep, moist soils, although it may also occur on shallow, dry soils (Juan *et al.*, 2006).

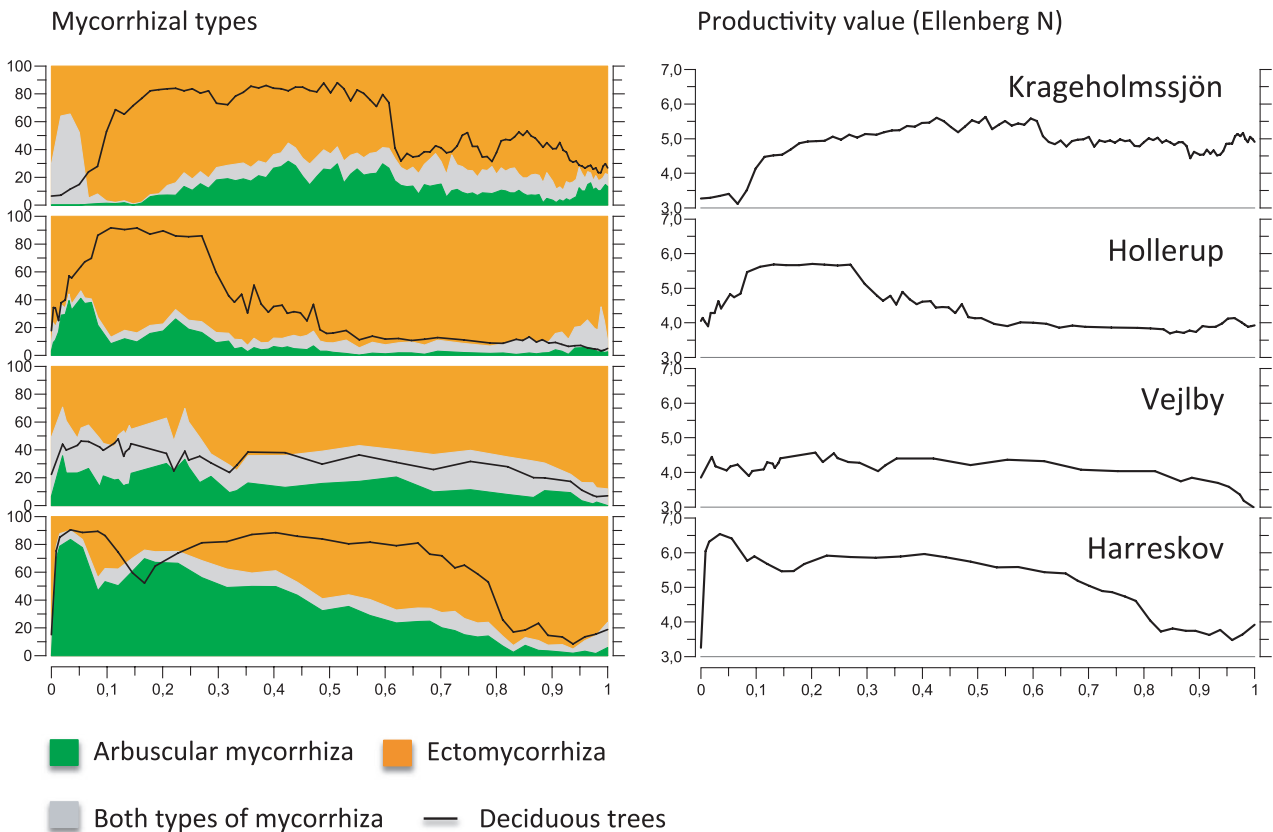


Figure 6 Frequencies of trees (as a percentage of all trees) according to mycorrhiza type through each warm stage. Abundance of deciduous trees (as a percentage of terrestrial vegetation) and Ellenberg N-values are shown for comparison. Depth (age for Krageholmssjön) scale was standardized to a scale from 0 to 1 for diagrammatic comparison.

