Postglacial climate changes and vegetation responses in northern Europe

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Abstract

Postglacial climate changes and vegetation responses were studied using a combination of biological and physical indicators preserved in lake sediments. Low-frequency trends, high-frequency events and rapid shifts in temperature and moisture balance were probed using pollen-based quantitative temperature reconstructions and oxygen-isotopes from authigenic carbonate and aquatic cellulose, respectively. Pollen and plant macrofossils were employed to shed light on the presence and response rates of plant populations in response to climate changes, particularly focusing on common boreal and temperate tree species. Additional geochemical and isotopic tracers facilitated the interpretation of pollen- and oxygen-isotope data.

The results show that the common boreal trees (*Betula* sp., *Pinus sylvestris*, *Picea abies*) were present in the Baltic region (~55°N) during the Lateglacial, which contrasts with the traditional view of species refuge locations in the south-European peninsulas during the glacial/interglacial cycles. The findings of this work are in agreement with recent paleoecological and genetic evidence suggesting that scattered populations of tree species persisted at higher latitudes, and that these taxa were likely limited to boreal trees. Moreover, the results demonstrate that stepwise changes in plant communities took place in concert with major climate fluctuations of the glacial/interglacial transition.

Postglacial climate trends in northern Europe were characterized by rise, maxima and fall in temperatures and related changes in moisture balance. Following the deglaciation of the Northern Hemisphere and the early Holocene reorganization of the ice-ocean-atmosphere system, the long-term temperature trends followed gradually decreasing summer insolation. The early Holocene (~11,700-8000 cal yr BP) was overall cool, moist and oceanic, although the earliest Holocene effective humidity may have been low particularly in the eastern part of northern Europe. The gradual warming trend was interrupted by a cold event ~8200 cal yr BP. The maximum temperatures, ~1.5-3.0°C above modern values, were attained ~8000-4000 cal yr BP. This mid-Holocene peak warmth was coupled with low lake levels, low effective humidity and summertime drought. The late Holocene (~4000 cal yr BP-present) was characterized by gradually decreasing temperatures, higher lake levels and higher effective humidity. Moreover, the gradual trends of the late Holocene were probably superimposed by higher-frequency variability. The spatial variability of the Holocene temperature and moisture balance patterns were tentatively attributed to the differing heat capacities of continents and oceans, changes in atmospheric circulation modes and position of sites and subregions with respect to large water bodies and topographic barriers.

The combination of physical and biological proxy archives is a pivotal aspect of this work, because non-climatic factors, such as postglacial migration, disturbances and competitive interactions, can influence reshuffling of vegetation and hence, pollen-based climate reconstructions. The

oxygen-isotope records and other physical proxies presented in this work manifest that postglacial climate changes were the main driver of the establishment and expansion of temperate and boreal tree populations, and hence, large-scale and long-term vegetation patterns were in dynamic equilibrium with climate. A notable exception to this pattern may be the postglacial invasion of Norway spruce (*P. abies*) and the related suppression of mid-Holocene temperate forest. This salient step in north-European vegetation history, the development of the modern boreal ecosystem, cannot be unambiguously explained by current evidence of postglacial climate changes.

The results of this work highlight that plant populations, including long-lived trees, may be able to respond strikingly rapidly to changes in climate. Moreover, interannual and seasonal variation and extreme events can exert an important influence on vegetation reshuffling. Importantly, the studies imply that the presence of diffuse refuge populations or local stands among the prevailing vegetation may have provided the means for extraordinarily rapid vegetation responses. Hence, if scattered populations are not provided and tree populations are to migrate long distances, their capacity to keep up with predicted rates of future climate change may be lower than previously thought.

Acknowledgements

Contents

List of original publications

This thesis is based on the five (I-V) peer-reviewed articles listed below:

I.   **Heikkilä, M.** and Seppä, H. (2003). A 11,000 yr palaeotemperature reconstruction from the southern boreal zone in Finland. *Quaternary Science Reviews* 22, 541-554.

II.   **Heikkilä, M.**, Fontana, S.L. and Seppä, H. (2009). Rapid Lateglacial tree population dynamics and ecosystem changes in the eastern Baltic region. *Journal of Quaternary Science* 24, 802–815.

III. Seppä, H., Alenius, T., Bradshaw, R.H.W., Giesecke, T., **Heikkilä, M.** and Muukkonen, P. (2009). Invasion of Norway spruce (*Picea abies*) and the rise of the Boreal ecosystem in Fennoscandia. *Journal of Ecology* 24, 802–815.

IV.   **Heikkilä, M.** and Seppä, H. (2010). Holocene climate dynamics in Latvia, eastern Baltic region: a pollen-based summer temperature reconstruction and regional comparison. *Boreas*, in press.

V.   **Heikkilä, M.**, Edwards, T.W.D., Seppä, H. and Sonninen, E. Sediment isotope tracers from Lake Saarikko, Finland, and implications to Holocene hydroclimatology. *Quaternary Science Reviews*, submitted.

Author's contributions

The author carried out the fieldwork, prepared and analysed pollen and isotopic samples from lake sediments for all studies. S. Fontana prepared and analysed macrofossils and carried out the loss-on-ignition analysis for Paper II, and E. Sonninen analysed lake water isotopes for Paper V. Paper III contains original material from T. Alenius, R. Bradshaw, T. Giesecke and P. Muukkonen.

The preparation of manuscripts was shared as follows:
I.   H. Seppä was responsible for preparing the manuscript, M.Heikkilä prepared the figures and contributed to writing.
II.   M. Heikkilä was responsible for preparing the manuscript, S. Fontana and H. Seppä provided comments and contributions.
III. H. Seppä prepared the manuscript. All authors contributed.
IV.   M. Heikkilä prepared the manuscript. H. Seppä commented and contributed.
V.   M. Heikkilä prepared the manuscript, T.W.D. Edwards and H. Seppä commented and contributed.

Abbreviations

B/A	= Bølling/ Allerød
cal yr BP	= calibrated years before present
DIC	= dissolved inorganic carbon
DIN	= dissolved inorganic nitrogen
GMWL	= Global Meteoric Water Line
HCl	= hydrochloric acid
HF	= hydrofluoric acid
KOH	= potassium hydroxide
LEL	= local evaporation line
LGM	= Last Glacial Maximum
LMWL	= Local Meteoric Water Line
LOI	= loss on ignition
MAT	= modern analogue technique
NAO	= North Atlantic Oscillation
PAR	= pollen accumulation rate
PCA	= principal components analysis
SIS	= Scandinavian Ice Sheet
SLAP	= Standard Light Antarctic Precipitation
T_{ann}	= mean annual temperature
T_{jul}	= mean July temperature
T_{summer}	= mean summer (MJJA) temperature
TOC	= total organic carbon
TON	= total organic nitrogen
VPDB	= Vienna Pee Dee Belemnite
VSMOW	= Vienna Standard Mean Ocean Water
WA-PLS	= weighted averaging partial least squares
YD	= Younger Dryas

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1 Introduction

1.1 Lake sediments as an archive of past climate and vegetation changes

The fields of paleolimnology, -climatology, -hydrology and -ecology have benefited from the recent spurt of climate change research, highlighted by a whole chapter devoted to paleoclimate in the 4th IPCC Assessment Report (Jansen *et al.* 2007). A retrospective, long-term perspective on climate change provides a grasp of underlying mechanisms and low-frequency patterns that may influence higher frequency climate variability. In addition, since it is known that low-frequency trends have been interrupted by short-term events and periods of rapid change in the past (Alley & Ágústsdóttir 2005; Broecker 2006; Overpeck & Cole 2006), prospects on climate system thresholds and ecosystem responses to abrupt climate fluctuations are in the scope of paleoclimatologists as well. Moreover, the discipline of paleoclimatology helps to build understanding of climate forcings and, particularly in liaison with climate modelling, provides a powerful means to probe past, present and future climate behaviour.