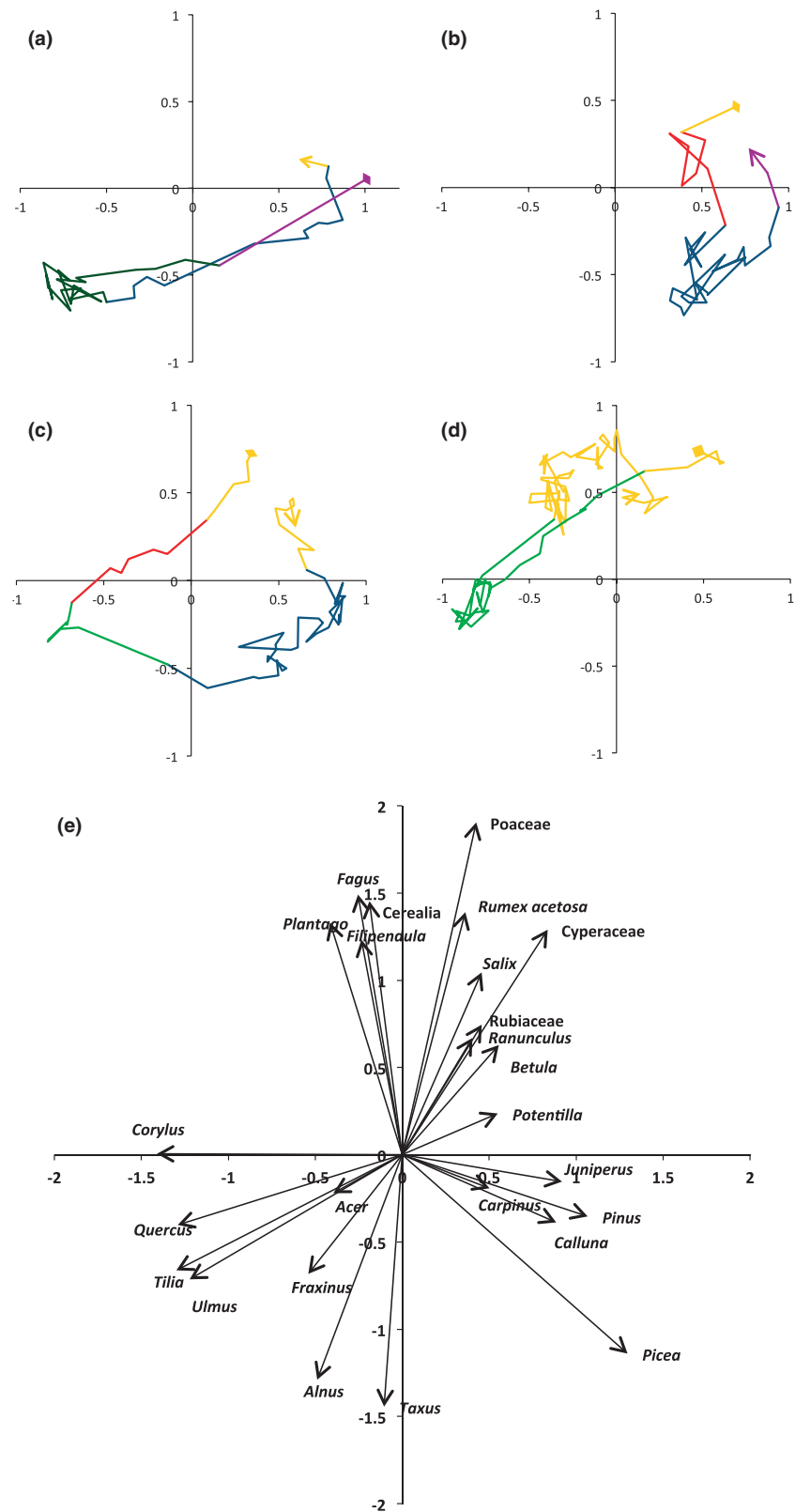


Figure 7 Principal components analysis (PCA) ordination scatterplots of sample (a–d) and pollen-type (e) scores. Different warm stages are displayed separately: (a) Harreskov, (b) Vejlbj, (c) Hollerup, (d) Krageholmsjön. The lines connect sample scores in chronological order, with an arrow at the youngest layer. Line colours refer to vegetation units as identified by cluster analysis (Fig. 8).

Deciduous forest with hazel/oak was the only deciduous phase at Hollerup (Eemian) and Krageholmsjön (Holocene). Dominated mainly by hazel and other shade-intolerant trees [oak, ash, and alder (*Alnus*)], this vegetation appears to have been

open (80–95% forest cover) and probably patchy. Deciduous phases are of quite variable duration: absent from the Holsteinian, short in the Eemian, and longer in the Harreskovian and the Holocene.

Ward's hierarchical clustering (*R*-squared distance)

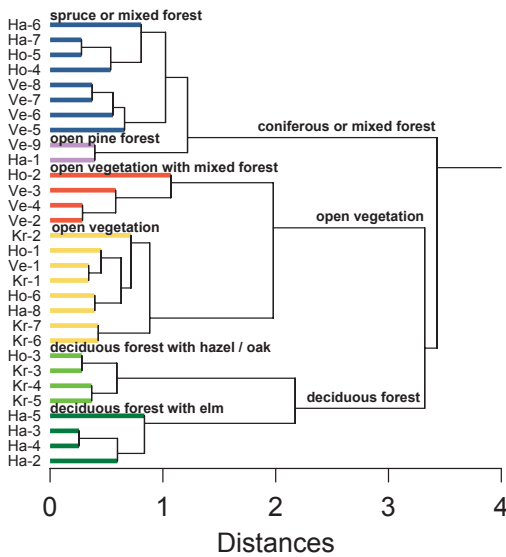


Figure 8 Classification dendrogram for Ward's hierarchical clustering of averaged REVEALS estimates of vegetation abundance for each zone as identified by the zonation procedure applied to each vegetation diagram of Figs 2–5. Zones have the same labelling as in the vegetation diagrams of Figs 2–5. Colours of terminal nodes correspond to the colouring of the right-hand columns in the vegetation diagrams.

Spruce or mixed forest developed during each of the three interglacials, but not the Holocene. Through the Holsteinian, vegetation dominated by conifers was the only forest type established. It was exceptional in having rather open conditions during these phases (Ve 4–8), in which grasses and *Juniperus* were important throughout. Forests with spruce developed in the Harreskovian and the Eemian following deciduous phases. One of the most striking results of the REVEALS estimation is the apparent dominance of *Picea* during periods in which deciduous trees became less prominent and forest types more open. Periods of spruce domination generally ended with *Pinus* becoming co-dominant and the absence of the most thermophilous taxa. Forest cover during these stages was between 70 and 85%. Comparison with the duration estimates of the Eemian and Holsteinian published by Müller (1974a,b) suggests that the coniferous period at Hollerup lasted at least 6000 years, while the same period at Vejlbjy was at least 10,000 years long. The coniferous/mixed forest period was relatively long during the Holsteinian, of intermediate duration in the Eemian, apparently short in the Harreskovian and virtually absent from the Holocene. This variation is inversely related to the duration of the preceding deciduous period. Interestingly, low but consistent pollen counts of *Abies* and *Pterocarya* (see Appendix S1b) may indicate that these taxa persisted through the late coniferous phase of the Holsteinian. *Pterocarya* is likely to have grown on temporarily inundated riversides, as *Pterocarya fraxinifolia*

(Poir.) Spach does today along the southern coasts of the Black and Caspian seas (Sheykholislami & Ahmadi, 2009). Considering the very high pollen productivity of *Pterocarya* (Filipova-Marinova *et al.*, 2010), interglacial pollen records in Northern Europe perhaps reflect long-distance transport rather than local presence.

In summary, open vegetation developed at the beginning and end of all the warm stages examined here, while coniferous and mixed forests occurred in all except the Holocene, and productive deciduous forests grew in all except the Holsteinian.