Sediments buried in lake bottoms are a focal archive in the study of past environmental change in the continental realm (Fritz 1996; Battarbee 2000; Smol & Douglas 2007). Lake deposits provide continuous, high- to relatively high resolution sequences that embody a richness of physical, chemical and biological "proxies", tracers that can be used to infer paleoclimate, -hydrology, -soils and –vegetation (Fig 1). In the beginning of the 21st century, research on past climates and vegetation based on lake sediment archives has undergone an explosive growth, accompanied by increasingly detailed quantitative reconstructions (e.g., Lotter *et al.* 1997; Seppä & Birks 2001; Korhola *et al.* 2002; Davis *et al.*

2003; Gaillard *et al.* 2008; Seppä *et al.* 2009b), very high temporal resolution (e.g., Hu *et al.* 1999; von Grafenstein *et al.* 1999a; Snowball *et al.* 2002; Tiljander *et al.* 2003; Veski *et al.* 2004; Ojala & Alenius 2005; Haltia-Hovi *et al.* 2007), multi-proxy and multi-site studies (e.g., Birks & Ammann 2000; Axford *et al.* 2009; Kaufman 2009) and joint use of proxy data and climate modeling (Masson *et al.* 1999; Rimbu *et al.* 2004; Wiersma & Renssen 2006; Braconnot *et al.* 2007; Mann *et al.* 2009; Renssen *et al.* 2009).

Temporally, lake sequences in northern Europe normally cover the past 15,000 to 9,000 years, depending on the location of the site with respect to the receding Scandinavian Ice Sheet (SIS). Resolution of lake sediment studies varies from seasonally or annually resolved lake varves to dozens or hundreds of years per sample depending on the sediment accumulation rate and resuspension of sediment layers in the lake bottom. Moreover, selected analysis interval influences data resolution. As an example, a sediment sequence that accumulated at a constant rate is divided into 1-cm-thick subsamples, each representing 50 years in time. Analyses are carried out continuously on every subsample (data represents continuous 50-year time slices), or perhaps on every second sample (data represents 50-year time slices with 50-year gaps in between) or on every fifth sample (data represents 50-year time slices with 200-year gaps in between). Because of the laborious nature of many analytic techniques, lower resolution is sometimes applied to the whole sequence whereas higher resolution is applied to sections of particular interest.

Determining an absolute age for each subsample - and an absolute chronology for the sequence - is a crucial step of any study involving stratigraphical lake sediment analyses. Incremental dating based on cyclic accumulation of sediment components, just like annual bands in tree-rings and continental glacier cores, can
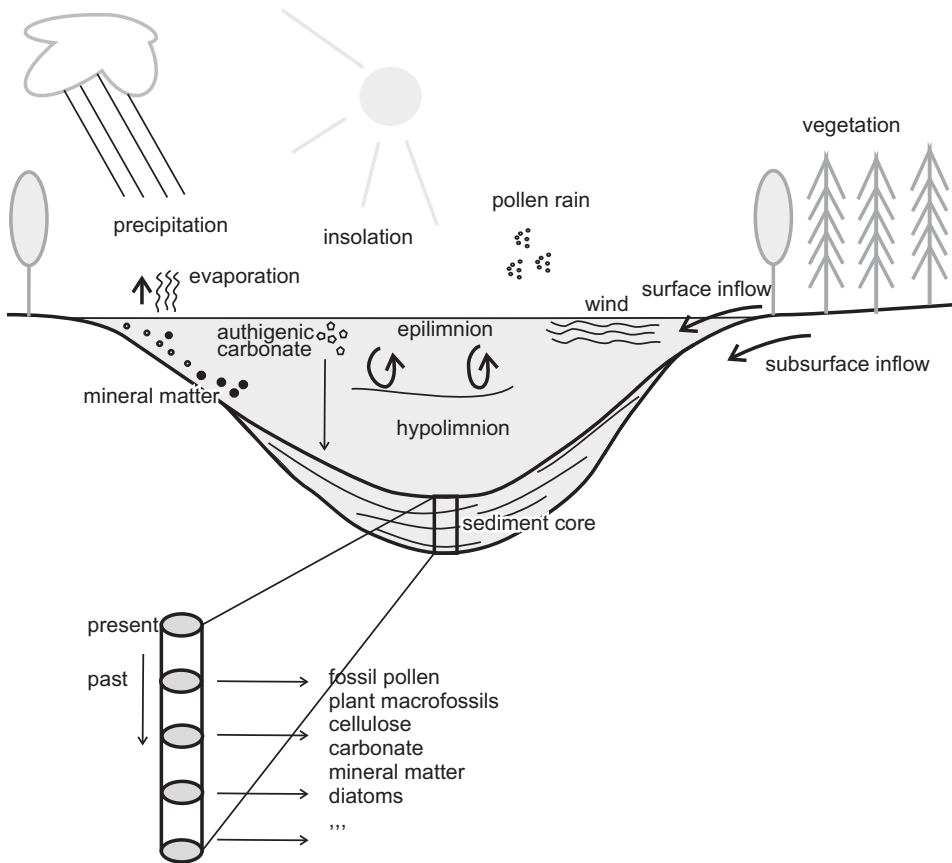
Figure 1. A scheme of a potential study lake illustrating some factors that influence lake system and components that are preserved in lake sediments.

be employed for seasonally and annually varved lake sediment sequences. Otherwise, chronological control is usually based on radiometric dating methods that utilize the radioactive decay of certain isotopes, such as lead (^{210}Pb), cesium (^{137}Cs) and carbon (^{14}C) (Libby 1955; Walker 2005). Most typically AMS (Accelerator Mass Spectrometer) radiocarbon dating is employed for lake sediment sequences of postglacial age. The use of terrestrial plant macrofossils is recommended, because bulk sediment can contain bedrock-derived ^{14}C-poor carbon (Deevey *et al.* 1954; Törnqvist *et al.* 1992; Grimm *et al.* 2009). However, also macrofossils from arctic and bo-

real regions commonly involve ages diverging from age-depth relations. It has been shown that macrofossil type can affect radiocarbon dating results; e.g., wood and charcoal from long-lived trees are often older than other macrofossils and filamentous leaves are more easily contaminated by modern carbon than other tissue types (Turney *et al.* 2000; Oswald *et al.* 2005). Sometimes stratigraphic characteristics of known age, e.g., layers of ash from volcanic eruptions (tephra) (Wohlfarth *et al.* 2006; Newton *et al.* 2007) or regionally recognized features in pollen spectra, can be used as time anchors to facilitate chronological control.

Climate influences lakes in complex ways, e.g., by directly changing the lake level, thermal stratification and the isotopic composition of lake water, via effects on catchment properties, terrestrial and aquatic ecosystems (Fritz 1996; Battarbee 2000; Fritz 2003). In addition, in-lake and sedimentary processes can alter the properties or representation of the proxy. The intricacy of lake sediment archives can be successfully addressed by careful site selection and by understanding the nature of the proxy(ies) employed. In this work, biological assemblages of pollen and plant macrofossils were used together with stable isotopes in lake sediment cellulose, authigenic carbonate and bulk organics. Interpretations were facilitated by accompanying assessments of present-day environments, namely, modern spatial pollen-climate relations and modern isotope hydrology. The linkage of biological and physical proxies is an essential aspect of this work. Since climate reconstructions based on pollen may be influenced by postglacial migration of plants (Birks 1986; Svenning & Skov 2004, 2005), physical methods can serve as a key to understanding climate-vegetation relations. The following subsections briefly describe the principles of the use of the proxy methods applied in this work.

1.2 Reconstructing past vegetation and climate from pollen and plant macrofossils

Pollen and plant macrofossils preserved in lake sediments derive from flora and vegetation surrounding the catchment, and therefore reflect the ecological and climatologic conditions in which the plants grew. Already in the beginning of the 20th century, the first pollen diagrams and macrofossils derived from peat bogs in Fennoscandia were used to interpret past climate changes (Andersson 1902, 1909; von Post 1925; Iversen 1944; von Post 1946; Iversen 1954). Pollen grains are produced and dispersed abundantly and are often frequent in postglacial, organic-rich lake sediments. However, the application of fossil pollen assemblages to infer past vegetation and climate is hampered by the complex relation between the spatial distribution of plants in the landscape and the proportions of pollen types in sediment due to differential production, dispersal and preservation of pollen types (Jacobson & Bradshaw 1981; Bradshaw & Webb 1985; Sugita 1994; Davis 2000). In addition, pollen grains are typically identified to genus or family level, and the low taxonomic resolution can complicate ecological and climatic inferences. However, species diversity is relatively low in northern Europe, and many tree pollen types, for example, can be assigned to species level, which facilitates ecological interpretations. Plant macrofossils are produced in lesser amounts, and due to their commonly larger size, are not dispersed far from the location of the original plant. In addition, taxonomic resolution of macrofossil analysis is generally much higher than that of pollen analysis. While pollen assemblages give numerical data on the proportions of plants in the landscape, plant macrofossils can be employed to assess whether the species was actually growing in situ. Pollen assemblages can be used to derive quantitative temperature estimates (Birks 1998, 2003), whereas the presence of plant macrofossils can be used to infer climatic conditions given the knowledge of modern ecological optima and tolerances of species (Birks & Birks 2003). Hence, the joint use of pollen and plant macrofossils is encouraged in the study of past climate and vegetation (Birks & Birks 2000; Tinner & Theurillat 2003), particularly if assessing the local presence of species is crucial. For example, in treeless and tree-line environments where far-transported pollen is present in greater proportions and in the study of species migration and population histories, studying both pollen and macrofossils can be advantageous.