DISCUSSION

Ellenberg N-values

Ellenberg *et al.* (1992) originally interpreted the N-value as an index of the amount of nitrogen available during the growing season. However, a number of studies in grassland and heathland communities have shown high correlations between mean Ellenberg N site scores and biomass production (Melman *et al.*, 1988; Hill & Carey, 1997; Schaffers & Šýkora, 2000; Diekman, 2003; Wagner *et al.*, 2007) or with standing crop (Ertsen *et al.*, 1998). In contrast, correlations with soil N-related measures are reported as absent or weak (Hill & Carey, 1997; Schaffers & Šýkora, 2000; Diekman, 2003). Ellenberg did not propose an index for phosphorus (P), but, based on the studies cited above, the Ellenberg N value calculated for vegetation seems to describe soil nutrient status and generally reflects the ability of the soil to produce plant biomass. Hill & Carey (1997) accordingly suggested that Ellenberg's 'N' should be interpreted as a productivity value rather than as an indicator of soil nitrogen availability, a suggestion we follow here. Although not shown by direct empirical studies, it seems reasonable to assume that above-ground productivity of trees is also strongly positively correlated with Ellenberg's N.

Controls of productivity and openness through warm stages

At all four sites, PCA results show a trajectory from top right to bottom left, then right and finally back to the top again (Fig. 7). If axes 1 and 2 represent soil and light gradients, this pattern represents a progression from relatively open vegetation to closed forest on fertile soils, then soil impoverishment followed by a gradual re-opening of the forest. While the Hollerup (Eemian) site shows strong variance along both soil and light gradients, the light gradient was dominant at Vejlbjy (Holsteinian), while the soil gradient was prominent at Harreskov (Harreskovian). Krageholmssjön (Holocene) differs from the rest, showing pronounced variation along the soil gradient, while tending towards open landscapes in the middle/late part.

The same general trends are evident in the Ellenberg values. Despite the problems associated with the indicator values of

grasses and sedges mentioned above, there are clear indications that early forest types were less productive (i.e. had lower N-values) than immediately succeeding types. Maximum soil fertility and maximum plant productivity seem to have developed within the first third of the Pleistocene warm stages, while this process was slightly delayed for the Holocene.

Our analysis of time-series of forest cover, productivity, soil reaction and light estimates, as well as interpretations of ordination axes, lead us to suggest the following, generalized pattern of warm-stage development: initially, open vegetation or pioneer vegetation was replaced by denser vegetation of mostly deciduous trees, demanding in terms of soil nutrients. This highly productive vegetation was replaced by forests of tree species that were less demanding in terms of soil nutrients. These forest types generally had a higher representation of conifers, became increasingly open, and were ultimately replaced by very open forest types at the transition to the next cold phase. Possible controls on productivity and openness include climate, fire, grazing and soils, each of which is discussed below.

Climate

Most reconstructions of interglacial climate in Central Europe are based on pollen data (e.g. Kühl & Litt, 2007; Brewer *et al.*, 2008) and are therefore not independent of the data we have used. Tzedakis *et al.* (2009) argue that the cooler climates of MIS 13–19 (assumed to include the Harreskovian interglacial) recorded by Jouzel *et al.* (2007) were related to relatively low atmospheric CO₂ concentrations. Later interglacials had higher CO₂ concentrations and were presumably warmer. Marine and lacustrine isotope data from the Eemian suggest that temperature peaked during the early interglacial, followed by a gradual decrease towards the end (Litt *et al.*, 1996; Shackleton *et al.*, 2002). The same pattern seems to hold for the Holocene and MIS 7–9, but during MIS 11–17 the temperature peak occurs later (Jouzel *et al.*, 2007; Orbelli *et al.*, 2010). Climate changes at the onset of each warm stage triggered a prolonged adjustment in plant distributions. If climate were the only control of biomass production, however, the timing of peaks in temperature and productivity during each warm stage would be expected to match. As described above, productivity and forest density peaked in early parts of warm stages thus not always in synchronicity with temperature peaks. Still, climate may have been important in shaping fire regimes (see below), which could have had important implications for past biomass (Power *et al.*, 2008).

Fire

Coxon *et al.* (1994) concluded, from the frequent occurrence of macroscopic charred wood in Irish Gortian deposits, that fire was an important environmental factor in the Holsteinian interglacial in Ireland. Fires during this interglacial could have been fuelled by flammable *Pinus–Calluna* vegetation. Frequent fires would not preclude the continuous presence of fire-

intolerant *Juniperus*, because this shrub could have been part of post-fire succession. Generally coniferous forest is more flammable than deciduous forest and it is likely that the openness of coniferous forest observed during warm stages was, to some extent, controlled by fire. This hypothesis remains to be tested in places other than the Irish Holsteinian site.

In contrast to the interglacials, natural fire regimes of the early and mid-Holocene are relatively well documented in southern Scandinavia (Odgaard, 1994; Carcaillet *et al.*, 2002; Greisman & Gaillard, 2009; Olsson *et al.*, 2010) although some uncertainty persists as to the role of Mesolithic human populations in burning (Regnell *et al.*, 1995). High fire frequencies have been documented for the period 8000–4000 cal. yr BP in southern Scandinavia (e.g. Odgaard, 1994; Greisman & Gaillard, 2009; Olsson *et al.*, 2010) and these fires caused recurrent vegetation disturbances, especially on less fertile soils with more flammable vegetation (e.g. pine or dwarf shrubs).

Grazing

Thanks to a rather extensive fossil record, knowledge of the large herbivores present in central European warm stages is relatively good. This is true for the Holsteinian and certainly so for the Eemian and Holocene (Kurtén, 1968; Bradshaw & Mitchell, 1999; Bradshaw *et al.*, 2003), but not so for the Harreskovian (Aaris-Sørensen, 1998). Large herbivores characteristic of the interglacials include species of elephant, rhinoceros, bison, aurochs, deer and moose (Bradshaw *et al.*, 2003) and there is no reason to suppose that the fauna of an early mid-Pleistocene interglacial, such as the Harreskovian, would have lacked these animals. The horse seems to have been a characteristic animal of the Holsteinian, while apparently absent from Eemian landscapes (Bradshaw *et al.*, 2003). The Holocene fauna of north-western Europe was completely different, lacking species of elephant, rhinoceros and giant deer, leaving aurochs as the dominant large grazer. Faunal population sizes during the warm stages are unknown. With the exception of the Holocene, the lack of high-resolution temporal records of mammalian fossils precludes an analysis of the faunal record in relation to warm-stage vegetation phases. Radiocarbon-dated aurochs remains from Denmark indicate that these animals were most common from 10,000–9000 cal. yr BP, after which their populations went into sharp decline as a result of Mesolithic hunting (Aaris-Sørensen, 1998). In Sweden, it seems that the aurochs was already extinct by 7500 cal. yr BP (Ekström, 1993), while Jutland aurochs in contact with the central European population survived until about 3000 cal. yr BP (Aaris-Sørensen, 2009).

It is difficult to evaluate the effects of large herbivores on vegetation through the more open periods. However, our openness reconstructions indicate that periods with maximum Ellenberg N-values and deciduous-dominant forest must generally have supported dense vegetation, a finding that gives little support to the landscape scenario known as the

'wood-pasture hypothesis' (Vera, 2000). Locally, grazing may have added to the openness of forests, but testing this theory of patchy landscapes would require more pollen data from small interglacial basins (reflecting stand-scale vegetation – see Sugita, 1994) than is currently available. A small-basin study at Egersund (Andersen, 1975; van Geel & Andersen, 1988) seems to support the existence of dense forest during the Eemian deciduous forest period, but quantitative reconstruction using the LOVE model (Sugita, 2007c) of the vegetation has not been attempted. In his meta-analysis of fossil plant and mammal records, Svenning (2002) concludes that the resource areas of large interglacial herbivores would have focused on river valleys, while upland ecosystems were probably closed forest, little influenced by grazing.

Soils

Our data (Table 1, Figs 2–6) clearly indicate that trees dependent entirely or partly on arbuscular mycorrhiza (P-scavengers: *Taxus*, *Ulmus*, *Fraxinus*, *Acer*) were dominant only during the early and/or deciduous phases of the interglacials. In contrast, P-mining type (ectomycorrhizal) trees were often frequent throughout warm stages, but were the only dominants of later forest stages. This observation is in accordance with the long-term soil nutrient model outlined above. If P were not becoming less available during each warm stage, it would be expected that trees with a scavenging strategy would also be common in later phases. The gradual decline of productivity from early peak values is probably related to slow P-depletion in soils. Fire may have contributed to this productivity decline by opening forest gaps and encouraging the expansion of flammable, fire-tolerant species (conifers, *Calluna*). Because conifers and *Calluna* can also cause rapid podzolization, a feedback loop may form between fire, soil impoverishment, vegetation flammability and openness.

Trends in productivity development are roughly identical in the four warm stages, irrespective of dominant soil types (Appendix S2). The Holsteinian (Vejlby) differs slightly by having generally lower productivity values and a less pronounced peak in the early part of the warm stage. It is possible that soil P at the beginning of the Holsteinian was lower than at the beginning of the other warm stages. Generally low soil-P levels would be consistent with the predominance of *Alnus* during most of the Holsteinian. *Alnus* is one of the few northern temperate plants to possess cluster roots for effective P-mining (Table 1) on top of its symbiosis with N-fixing actinomycetes (Bond *et al.*, 1954).

Methodological issues associated with regional vegetation reconstruction and Ellenberg indices

In the forest phases, REVEALS estimates of Cyperaceae are generally below 2%; hence it does not influence greatly the total proportion of open-land cover, even though it may not be exclusively part of the terrestrial vegetation. In the early and late phases of each warm stage, however, it is probable that

some of the Cyperaceae pollen represents plants growing on the lake margins; thus the inclusion of Cyperaceae as a terrestrial taxon might overestimate the proportion of open land somewhat during those periods.

Some of the complications in the REVEALS reconstruction are related to model assumptions, in particular that pollen production of individual taxa is constant through space and time. PPEs obtained so far in Europe (Broström *et al.*, 2008) show geographical and elevational variation. Moreover, it is unlikely that pollen production has been stable through time due to, for instance, climate changes (Hicks, 2006). Basin size is an important parameter in governing the source-area of pollen and needs to be sufficiently large to provide a regional-scale signal. Information about the size of basins during the studied interglacials is incomplete but, according to the available cores and exposures, the two smaller sites (Harreskov, Hollerup) were probably larger than indicated (see Materials and Methods). The good pollen-stratigraphical correlation of the Danish interglacials with other interglacial pollen-sequences in northern-central Europe (Müller, 1974a; Zagwijn, 1975, 1996; Hahne, 1996) indicates that they are representative of broad-scale changes. Although land–sea configurations have varied through the Middle and Late Quaternary, setting Z_{\max} to 100 km probably means inclusion of larger areas of sea (non-pollen producing areas, Fig. 1). However, a sensitivity test shows there are no significant differences in vegetation estimations, when using 100, 50 or 25 km radii (Spearman rank correlation tests showed no significant differences in REVEALS estimates – $P < 0.001$, $\rho = 0.99$).

Calculation of Ellenberg indicator values is somewhat hampered by the limited taxonomic resolution of pollen data. The families of Poaceae and Cyperaceae, both represented by only one pollen type, comprise a large number of species with marked differences in soil preferences. Exclusion of these families causes a loss of ecological information and, for this reason, the Ellenberg indicator values in the forest phases should be regarded as more reliable than values in the very early and very late phases, in which grasses, sedges and herbs were prominent. In spite of these methodological issues, we regard the REVEALS-based reconstructions as the best available estimates for vegetation density and the balance between conifers and deciduous forest cover during warm stages.

CONCLUSIONS

Our results based on REVEALS vegetation estimates and Ellenberg indices suggest a consistent pattern in warm stages of initially rising productivity, followed by a long, slow decline. The P-acquisition strategies of dominant trees indicate that the decline reflects P-depletion in soils. This pattern seems to override possible differences due to soil types, climate and disturbance.