Understanding the source area of pollen has been a longstanding challenge of pollen-based vegetation reconstructions, since a well-developed theory dealing with the relation between the spatial distribution of plants in the landscape and the percentages of pollen in sediment has been lacking (Davis 2000). As described above, plant macrofossils can facilitate interpretation of pollen diagrams, mainly by their capability of assessing the local presence of key taxa. In addition, empirical and theoretical studies have led to the development of correction factors and models that aim to quantitatively relate pollen loading to surrounding vegetation (Prentice 1985; Prentice 1988; Sugita 1994, 2007a, 2007b; Calcote 1995). Another approach is to calculate pollen accumulation rates (PAR = grains/cm^2/yr) (Davis & Deevey 1964) instead of commonly-employed pollen percentages. Pollen percentages are "closed" data: a change in the abundance of one taxon leads to changes in percentage values of all other taxa even if there was no actual change in pollen loading or population size. The PAR value of a taxon, on the other hand, is independent on values of the relative abundance of other taxa and directly dependent on the abundance of plants in the surrounding landscape. Hence, PAR data has been used to study tree-line dynamics and to reconstruct past changes in plant populations (e.g., Ritchie 1969; Hyvärinen 1975; Gajewski *et al.* 1993; Giesecke 2005; Seppä & Hicks 2006; Tinner *et al.* 2009). However, early work showed great variability of PAR between and within lakes, and it became apparent that sedimentation processes alter original pollen loading (Davis & Brubaker 1973; West 1973; Davis *et al.* 1984; Davis 2000). Deriving PAR values from lake sediment pollen involves addition of marker grains in pollen samples (Stockmarr 1972) and requires well-dated sequences from stable sedimentary basins. Recently, new interest has arisen and a growing number of studies have employed PAR values in the study of plant population dynamics, including quantitative vegetation reconstructions, thanks to the improved understanding of pollen-vegetation relations and modern PAR-values, better precision of pollen analytic techniques and enhanced chronological control (Hicks 2001; Seppä & Hicks 2006; Gerasimidis *et al.* 2008; Giesecke & Fontana 2008; Hättestrand *et al.* 2008; Seppä *et al.* 2009a).

The study of climate using fossil pollen traditionally involves two steps: the reconstruction of vegetation from pollen assemblages, and the reconstruction of climate from vegetation. Today, most pollen-based climate reconstructions yield to quantitative estimates and are performed based on the knowledge of modern spatial relations between pollen derived from surface sediments and corresponding meteorological measurements (e.g., 30-yr climate normals). These numerical reconstructions involve two steps: 1) the determination of modern-day pollen-climate relations (transfer functions) based on a calibration dataset, and 2) the "space for time" substitution, i.e., the use of transfer functions to derive climate estimates from stratigraphical pollen assemblages (Birks 1998, 2003). Several numerical techniques have been used to derive quantitative transfer functions, the most commonly used being the modern analogue technique (MAT) (Overpeck *et al.* 1985; Guiot 1990; Davis *et al.* 2003; Jackson & Williams 2004; Williams & Shuman 2008) and weighted averaging (partial least squares) [WA(PLS)] (ter Braak & Juggins 1993; ter Braak 1995; Lotter *et al.* 1997; Birks 1998; Seppä *et al.* 2004; Finsinger *et al.* 2007).

MAT involves calculating compositional dissimilarity between a fossil sample and each member of the calibration dataset, and the environmental characteristics of n most similar modern samples are averaged and assigned to the fossil sample (Williams & Shuman 2008). WA and WA-PLS are ecologically realistic, as they

take into account typically unimodal responses of species to environmental variables (ter Braak & Juggins 1993; ter Braak 1995). In WA, optima for each pollen taxon is calculated as an average of climate values at lake sites in the calibration dataset, and weighted by taxa abundances (ter Braak & Looman 1986). WA-PLS, in turn, employs the principles of both WA and PLS, a linear regression method that guards against multi-collinearity by selecting a limited number of orthogonal components. In WA-PLS, these components are selected to maximize the covariance between the vector of weighted averages of climate variables and species. WA-PLS usually performs better than WA, because WA-PLS takes into account residual correlations in biological data (ter Braak & Juggins 1993; Birks 2003). Hence, WA-PLS is a simple and robust method that performs well with data that contain structured noise in the form of secondary environmental gradients (ter Braak & Juggins 1993; Birks 2003). The computations involved in WA-PLS are simple. Hence, the advantages of WA-PLS include the possibility for computer-intensive cross-validation and error estimation methods, e.g., bootstrapping and jack-knifing. Essentially, WA-PLS is based on the basic idea of indicator species employed in Quaternary paleoclimatology for more than a century, namely, that species abundances are dependent on limiting ranges of climate variables. However, the contemporary "multivariate indicator species approach" is based on large assemblages (e.g., matrices of 50-300 pollen taxa, 1-10 climate variables and 50-200 lake surface sediment samples) and involves computer-intensive performance testing and validation procedures.

1.3 Reconstructing past hydroclimatology using stable isotopes

The excellent suitability of water isotope tracers ($^{18}O/^{16}O$ and $^2H/^1H$) for probing past hydroclimatology and atmospheric circulation stems from the known and measurable physical behavior of two rare, heavy isotopologues ($^1H^2H^{16}O$ and $^1H^1H^{18}O$) compared to common light water ($^1H^1H^{16}O$) that leads to mass-dependent isotopic partitioning among the phases of the global water cycle (Craig 1961; Gat 1996; Edwards *et al.* 2004). Isotopic composition of water is expressed as δ-values (δ^{18}O or δ^{2}H) as follows:

$$\delta_{sample} = 1000 \times \left[R_{sample}/R_{VSMOW} - 1 \right] \quad (1)$$

where δ represents deviations per mil (‰) from the VSMOW standard, and R is $^{18}O/^{16}O$ or $^2H/^1H$.

The covariance between oxygen and hydrogen in the global water cycle is most elegantly seen as linear regression through the isotopic composition of precipitation at global scale, the global meteoric water line (GMWL), expressed as

$$\delta\ ^2H = 8 \times \delta^{18}O - 10 \quad (2)$$

At high-latitudes, δ^{18}O and δ^{2}H of precipitation generally correlate with temperature, mainly due to Rayleigh distillation, i.e., progressive rainout of heavy isotopic species (lowering of δ^{18}O or δ^{2}H) during the poleward transport of air parcels from the common moisture source in the subtropics (Dansgaard 1964; Rozanski *et al.* 1992; Araguás-Araguás *et al.* 2000). Hence, oxygen and hydrogen isotopes preserved in proxy archives, such as ice cores (e.g., Dahl-Jensen *et al.* 1998; Johnsen *et al.* 2001), speleothems (Lauritzen & Lundberg 1999; Sundqvist *et al.* 2007), and lake sediments (von Grafenstein *et al.* 1998), have been used to infer paleotemperatures. However, several proxy- and model-based examples demonstrate the influence of atmospheric circulation

changes and other non-temperature-dependent factors on the isotopic composition of precipitation (Edwards *et al.* 1996; Fricke & O'Neil 1999; Hammarlund *et al.* 2002; Noone & Simmonds 2002; Masson-Delmotte *et al.* 2005; Birks & Edwards 2009; Feng *et al.* 2009). In essence, the isotopic composition of precipitation is a result of the isotopic composition of the initial vapour source and concurrent hydroclimatological conditions, subsequent distillation, evaporation and mixing of the air-mass as well as conditions at the site of rainfall (Gat 1996; Araguás-Araguás *et al.* 2000). Atmospheric circulation has an intrinsic effect on any one of these factors, and thereby a change in atmospheric dynamics leads to alteration of the isotopic fingerprint of precipitation.

Water- and isotope-mass balances of lake basins are controlled by inputs (precipitation, surface and subsurface runoff) and outputs (evaporation and outflow). Isotopic composition of surface runoff and groundwater in northern Europe closely resemble that of annual mean precipitation (Darling *et al.* 2003; Kortelainen & Karhu 2004). Lake water isotopic composition, on the other hand, may be notably modified by surface evaporation during the open water season as well as precipitation seasonality, spring snowmelt and flooding (Gibson & Edwards 2002; Brock *et al.* 2008; Gibson *et al.* 2008; Yi *et al.* 2008; Brock *et al.* 2009; Jonsson *et al.* 2009b). In the conceptual δ^{18}O-δ^2H space (Fig. 2), the isotopic composition of lake water is commonly displaced from the linear trajectory formed by the isotopic composition of weighted monthly precipitation at the locality (local meteoric water line, LMWL). The distance of lake water from the input water on the
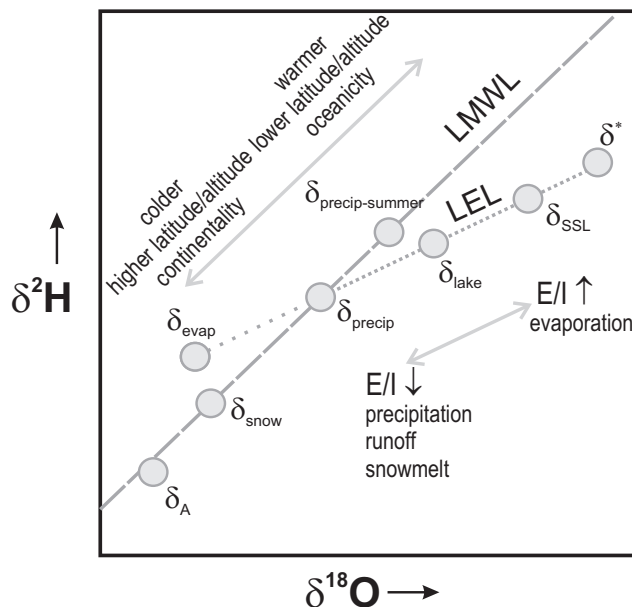
Figure 2. A conceptual scheme of water isotopic compositions for a particular high-latitude region. Local Meteoric Water Line (LMWL) forms a linear trajectory based on the isotopic labeling of local precipitation; shown are the δ-values for atmospheric moisture (δ_A), snow (δ_{snow}), weighted mean annual precipitation (δ_{precip}), summer precipitation ($\delta_{precip-summer}$). Surface waters undergoing evaporation lie along the Local Evaporation Line (LEL): δ_{lake} is the isotopic composition of a lake, δ_{SSL} the isotopic composition of a terminal steady-state lake, and δ* the theoretical isotopic composition of a lake nearing desiccation, respectively. The isotopic composition of evaporated vapour (δ_{evap}) lies on the other side of the LWML on an extension to LEL. The evaporation-to-inflow (E/I) ratio expresses the lake water balance that can be calculated employing the isotopic compositions of water budget components (Gonfiantini 1986; Gibson & Edwards 2002; Yi *et al.* 2008).

LMWL reflects the lake water balance in terms of evaporation-inflow ratio (E/I). In high-latitude lakes, positive excursions in the distance from the LMWL arise from summertime evaporative enrichment, whereas negative excursions are accounted for by spring snowmelt or dilution by annual precipitation and groundwater.

Past changes in lake water oxygen isotopic composition are inferred from sedimentary compounds, traditionally from carbonates (Epstein *et al.* 1953; Stuiver 1970; Talbot 1990; Ito 2001), and more recently from diatom silica and aquatic cellulose (Edwards & McAndrews 1989; Shemesh *et al.* 2001; Wolfe *et al.* 2001a; Leng & Barker 2006; Wolfe *et al.* 2007). The latter two are ubiquitously present in non-carbonate-precipitating, acidic lakes lying on the crystalline bedrock of northern Europe. In addition to their universal representation in lake sediments, diatom silica and aquatic cellulose have become increasingly attractive due to recent amendments in the understanding of the processes that influence their isotopic composition, together with progress in sediment cleaning and analytic techniques (Leng & Barker 2006; Wolfe *et al.* 2007; Tyler *et al.* 2008; Yi 2008; St. Amour 2009). Carbonate and silica formation involve temperature-dependent isotopic fractionation (Epstein *et al.* 1953; Kim & O'Neil 1997; Leng *et al.* 2001; Leng & Marshall 2004; Leng & Barker 2006), whereas aquatic cellulose is synthesized without temperature effects, and can be directly used as a proxy for oxygen isotopic composition of lake water (Wolfe *et al.* 2001a; Wolfe *et al.* 2007). Hence, combining isotopic analyses of cellulose with analyses of carbonate or silica potentially enables reconstruction of changes in lake water temperature (Klisch *et al.* 2007; Rozanski *et al.* 2010). Fundamental assumptions in the use of any sedimentary compound to infer lake water oxygen isotopic composition are that 1) they are of aquatic origin and record the isotopic composition of the lake water from which they form, 2) preparation of samples prior to isotopic measurements successfully removes contaminants or they do not interfere with the analysis and 3) fractionation factor ($\alpha_{(carbonate/diatom/cellulose)-water}$) and behavior are understood.

Diatoms are photosynthetic algae and thus occur naturally in lakes. However, contamination can be a major problem since the analysis of diatom silica will liberate oxygen from any other oxygen-bearing mineral present in the sample (Leng & Barker 2006; Brewer *et al.* 2008). Diatom species-specific fractionation differences are unlikely (Shemesh *et al.* 2001; Jonsson *et al.* 2009a), but $\alpha_{diatom-water}$ is influenced by temperature (-0.5 to -0.2‰/°C) (Juillet-Leclerc & Labeyrie 1987; Leng & Barker 2006). Carbonate, in turn, can be derived from the catchment bedrock or overburden and such detrital particles should be eliminated from paleohydrologic and -climatic studies by e.g., examining the mineralogical properties or grain-size (Kelts & Hsü 1978; Hammarlund & Buchardt 1996; Ito 2001; Mangili *et al.* 2009). In closed-lake (long residence time) conditions, oxygen and carbon isotopic composition of in-lake produced carbonate show correlation (Talbot 1990). Biogenic carbonate refers to shells of crustaceans and mollusks living in the lake, whereas authigenic carbonate is homogenous marl that is precipitated when the $CaCO_3$ concentration attains supersaturation (Kelts & Hsü 1978; Hodell *et al.* 1998), often as a result of photosynthetic removal of CO_2 during the summertime. Temperature-dependence of carbonate fractionation (-0.24‰/°C) has been empirically derived, and $\alpha_{carbonate-water}$ varies between from ~1.032 to ~1.029 in relation to water temperatures of 10-25 °C (Epstein *et al.* 1953; Friedman & O'Neil 1977; Hays & Grossman 1991; Kim & O'Neil 1997). Additionally, precipitation of biogenic carbonate incorporates species-specific fractionation factors (von Grafenstein *et al.*

1999b). Fractionation between oxygen isotopic composition of aquatic cellulose and the lake water available during the cellulose synthesis has been constrained between 1.025-1.030 in field and laboratory studies (Yakir & DeNiro 1990; Wolfe *et al.* 2001b; Sternberg *et al.* 2003; Wolfe *et al.* 2007), and a constant $\alpha_{cellulose-water}$ of 1.028 is employed (Edwards *et al.* 1985; Edwards & McAndrews 1989; Wolfe *et al.* 2001b; Wolfe *et al.* 2007; Yi 2008). Terrestrial cellulose is eliminated by sieving the samples to exclude plant macrofossils and by routinely involving studies of carbon:nitrogen (C/N) elemental and isotopic analyses (Wolfe *et al.* 2007; St. Amour 2009). Sediment C/N values greater than 20 are normally considered to derive from protein-poor vascular plants, whereas C/N values of 4-10 are thought to originate from protein-rich aquatic phytoplankton (Meyers & Lallier-Vergès 1999; Meyers 2003). Hence, higher C/N ratios potentially reflect lower aquatic productivity and greater proportion of terrestrial organic matter in the sediment. However, C/N ratios are controlled by nitrogen availability as well, and higher values are commonly caused by nitrogen limitation (Brahney et al. 2006; Elser et al. 2009).