The coniferous phases of the interglacials appear to have been more open than previously assumed, but the deciduous forest phases were probably dominated by dense forest stands. This result gives little support to the hypothesis that at

landscape-scale grazing by large herbivores could prevent dense forests from dominating temperate fertile upland soils during the deciduous stages.

ACKNOWLEDGEMENTS

We acknowledge Shinya Sugita for providing us with an unreleased version of the computer program REVEALS v. 4.1.9, for advice for formatting data for input, and for the choice of Z_{\max} . We also thank Christian Kronborg for discussions about Quaternary stratigraphy and information about the lithology of Danish glacial deposits. The manuscript was improved by suggestions from Thomas Giesecke, Jens-Christian Svenning and an anonymous reviewer as well as by linguistic suggestions from Simon Connor. This study was supported through a postdoctoral scholarship from the Carlsberg Foundation to Petr Kuneš. We also acknowledge the NordForsk-sponsored LANDCLIM network and its members for inspiring workshops and useful discussions on topics related to the present paper, in particular REVEALS applications.

REFERENCES

- Aaris-Sørensen, K. (1998) *Danmarks forhistoriske dyreverden*. Gyldendal, Copenhagen.
- Aaris-Sørensen, K. (2009) Diversity and dynamics of mammalian fauna in Denmark throughout the last glacial-interglacial cycle, 115–0 kyr BP. *Fossils and Strata*, **57**, 1–59.
- Aitchison, J. (1986) *The statistical analysis of compositional data*. Chapman and Hall, London.
- Andersen, S. (1969) Interglacial vegetation and soil development. *Meddelelser fra Dansk Geologisk Forening*, **19**, 90–102.
- Andersen, S. (1970) The relative pollen productivity and pollen representation of North European trees, and correction factors for tree pollen spectra: determined by surface pollen analyses from forests. *Danmarks Geologiske Undersøgelse, II. række*, **96**, 1–99.
- Andersen, S.T. (1965) Interglacialer og interstadialer i Danmarks kvartær. *Meddelelser fra Dansk Geologisk Forening*, **1965**, 486–506.
- Andersen, S.T. (1967) Kvartærtiden. Istider og mellemistider i Danmark. *Danmarks Natur 1, Landskabernes opståen* (ed by A. Nørrevang and T.J. Meyer), pp. 199–250. Politikens Forlag, Copenhagen.
- Andersen, S.T. (1975) The Eemian freshwater deposit at Egernsund, south Jylland, and the Eemian landscape development in Denmark. *Danmarks Geologiske Undersøgelse, Årbog*, **1974**, 49–70.
- Andersen, S.T. (1994) History of the terrestrial environment in the Quaternary of Denmark. *Bulletin of the Geological Society of Denmark*, **41**, 219–228.
- Ber, A. (2005) Polish Pleistocene stratigraphy – A review of interglacial stratotypes. *Netherlands Journal of Geosciences—Geologie en Mijnbouw*, **84**, 61–76.
- Ber, A. (2006) Pleistocene interglacials and glaciations of northeastern Poland compared to neighbouring areas. *Quaternary International*, **149**, 12–23.
- Berglund, B. (ed.) (1991) *The cultural landscape during 6000 years in southern Sweden: the Ystad Project*. Munksgaard, Copenhagen.
- Birks, H.J.B. (1986) Late-Quaternary biotic changes in terrestrial and lacustrine environments, with particular reference to north-west Europe. *Handbook of Holocene palaeoecology and palaeohydrology* (ed. by B. Berglund), pp. 3–65. John Wiley & Sons, Chichester.
- Birks, H.J.B. & Birks, H.H. (2004) Paleocology: the rise and fall of forests. *Science*, **305**, 484–485.
- Björck, S., Noe-Nygaard, N., Wolin, J., Houmark-Nielsen, M., Hansen, H.J. & Snowball, I. (2000) Eemian lake development, hydrology and climate: a multi-stratigraphic study of the Hollerup site in Denmark. *Quaternary Science Reviews*, **19**, 509–536.
- Bond, G., Fletcher, W. & Ferguson, T. (1954) The development and function of the root nodules of *Alnus*, *Myrica* and *Hippophae*. *Plant and Soil*, **5**, 309–323.
- ter Braak, C.J.F. (1995) Calibration. *Data analysis in community and landscape ecology* (ed. by R.H.G. Jongman, C.J.F. ter Braak and O.F.R. van Tongeren), pp. 78–90. Cambridge University Press, Cambridge.
- ter Braak, C.J.F. & Barendregt, L.G. (1986) Weighted averaging of species indicator values: its efficiency in environmental calibration. *Mathematical Biosciences*, **78**, 57–72.
- ter Braak, C.J.F. & Šmilauer, P. (2002) *CANOCO reference manual on CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5)*. Microcomputer Power, Ithaca, NY.
- Bradshaw, E.G., Rasmussen, P. & Odgaard, B.V. (2005) Mid-to late-Holocene land-use change and lake development at Dallund Sø, Denmark: synthesis of multiproxy data, linking land and lake. *The Holocene*, **15**, 1152–1162.
- Bradshaw, R.H.W. & Mitchell, F.J.G. (1999) The palaeoecological approach to reconstructing former grazing–vegetation interactions. *Forest Ecology and Management*, **120**, 3–12.
- Bradshaw, R.H.W., Hannon, G.E. & Lister, A.M. (2003) A long-term perspective on ungulate–vegetation interactions. *Forest Ecology and Management*, **181**, 267–280.
- Brewer, S., Guiot, J., Sánchez-Goñi, M.F. & Klotz, S. (2008) The climate in Europe during the Eemian: a multi-method approach using pollen data. *Quaternary Science Reviews*, **27**, 2303–2315.
- Broström, A., Sugita, S. & Gaillard, M.J. (2004) Pollen productivity estimates for the reconstruction of past vegetation cover in the cultural landscape of southern Sweden. *The Holocene*, **14**, 368–381.
- Broström, A., Nielsen, A.B., Gaillard, M., Hjelle, K., Mazier, F., Binney, H., Bunting, J., Fyfe, R., Meltsov, V., Poska, A., Räsänen, S., Soepboer, W., Stedingk, H., Suutari, H. & Sugita, S. (2008) Pollen productivity estimates of key European plant taxa for quantitative reconstruction of past vegetation: a review. *Vegetation History and Archaeobotany*, **17**, 461–478.

- Carcaillet, C., Almquist, H., Asnong, H. *et al.* (2002) Holocene biomass burning and global dynamics of the carbon cycle. *Chemosphere*, **49**, 845–863.
- Cleveringa, P., Meijer, T., van Leeuwen, R.J.W., de Wolf, H., Pouwer, R., Lissenberg, T. & Burger, A.W. (2000) The Eemian stratotype locality at Amersfoort in the central Netherlands: a re-evaluation of old and new data. *Geologie en Mijnbouw–Netherlands Journal of Geosciences*, **79**, 197–216.
- Coxon, P., Hannon, G. & Foss, P. (1994) Climatic deterioration and the end of the Gortian Interglacial in sediments from Derrynadivva and Burren Townland, near Castlebar, County Mayo, Ireland. *Journal of Quaternary Science*, **9**, 33–46.
- Davis, O.K. (1995) Climate and vegetation patterns in surface samples from arid western U.S.A.: application to Holocene climatic reconstructions. *Palynology*, **19**, 95–117.
- Desprat, S., Sánchez Goñi, M., Turon, J., McManus, J., Loutre, M., Duprat, J., Malaizé, B., Peyron, O. & Peypouquet, J. (2005) Is vegetation responsible for glacial inception during periods of muted insolation changes? *Quaternary Science Reviews*, **24**, 1361–1374.
- Diekmann, M. (2003) Species indicator values as an important tool in applied plant ecology – a review. *Basic and Applied Ecology*, **4**, 493–506.
- Eisenhut, G. (1961) *Untersuchungen über die Morphologie und Ökologie der Pollenkörner heimischer und fremdländischer Waldbäume* (translated into English by T.S. Jackson and P. Jaumann, 1989). Paul Parey, Hamburg.
- Ekström, J. (1993) The late Quaternary history of the urus (*Bos primigenius* Bojanus 1827) in Sweden. *LUNDQUA Thesis*, **29**, 100–129.
- Ellenberg, H., Weber, H., Düll, R., Wirth, V., Werner, W. & Paulißen, D. (1992) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, **18**, 1–248.
- Ertsen, A.C.D., Alkemade, J.R.M. & Wassen, M.J. (1998) Calibrating Ellenberg indicator values for moisture, acidity nutrient availability and salinity in the Netherlands. *Plant Ecology*, **135**, 113–124.
- Filipova-Marinova, M.V., Kvavadze, E.V., Connor, S.E. & Sjögren, P. (2010) Estimating absolute pollen productivity for some European Tertiary-relict taxa. *Vegetation History and Archaeobotany*, **19**, 351–364.
- Fritzboeger, B. & Odgaard, B. (2010) Skovenes historie. *Naturen i Danmark, bd. 4, Skovene* (ed. by P.F. Møller and K.S. Jensen), pp. 55–88. Gyldendal, Copenhagen.
- Fromm, K. (1994) Paläomagnetische Bestimmungen an Quartärsedimenten in Nordwest-Deutschland. *Geologisches Jahrbuch*, **A 134**, 229–257.
- Gaillard, M.-J. (1984) *A palaeohydrological study of Kragholmssjön (Scania, south Sweden): regional vegetation history and water-level changes*. LUNDQUA Report, 25, Department of Quaternary Geology, Lund University.
- van Geel, B. & Andersen, S. (1988) Fossil ascomycetes of the parasitic fungus *Ustilina deusta* in Eemian deposits in Denmark. *Review of Palaeobotany and Palynology*, **56**, 89–93.
- Geyh, M.A. & Müller, H. (2005) Numerical Th-230/U dating and a palynological review of the Holsteinian/Hoxnian Interglacial. *Quaternary Science Reviews*, **24**, 1861–1872.
- Granoszewski, W. (2003) Late Pleistocene vegetation history and climatic changes at Horoski Duze, eastern Poland: a palaeobotanical study. *Acta Palaeobotanica*, **4**(Suppl.), 3–95.
- Gregory, P. (1973) *The microbiology of the atmosphere*. Leonard Hill, Aylesbury.
- Greisman, A. & Gaillard, M.-J. (2009) The role of climate variability and fire in early and mid Holocene forest dynamics of southern Sweden. *Journal of Quaternary Science*, **24**, 593–611.
- Hahne, J. (1996) The interglacial site of Hunterburg near Quakenbrück (NW Germany). *The early Middle Pleistocene in Europe* (ed. by C. Turner), pp. 181–186. Balkema, Rotterdam.
- Harley, J.L. & Harley, E.L. (1987) A check-list of mycorrhiza in the British flora—addenda, errata and index. *New Phytologist*, **107**, 741–749.
- Hellman, S.E.V., Gaillard, M.-J., Broström, A. & Sugita, S. (2008a) The REVEALS model, a new tool to estimate past regional plant abundance from pollen data in large lakes: validation in southern Sweden. *Journal of Quaternary Science*, **23**, 21–42.
- Hellman, S.E.V., Gaillard, M.-J., Broström, A. & Sugita, S. (2008b) Effects of the sampling design and selection of parameter values on pollen-based quantitative reconstructions of regional vegetation: a case study in southern Sweden using the REVEALS model. *Vegetation History and Archaeobotany*, **17**, 445–459.
- Hicks, S. (2006) When no pollen does not mean no trees. *Vegetation History and Archaeobotany*, **15**, 253–261.
- Hill, M.O. & Carey, P.D. (1997) Prediction of yield in the Rothamsted Park grass experiment by Ellenberg indicator values. *Journal of Vegetation Science*, **8**, 579–586.
- Hill, M.O., Mountford, J.O., Roy, D.B. & Bunce, R.G.H. (1999) *Ellenberg's indicator values for British plants*. ECOFACT, Vol. 2, Technical Annex. Institute of Terrestrial Ecology, Huntingdon, UK.
- Iversen, J. (1957) The bearing of glacial and interglacial epochs on the formation and extinction of plant taxa. *Uppsala Universitets Årsskrift*, **1958**, 6.
- Johnson, S. (1967) Hierarchical clustering schemes. *Psychometrika*, **32**, 241–254.
- Jouzel, J., Masson-Delmotte, V., Cattani, O. *et al.* (2007) Orbital and millennial Antarctic climate variability over the past 800,000 years. *Science*, **317**, 793–796.
- Juan, T., Sagrario, A., Jesús, H. & Cristina, C.M. (2006) Red fox (*Vulpes vulpes* L.) favour seed dispersal, germination and seedling survival of Mediterranean Hackberry (*Celtis australis* L.). *Acta Oecologica*, **30**, 39–45.
- Juggins, S. (2003) *C2 user guide. Software for ecological and palaeoecological data analysis and visualisation*. University of Newcastle, Newcastle upon Tyne.
- Kirby, K.J. (2004) A model of natural wooded landscape in Britain as influenced by large herbivory activity. *Forestry*, **77**, 405–420.