Changes in lake productivity and nutrient cycling can be studied to aid interpretation of oxygen isotope-inferred past hydroclimatology. The isotopic composition of dissolved inorganic carbon (DIC) pool and dissolved inorganic nitrogen (DIN) pool in the lake's past can be inferred from organic matter or carbonate carbon, and organic matter, respectively. For isotopic composition of carbon ($\delta^{13}C$),

$$\delta_{sample} = 1000 \times \left[R_{sample} / R_{VPDB} - 1 \right] \quad (3)$$

where δ represents deviations per mil (‰) from the VPDB standard, and R is $^{13}C/^{12}C$. For nitrogen ($\delta^{15}N$),

$$\delta_{sample} = 1000 \times \left[R_{sample} / R_{VPDB} - 1 \right] \quad (4)$$

where δ represents deviations per mil (‰) from the AIR standard, and R is $^{15}N/^{14}N$.

Isotopic composition of DIC is influenced by processes including photosynthetic productivity, isotopic exchange with atmospheric CO_2, in-lake recycling of organic matter and catchment-derived DIC sources. Both carbon isotope composition of carbonate ($\delta^{13}C_{carb}$) and organic matter ($\delta^{13}C_{org}$) reflect the isotopic composition of DIC, but their compositions are modified by slightly different processes. Productivity-induced carbonate precipitation takes place in the lake epilimnion during the open-water season (Kelts & Hsü 1978; Hodell *et al.* 1998; Wittkop *et al.* 2009), and formed carbonate is subsequently settled in the water column and sediment surface. The isotopic composition of carbon in organic matter, on the other hand, is influenced by both productivity and in-lake respiration. In particular, thermally stratified and deep lakes allow $\delta^{13}C_{org}$ to be significantly modified due to respiration and diagenesis in the water column and lake bottom. Fractionation between DIC and photosynthetically produced organic matter in typical lake water temperatures is around -20‰ (Meyers & Lallier-Vergès 1999), hence, $\delta^{13}C_{carb}$-$\delta^{13}C_{org}$ separation should be close to this value if only photosynthetic assimilation was involved. In addition to in-lake respiration of organic matter, enhanced kinetic fractionation due to proton-pumping by certain algae during photosynthesis (Hammarlund *et al.* 1997), and contributions of bacterial organic matter in eutrophic and anoxic conditions (Li *et al.* 2008) have been related to greater separation between $\delta^{13}C_{carb}$ and $\delta^{13}C_{org}$.

Algae favour isotopically lighter ^{14}N in assimilation of organic matter. If dissolved DIN is readily available, $\delta^{15}N$ of photosynthetic matter resembles that of DIN. However, when the DIN pool is limited, reduced discrimination against ^{15}N gives rise to progressively enriched $\delta^{15}N$ values (Talbot 2001; Brahney *et al.* 2006). In con-

ditions of extreme nitrogen limitation, generally in highly eutrophic lakes, algae capable of nitrogen fixation dominate and $\delta^{15}N$ values are close to those of atmospheric N_2 (0‰). In addition to productivity, DIN availability is controlled by hydrological regime. Mild winters and ample precipitation allow nitrogen recharge from the catchment to the lake throughout the year, while deep snowpack followed by rapid spring snowmelt and hydrological flushing can lead to DIN limitation in the early summer (Bergström *et al.* 2008). Beyond nitrogen availability, processes such as denitrification and uptake of ammonium influence $\delta^{15}N$ fingerprint particularly under eutrophic and anoxic conditions (Talbot 2001; Li *et al.* 2008).

1.4   Objectives of the study

This work employs lake sediment pollen and isotopic tracers in order to investigate long-term climatic trends and short-term climatic events, along with large-scale responses of ecosystems to postglacial climate changes in forested northern Europe. The pollen records manifest changes in the abundances of plant communities, particularly the dynamics of tree populations. In combination with a calibration set incorporating the modern numerical pollen-climate relations, pollen records enable reconstruction of quantitative temperature histories. Joint records of pollen and plant macrofossils, in turn, are crucial for the assessment of the local presence of key plant taxa. The stable oxygen isotope records are invaluable in tracing atmospheric circulation dynamics and in assessing moisture balance changes associated with the pollen-inferred temperature patterns. Moreover, the combination of biological and physical proxy sources allows a viable study of vegetation responses to climate changes.

The broad scope of the study was to elucidate understanding of postglacial climate changes and vegetation responses in eastern Fennoscandia and the Baltic region. Particular interest was on paleotemperatures and moisture balance, past atmospheric circulation patterns and responses of tree populations to both gradual and abrupt climate changes. The following specific questions were addressed:

- How did vegetation and tree populations respond to prominent climate changes of the Lateglacial-Holocene transition (~15,000-10,000 cal yr BP)?
- What was the magnitude and trend of temperature change during the past 10,000 years and what kind of regional patterns could be detected?
- What was the pattern of change in moisture balance during the past 10,000 years and what kind of regional patterns could be detected?
- What was the nature of abrupt climatic events?
- Could postglacial temperature and moisture balance changes be related to changes in atmospheric circulation modes and seasonality?
- How did forest ecosystems and tree populations respond to low-frequency and high-frequency climate changes during the past 10,000 years?
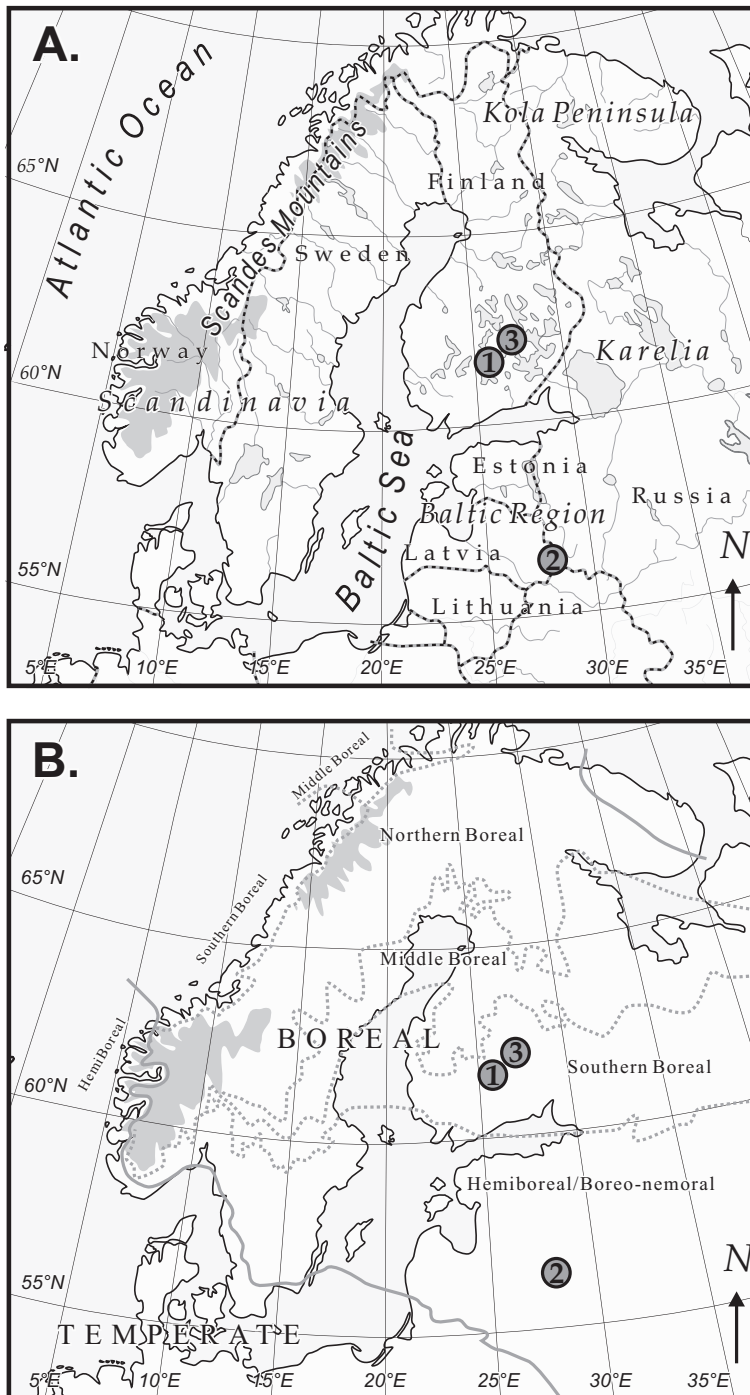
Figure 3. A map of the study region and sites with (A) geographical nomenclature and (B) vegetation zonation. 1. Lake Laihalampi, 2. Lake Kurjanovas, 3. Lake Saarikko.

2 Materials and methods

2.1 Study area and sites

The three study sites (Table 1, Fig. 3A) are located in the southern part of the boreal forest zone, in the ecotone between the boreal and temperate (nemoral) ecosystems of northern Europe (Ahti *et al.* 1968; Esseen *et al.* 1997) (Fig. 3B). While most of western and central Europe is used for agriculture, large forested regions remain in the northern and eastern parts of the continent. The boreal ecosystem, situated roughly between 56°N to 69°N in Fennoscandia (Scandinavia, Finland, Kola Peninsula and Karelia) and in the Baltic region, is composed of forests dominated by two coniferous tree species: Norway Spruce *(Picea abies)* and Scots Pine *(Pinus sylvestris)*. Typical deciduous tree species are silver birch *(Betula pubescens)*, downy birch *(B. pendula)*, common aspen *(Populus tremula)*, rowan *(Sorbus aucuparia)*, black alder *(Alnus glutinosa)*, grey alder *(A. incana)* and goat willow *(Salix caprea)* (Esseen *et al.* 1997). The ecotone between the boreal and temperate ecosystems is commonly designated as the hemiboreal or boreo-nemoral vegetation zone. In the hemiboreal zone, temperate broad-leaved trees such as ash *(Fraxinus excelsior)*, pedunculate oak (*Quercus robur*), small-leaved lime *(Tilia cordata)*, wych elm *(Ulmus glabra)* and hazel *(Corylus avellana)* thrive particularly on better soils. These thermophilous tree species reach their northern distribution limits between 60°N and 65°N, with ranges of *C. avellana* and *U. glabra* extending to more oceanic areas than those of *Q. robur* and *T. cordata* (Hultén 1950; Jalas & Suominen 1972–1999; Giesecke *et al.* 2008).

Particularly on the eastern side of the Scandes mountain range where topography does not have a major influence on climate patterns, the distinct vegetation zonation (Fig. 3B) follows the northward decreasing growing season length, sum of growing degree days and annual mean temperature. Temperature variation shows a clear seasonal cycle: the difference between the coldest and warmest months is ~10-20°C (Isemer *et al.* 2008). Seasonality increases northeastward from the Atlantic coast, and local differences are experienced e.g., with respect to the distance from the main water bodies (Johannessen 1970; New *et al.* 2002; Isemer *et al.* 2008). Precipitation is moderate throughout the year with slightly higher amounts during the autumn months and an annual average of 600-700 mm/year in the Fennoscandian mainland. Duration of seasonal snow cover increases northeastward, lasting from several days on the southwestern Atlantic coast to 7-8 months north of the Arctic Circle (Kitaev *et al.* 2006).

The spatial and seasonal distribution of climate variables is closely linked to the atmospheric circulation regime in the region. Dominating westerly, oceanic air-flow from the Atlantic Ocean plays a crucial role in shaping the climates of northern Europe (Johannessen 1970; Marshall *et al.* 2001; Isemer *et al.* 2008). Westerly air-masses are the reason for mild winters and unstable weather pattern particularly in the western and southwestern part of Fennoscandia, but also further east in the Fennoscandian mainland and in the Baltic region (Jaagus *et al.* 2003; Draveniece 2006). Westerly flow is strongest in January and February when the Icelandic Low and the Azores High are well developed and the mean pressure gradient over northern Europe intensifies, consistent with typically positive winter North Atlantic Oscillation (NAO) (Chen 2000; Marshall *et al.* 2001; Isemer *et al.* 2008; Jaagus 2009). Negative winter NAO on the other hand, leads to severely cold winter conditions and more extensive ice-cover over the Baltic Sea (Marshall *et al.* 2001; Omstedt & Chen 2001). The summer months are characterized with more typical meridional circulation (Isemer *et al.* 2008; Jaa-

Table 1. Details of the lake sites sampled for this study.

	Lake Laihalampi, Finland	Lake Kurjanovas, Latvia	Lake Saarikko, Finland
Coordinates	61°29′ N; 26°05′ E	56°31′ N; 27°59′ E	62°15′N; 27°40′E
Size	25.5 ha	160 ha	8.5 ha
Depth	1.2 m	5.8 m	3.4 m
Modern vegetation zone	southern boreal	hemiboreal (boreo-nemoral)	southern boreal
	<u>Dates</u>: Six ^{14}C dates of bulk sediment, fixed date for basin deglaciation and core top (8 data points) <u>Calibration</u>: INTCAL98 <u>Age-depth model</u>: Non-parametric weighted regression (generalized linear modeling)	<u>Dates</u>: Three ^{14}C dates of plant macrofossils, fixed dates for three pollen-stratigraphical events (6 data points) (paper II), ^{14}C dates of seven plant macrofossils, fixed date for core top (8 data points) (paper IV) <u>Calibration</u>: INTCAL04 <u>Age-depth model</u>: Bayesian deposition model (II), second-order polynomial regression (IV)	<u>Dates</u>: Seven ^{14}C dates of *Pinus* and *Betula* macrofossils, fixed date for core top (8 data points) <u>Calibration</u>: INTCAL04 <u>Age-depth model</u>: Second-order polynomial regression
Sample analyses	• pollen • LOI	• pollen • plant macrofossils • LOI	• δ^{18}O and δ^{2}H of lake water (2-yr monitoring) • δ^{18}O from cellulose and carbonate • δ^{13}C from carbonate and bulk organic matter • δ^{15}N from bulk organic matter • C and N elemental content from bulk organic matter • LOI
Numerical analyses	• pollen-based T_{ann} reconstruction (2-component WA-PLS) (I) • cross-correlations of important tree taxa (III)	• PCA of Lateglacial pollen data (II) • pollen-based T_{summer} reconstruction for the Holocene (2-component WA-PLS) (IV)	
Paper	I, III	II, IV	V

gus 2009). Meridional, anticyclonic conditions give rise to high temperatures and infrequent precipitation, whereas zonal, cyclonic air-flow leads to cool, moist summers (Chen & Hellström 1999; Jaagus 2009). An extreme case of the anticyclonic pattern is atmospheric blocking, a recurrent stationary high-pressure system causing divergence of the westerly storm-tracks and giving rise to severely long, dry and warm spells of summer climate (Busuoic *et al.* 2001; Jaagus 2009). Strong summer anticyclones over Fennoscandia are often related to positive summer NAO (SNAO) (Cassou *et al.* 2005; Folland *et al.* 2009; Jones & Lister 2009), particularly when a positive pressure anomaly centre is located over southern Scandinavia, and to positive a Eurasian/Scandinavian teleconnection pattern when anticyclone is over eastern Fennoscandia or western Russia (Barnston & Livezey 1987; Jaagus 2009).