- Koutsodendris, A., Müller, U.C., Pross, J., Brauer, A., Kotthoff, U. & Lotter, A.F. (2010) Vegetation dynamics and climate variability during the Holsteinian interglacial based on a pollen record from Dethlingen (northern Germany). *Quaternary Science Reviews*, **29**, 3298–3307.
- Krzyszowski, D., Bottger, T., Junge, F.W., Kuszell, T. & Nawrocki, J. (1996) Ferdynandovian interglacial climate reconstructions from pollen successions, stable-isotope composition and magnetic susceptibility. *Boreas*, **25**, 283–296.
- Kühl, N. & Litt, T. (2007) Quantitative time-series reconstructions of Holsteinian and Eemian temperatures using botanical data. *The climate of the past interglacials* (ed. by F. Sirocko, M. Claussen, M.F. Sánchez-Goñi and T. Litt), pp. 239–254. *Developments in Quaternary Science*, Vol. 7. Elsevier, Amsterdam, Oxford.
- Kurtén, B. (1968) *Pleistocene mammals of Europe*, reprinted 2007 edn. Aldine Transaction, New Brunswick.
- Lambers, H., Shane, M.W., Cramer, M.D., Pearse, S.J. & Veneklaas, E.J. (2006) Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. *Annals of Botany*, **98**, 693–713.
- Lambers, H., Raven, J.A., Shaver, G.R. & Smith, S.E. (2008) Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology and Evolution*, **23**, 95–103.
- Litt, T., Junge, F.W. & Böttger, T. (1996) Climate during the Eemian in north-central Europe – a critical review of the palaeobotanical and stable isotope data from central Germany. *Vegetation History and Archaeobotany*, **5**, 247–256.
- Mamakowa, K. (2003) Pleistocen. *Palinologia* (ed. by S. Dybowa-Jachowicz and A. Sadowska), pp. 235–266. Instytut Botaniki W. Szafera, Polska Akademia Nauk, Kraków.
- Melman, T.C.P., Clausman, P.H.M.A. & Udo de Haes, H.A. (1988) The testing of three indicator systems for trophic state in grasslands. *Vegetatio*, **75**, 143–152.
- Mitchell, F.J.G. (2005) How open were European primeval forests? Hypothesis testing using palaeoecological data. *Journal of Ecology*, **93**, 168–177.
- Mossberg, B. & Stenberg, L. (2005) *Den nye nordiske Flora*. Gyldendal, Copenhagen.
- Müller, H. (1974a) Pollenanalytische Untersuchungen und Jahresschichtenzählung an der eem-zeitlichen Kieselgur von Bispingen/Luhe. *Geologisches Jahrbuch*, **21**, 149–169.
- Müller, H. (1974b) Pollenanalytische Untersuchungen und Jahresschichtenzählungen an der holstein-zeitlichen Kieselgur von Münster-Breloh. *Geologisches Jahrbuch*, **21**, 107–140.
- Nitychoruk, J., Bińka, K., Ruppert, H. & Schneider, J. (2006) Holsteinian interglacial = marine isotope stage 11? *Quaternary Science Reviews*, **25**, 2678–2681.
- Odgaard, B.V. (1994) The Holocene vegetation history of northern west Jutland, Denmark. *Opera Botanica*, **123**, 1–171.
- Odgaard, B.V. & Rasmussen, P. (2000) Origin and temporal development of macro-scale vegetation patterns in the cultural landscape of Denmark. *Journal of Ecology*, **88**, 733–748.
- Olsson, F., Gaillard, M.-J., Lemdahl, G., Greisman, A., Lanos, P., Marguerie, D., Marcoux, N., Skoglund, P. & Wäglind, J. (2010) A continuous record of fire covering the last 10,500 calendar years from southern Sweden — The role of climate and human activities. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **291**, 128–141.
- Orombelli, G., Maggi, V. & Delmonte, B. (2010) Quaternary stratigraphy and ice cores. *Quaternary International*, **219**, 55–65.
- Power, M.J., Marlon, J., Ortiz, N. *et al.* (2008) Changes in fire regimes since the Last Glacial Maximum: an assessment based on a global synthesis and analysis of charcoal data. *Climate Dynamics*, **30**, 887–907.
- Prentice, I.C. (1980) Multidimensional scaling as a research tool in Quaternary palynology: a review of theory and methods. *Review of Palaeobotany and Palynology*, **31**, 71–104.
- Prentice, I.C. (1985) Pollen representation, source area, and basin size: toward a unified theory of pollen analysis. *Quaternary Research*, **23**, 76–86.
- Regnell, M., Gaillard, M.-J., Bartholin, T.S. & Karsten, P. (1995) Reconstruction of environment and history of plant use during the late Mesolithic (Ertebølle culture) at the inland settlement of Bökeberg III, southern Sweden. *Vegetation History and Archaeobotany*, **4**, 67–91.
- Rzechowski, J. (1996) The Ferdynandovian Interglacial and its stratigraphical position in the Middle Pleistocene of Europe. *The early Middle Pleistocene in Europe* (ed. by C. Turner), pp. 279–293. Balkema, Rotterdam.
- Schaffers, A.P. & Sýkora, K.V. (2000) Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *Journal of Vegetation Science*, **11**, 225–244.
- Shackleton, N.J., Chapman, M., Sánchez-Goñi, M.F., Pailler, D. & Lancelot, Y. (2002) The classic marine isotope substage 5e. *Quaternary Research*, **58**, 14–16.
- Sheykholislami, A. & Ahmadi, T. (2009) The study of Caucasian walnut (*Pterocarya fraxinifolia* (Lam.) Spach.) in forests of Mashelak (Noshahr, Iran). *Botany Research Journal*, **2**, 28–33.
- Soepboer, W., Sugita, S. & Lotter, A.F. (2010) Regional vegetation-cover changes on the Swiss Plateau during the past two millennia: a pollen-based reconstruction using the REVEALS model. *Quaternary Science Reviews*, **29**, 472–483.
- Stevens, P.R. & Walker, T.W. (1970) The chronosequence concept and soil formation. *The Quarterly Review of Biology*, **45**, 333–350.
- Sugita, S. (1994) Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *Journal of Ecology*, **82**, 881–897.
- Sugita, S. (2007a) POLLSCAPE model. *Encyclopedia of Quaternary science* (ed. by A.E. Scott), pp. 2561–2570. Elsevier, Oxford.
- Sugita, S. (2007b) Theory of quantitative reconstruction of vegetation I: pollen from large sites REVEALS regional vegetation composition. *The Holocene*, **17**, 229–241.
- Sugita, S. (2007c) Theory of quantitative reconstruction of vegetation II: all you need is LOVE. *The Holocene*, **17**, 243–257.