The study region was covered by the SIS during the Weichselian glaciation, and all lakes were formed when the SIS margin shifted gradually northwards. During the Last Glacial Maximum (LGM) ~21,000–18 000 cal yr BP the southeastern sector of the SIS extended south to central Poland, Lithuania and northern Belarus (Fig. 4). Deglaciation of northern Europe
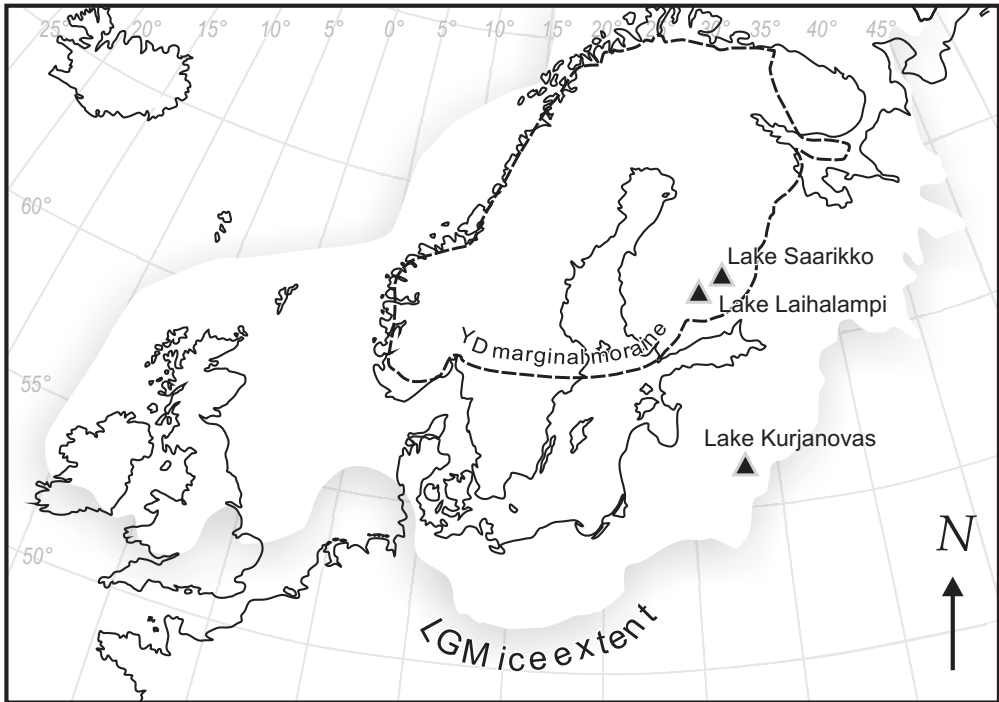
Figure 4. A map of northern Europe showing the study sites with respect to the LGM (Svendsen *et al.* 2004) and the Younger Dryas (Donner 1995) ice extent, respectively.

started when the temperature rose, but the ice margin retreat was punctuated by climatic oscillations. Substantial warming occurred during the Bølling/Allerød interstadial (B/A, Greenland Interstadial-1) ~14,700–12,900 cal yr BP (Rasmussen *et al.* 2006b) and the SIS margin retreated across Estonia and southern Sweden. During the Younger Dryas stadial (YD, Greenland Stadial-1) ~12,900–11,700 cal yr BP (Rasmussen *et al.* 2006b) the ice sheet margin was positioned over southern Fennoscandia (Fig. 4). Postglacial time, or the Holocene epoch, began ~11,700 cal yr BP and by ~9000 cal yr BP the SIS remnant located in northern Sweden had disappeared (Kleman *et al.* 1997). However, waters of the prehistoric stages of the Baltic Sea covered vast areas and the modern shoreline configuration was attained only during the mid-Holocene ~6000 cal yr BP.

2.2 Sediment sampling, stratigraphical analyses and dating

Lake Laihalampi (Paper I, III) and Lake Kurjanovas (II, IV) were sampled using a 100-cm-long and 10-cm-diameter Russian peat sampler, whereas sampling of Lake Saarikko (V) was performed using a Livingstone-type piston corer equipped with clear tubes, 180 cm in length and 10 cm in diameter. Recovered cores were described and photographed in the field, transferred and stored in the cold room at +4 °C. Subsampling was performed contiguously in 0.5- to 1-cm increments, and data are based on analyses at 1- to 4-cm intervals. Lake Laihalampi loss-on-ignition (LOI) and pollen analyses totaled 150 samples, whereas Lake Kurjanovas analyses included 175 samples for pollen analyses (Lateglacial and Holocene) and 63 samples for plant macrofossil analysis and LOI

analysis (Lateglacial). The number of analyses on Lake Saarikko samples was as follows: 115 for LOI, 144 for δ^{18}O from cellulose and for carbon and nitrogen elemental and isotopic analyses from bulk organic matter, and 55 for δ^{18}O and δ^{13}C from carbonate. Detailed descriptions of sampling and subsampling strategies can be found in each manuscript.

Sediment organic matter and carbonate content were estimated by LOI. First, water content was estimated by oven-drying the samples for 24 h at 105°C. The samples were then combusted in a muffle furnace, first at 500-550 °C for 3-5 hours and then at 950 °C for 2 hours. Results are expressed following Heiri *et al.* (2001) as percentages of weight loss of the sediment in each step in relation to the dry weight of the samples before combustion.

Chronological control was based on radiocarbon dating of bulk sediment (Lake Laihalampi) or terrestrial/telmatic macrofossils (Lakes Kurjanovas and Saarikko), and dates were calibrated using the INTCAL98 (Stuiver *et al.* 1998) or INTCAL04 (Reimer *et al.* 2004) data. In some cases, sample dates that clearly deviated from the overall age–depth relations were not used in age-depth models. Moreover, fixed dates for the core top (all Papers) and for other known stratigraphical events (Papers I, II) were employed. Details of strategies for chronological control and age-depth models for each sequence can be found in Table 1 and the corresponding manuscripts.

2.3 Pollen and plant macrofossil analyses

Pollen samples were prepared from volumetric samples of 0.5 or 1 cm³, treated with standard methods of KOH, HF and acetolysis (Moore *et al.* 1991). *Lycopodium* tablets (Stockmarr 1972) were added in order to estimate pollen concentrations and accumulation rates. At least 500 (Lake Laihalampi) or 700 (Lake Kurjanovas) terrestrial

pollen and spores were analysed to the lowest possible taxonomic level. Pollen and spore nomenclature followed Moore *et al.* (1991) with the following exceptions: *Achillea*-type and *Solidago*-type correspond to *Anthemis*-type and *Aster*-type of Moore *et al.* (1991), family Rubiaceae is congruent with *Galium*-type of Moore *et al.* (1991), oblong pollen grains with large lacunae from family Cyperaceae were termed *Carex*-type, and unidentified spores of the family Polypodiaceae are called *Dryopteris*-type. Modern reference collections were used for critical determinations. The remains of conifer stomata were identified from the pollen microscope slides to species level (*Picea abies, Pinus sylvestris*) when possible; identification was based on Sweeney (2004). Data of conifer stomata were critical for and presented in Paper II.

Pollen diagrams were prepared using the software packages TILIA and TILIA.GRAPH (Grimm 1990) or C2 (Juggins 2007). Percentages of terrestrial pollen and spore taxa were calculated on the basis of their total sum, percentages of aquatics on the basis of their total sum plus the total sum of terrestrial taxa, and percentages of *Sphagnum* on the basis of *Sphagnum* plus the total sum of terrestrial taxa. Pollen concentrations were calculated by multiplying the number of each pollen type by the ratio of the added and counted *Lycopodium* markers, and pollen accumulation rates from the pollen concentration values by multiplying the concentration values of each subsample by the sedimentation rate, respectively. Most data are reported as percentage values, but PAR values are employed in Paper III. Interpretation of population shifts was facilitated by performing principal components analysis (PCA) on Lake Kurjanovas Lateglacial pollen percentage data (Paper II) and cross-correlation analyses on Lake Laihalampi PAR data as well as on other pollen data (Giesecke 2005; Ojala & Alenius 2005; Alenius & Laakso 2006) pre-
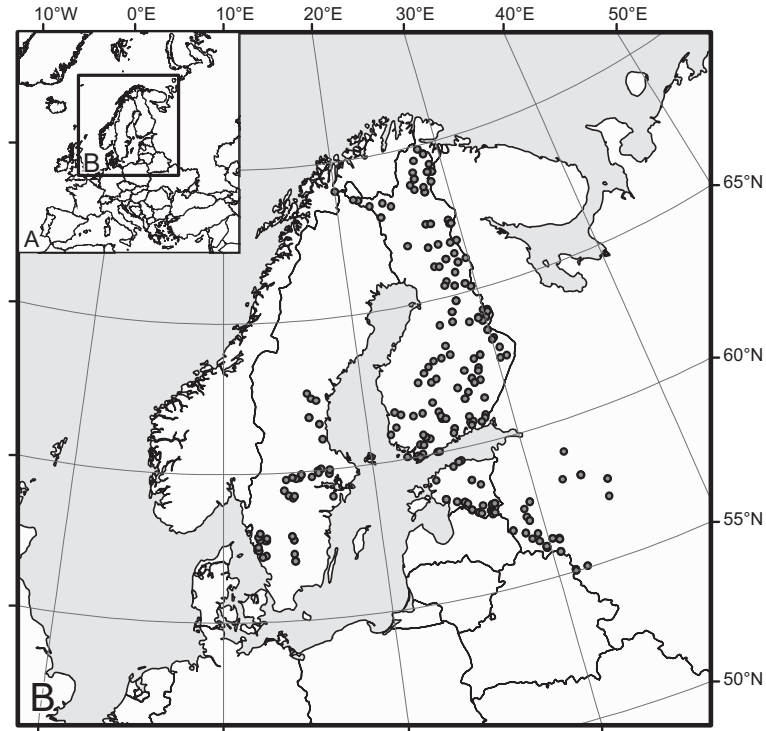
Figure 5. A map of the surface sample sites used to derive pollen-climate transfer functions.

sented in Paper III.