- Sugita, S., Gaillard, M.-J. & Broström, A. (1999) Landscape openness and pollen records: a simulation approach. *The Holocene*, **9**, 409–421.
- Svenning, J. (2002) A review of natural vegetation openness in north-western Europe. *Biological Conservation*, **104**, 133–148.
- Tauber, H. (1965) Differential pollen dispersion and the interpretation of pollen diagrams. *Geological Survey of Denmark, II. series*, **89**, 1–69.
- Taylor, L.L., Leake, J.R., Quirk, J., Hardy, K., Banwart, S.A. & Beerling, D.J. (2009) Biological weathering and the long-term carbon cycle: integrating mycorrhizal evolution and function into the current paradigm. *Geobiology*, **7**, 171–191.
- Thompson, K., Hodgson, J.G., Grime, J.P., Rorison, I.H., Band, S.R. & Spencer, R.E. (1993) Ellenberg numbers revisited. *Phytocoenologia*, **23**, 277–289.
- Tzedakis, P.C., Raynaud, D., McManus, J.F., Berger, A., Brovkin, V. & Kiefer, T. (2009) Interglacial diversity. *Nature Geoscience*, **2**, 751–755.
- Urban, B. (1995) Palynological evidence of younger Middle Pleistocene interglacials (Holsteinian, Reinsdorf and Schöningen) in the Schöningen open cast lignite mine (eastern Lower Saxony, Germany). *Mededelingen Rijks Geologische Dienst*, **52**, 175–186.
- Vera, F.W.M. (2000) *Grazing ecology and forest history*. CABI Publishing, New York.
- Wagner, M., Kahmen, A., Schlumprecht, H., Audorff, V., Perner, J., Buchmann, N. & Weisser, W. (2007) Prediction of herbage yield in grassland: how well do Ellenberg N-values perform? *Applied Vegetation Science*, **10**, 15–24.
- Wardle, D.A., Hornberg, G., Zackrisson, O., Kalela-Brundin, M. & Coomes, D.A. (2003) Long-term effects of wildfire on ecosystem properties across an island area gradient. *Science*, **300**, 972–975.
- Wardle, D.A., Walker, L.R. & Bardgett, R.D. (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science*, **305**, 509–513.
- Wilkinson, L. (1998) *SYSTAT, version 9*. SYSTAT, Evanston, IL.
- Zagwijn, W. (1975) Indeling van het Kwartair op grond van veranderingen in vegetatie en klimaat [Subdivision of the Quaternary based upon changes in vegetation and climate]. *Toelichtingen bij geologische overzichtskaarten van Nederland* (ed. by W.H. Zagwijn and C.J. van Staaldunin), pp. 109–114. Rijks Geologische Dienst, Haarlem.
- Zagwijn, W.H. (1996) The Cromerian Complex Stage of the Netherlands and correlation with other areas in Europe. *The early Middle Pleistocene in Europe* (ed. by C. Turner), pp. 145–172. Balkema, Rotterdam.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Simplified pollen-percentage diagram from (a) Hollerup, (b) Vejlbj and (c) Harreskov based on Andersen's (1965) analysis. Only common and important types are included.

Appendix S2 Surface geology of each site and information on lake sediment and inferred soil type during the period of maximum productivity (Ellenberg N).

Appendix S3 Pollen productivity estimates relative to Poaceae and fall speed of the pollen types used in the REVEALS reconstructions.

Appendix S4 List of ecological values used for calculating Ellenberg values (Hill *et al.*, 1999).

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCHES

Petr Kuneš is a postdoctoral fellow in palaeoecology at the Department of Geoscience, University of Aarhus, Denmark. His current research focuses on interglacial environment, quantitative reconstruction of vegetation and biostratigraphic correlation of pollen data.

Bent Vad Odgaard is a professor of palaeoecology at the Department of Geoscience, University of Aarhus, Denmark. His main research interests include terrestrial vegetation dynamics as well as palaeolimnology of the Holocene and interglacial periods based on pollen and plant macrofossil records.

Marie-José Gaillard is professor in botany (palaeoecology and vegetation history) at Linnaeus University, Kalmar, Sweden. Her current research focuses on quantitative Holocene land-cover reconstructions in north-western Europe based on pollen records and models of pollen–vegetation relationships, and on the Holocene history of forest, cultural landscapes and fire in southern Sweden.

Editor: Jens-Christian Svenning