Plant macrofossils for Paper II were analysed from samples of 8–21 cm³ of wet sediment with a stratigraphic thickness of 1 cm by S. Fontana. Samples were soaked overnight in 5% NaOH and sieved with a 150-mm mesh. Plant macrofossil remains were identified according to Bertsch (1941), Bialobrzeska and Truchanowiczowna (1960), Tomlinson (1985), Grosse-Brauckmann and Streitz (1992) and Van Dinter and Birks (1996).

2.4 Quantitative pollen-based reconstructions

The climate reconstructions were carried out using pollen-climate transfer functions generated for each pollen and spore type using weighted averaging partial least squares (WA-PLS) (ter Braak & Juggins 1993; Birks 2003). North Eu-

ropean pollen-climate calibration set (Seppä *et al.* 2004) initially used by Seppä & Birks (2001) has been spatially extended, and it now includes 231 pollen surface samples from lakes in Finland (113) (Seppä & Birks 2001), Estonia (24) (Seppä *et al.* 2004; Seppä & Poska 2004), Sweden (36) (Seppä *et al.* 2005; Antonsson 2006) and Russia (58) (Heikkilä & Seppä 2010; Salonen *et al.* in preparation). All lakes in the training set were selected according to the same specific criteria, and standardized methodology was employed in the collection, preparation, nomenclature and analysis of all samples. Pollen identification was harmonized and pollen analysis was carried out by few analysts. For this study (Paper IV), 24 new samples were collected from western Russia and included in the training set to ensure representation of broadleaved forest of the Baltic region and potential temperate mid-Holocene tree

Table 2. Characteristics and performance of the WA-PLS pollen-climate calibration sets used in Lake Laihalampi T_{ann} reconstruction (Paper I) and Lake Kurjanovas T_{summer} reconstruction (Paper IV).

	Training set for paper I	Training set for paper IV
Number of sample lakes	113	177
Number of pollen taxa[1]	84	105
Temperature range	-4.7 – 5.4 (T_{ann})	8.9 – 15.4 (T_{summer}, May to August)
Geographical coverage	Finland	forested Finland, Sweden and Estonia, western Russia
Root mean square error of prediction (RMSEP) (°C)	0.91	0.74
R^2 between predicted and measured temperature	0.85	0.74
Maximum bias (°C)	2.1	1.6

populations. Undisturbed temperate forest is rare inside its natural range in Europe due to extensive land use by humans, and potential modern sites are located in the eastern domain of Europe.

For the annual mean temperature (T_{ann}) reconstruction of Lake Laihalampi, 113 lakes in Finland (Paper I), and for the summer temperature reconstruction (T_{summer}) of Lake Kurjanovas, 177 lakes from Finland, Estonia, Sweden and Russia were used (Fig. 5). The modern temperature estimates for the surface-sample sites in Finland, Estonia and Sweden were extrapolated from the climate normals (1961–1990) of nearby meteorological stations, applying an adiabatic lapse rate of 0.57°C per 100-meter altitudinal increase (Laaksonen 1976). Modern temperature estimates for Russian sites were derived from the 10' gridded data set by New *et al.* (2002). Details of both calibration data sets are presented in Table 2. The model performance was tested by leave-one-out cross-validation, and two-component WA-PLS models were selected for temperature reconstructions based on the highest coefficient of determination (R_2), lowest root mean square error of prediction (RMSEP) and lowest maximum bias. Monte Carlo simulation implemented in the program WA-PLS (ter Braak & Juggins 1993) was used to calculate sample-specific error-estimates for reconstructed temperatures.

2.5 Elemental and stable isotope analyses

Organic carbon and nitrogen content and isotopic composition were analyzed from bulk organic matter. Carbonate was removed by placing vials filled with 10% HCl in a warm water bath (60 °C) for 2 h. Samples were rinsed with deionized water, and the procedure was repeated until the pH in vials reached that of the deionized water. Sample residue was then freeze-dried and dried samples were sieved with a 500-μm mesh to remove coarse debris. The fine fraction was used for total organic carbon (TOC), total nitrogen, stable carbon ($\delta^{13}C_{org}$) and nitrogen isotope ($\delta^{15}N$) analyses, performed using an elemental analyzer interfaced with a continuous-flow isotope ratio mass spectrometer in the University of Waterloo Environmental Isotope Laboratory. The total organic nitrogen (TON) and carbon:nitrogen (C/N) are reported as weight ratio corrected for inorganic nitrogen as suggested by Talbot (2001), and $\delta^{13}C_{org}$ and $\delta^{15}N$ values as δ-values with respect to VPDB and AIR standards, respectively.

Samples for sediment cellulose oxygen iso-

tope analysis were prepared from the same HCl-washed residue that was used for organic carbon and nitrogen measurements. Non-cellulose organic and inorganic matter was eliminated in four steps: lipids, resins and tannins with solvent extraction, lignin with bleaching, xylan, mannan and other polysaccharides with alkaline hydrolysis and Fe- and Mn-oxyhydroxides with leaching (Wolfe *et al.* 2001b; Wolfe *et al.* 2007). Cellulose δ18O was analyzed by high-temperature pyrolysis using an on-line continuous-flow isotope-ratio mass spectrometer at the University of Waterloo Environmental Isotope Laboratory. Results are expressed as δ-values with respect to the VSMOW standard. Analytical reproducibility estimated from repeat measurements on cellulose samples is ±0.4 ‰.

Samples for sediment carbonate oxygen and carbon isotope analysis were prepared from bulk carbonates. Selected sediment samples were freeze-dried and subsequently sieved using a 500-μm mesh to eliminate occasional *Chara* encrustations, mollusk and ostracod shells. The fine fraction was homogenized, and treated with sealed vessel phosphoric acid procedure of McCrea (1950). The resultant CO_2 was measured for isotope ratios with dual inlet VG Prism mass spectrometer. Results are expressed as δ-values with respect to VPDB standard. Analytical reproducibility based on repeated analyses on the standard materials is ±0.2‰ for oxygen and ±0.1‰ for carbon.

Samples of lake water and precipitation were analyzed for oxygen and hydrogen isotopes at the University of Helsinki Dating Laboratory. Results are reported relative to VSMOW using the δ-notation, normalized to SLAP values of −55.5‰ (δ18O) and −428‰ (δ2H) as recommended by Coplen (1996).

3 Results and Discussion

3.1 Lateglacial climate and vegetation responses

Paper II examines Lateglacial plant communities, tree populations and their responses to the major climate changes of the Lateglacial/Holocene transition. The common notion has been that during glacial times, temperate and boreal tree populations were restricted to far south of the continental ice sheets. In Europe, the suitable locations were in the Iberian, Italian and Balkan Peninsulas (Bennett *et al.* 1991). This view has, however, been recently amended by indications for smaller refuge populations of trees at higher-latitude locations (Kullman 2002; Willis & van Andel 2004; McLachlan *et al.* 2005; Anderson *et al.* 2006; Cheddadi *et al.* 2006; Feurdean *et al.* 2007; Kullman 2008; Binney *et al.* 2009; Väliranta *et al.* submitted), so called "cryptic refugia" (Stewart & Lister 2001). A more exact picture of refuge sites and colonization routes is complicated by the lack of evidence for populations *in situ,* e.g., plant macrofossils, remains of stomata and charcoal. The reversal of glacial climate to interglacial conditions involved drastic changes in temperature and seasonality (Denton *et al.* 2005; Overpeck & Cole 2006), exerting an influence on reshuffling and migration of plant populations. The potential refuge populations and reassembling of taxa in response to the major climatic transition in the southeastern sector of the SIS were studied employing fossil pollen spectra, plant macrofossils and conifer stomata from the Lake Kurjanovas sediment sequence.

3.1.1 Rapid, stepwise nature of environmental changes

Lake Kurjanovas probably formed before ~16,000 cal yr BP shortly after the SIS had retreated (Fig. 4, and Fig. 1 in Paper II). Pollen and macrofossil remains (Fig. 6, and Figs. 4 and
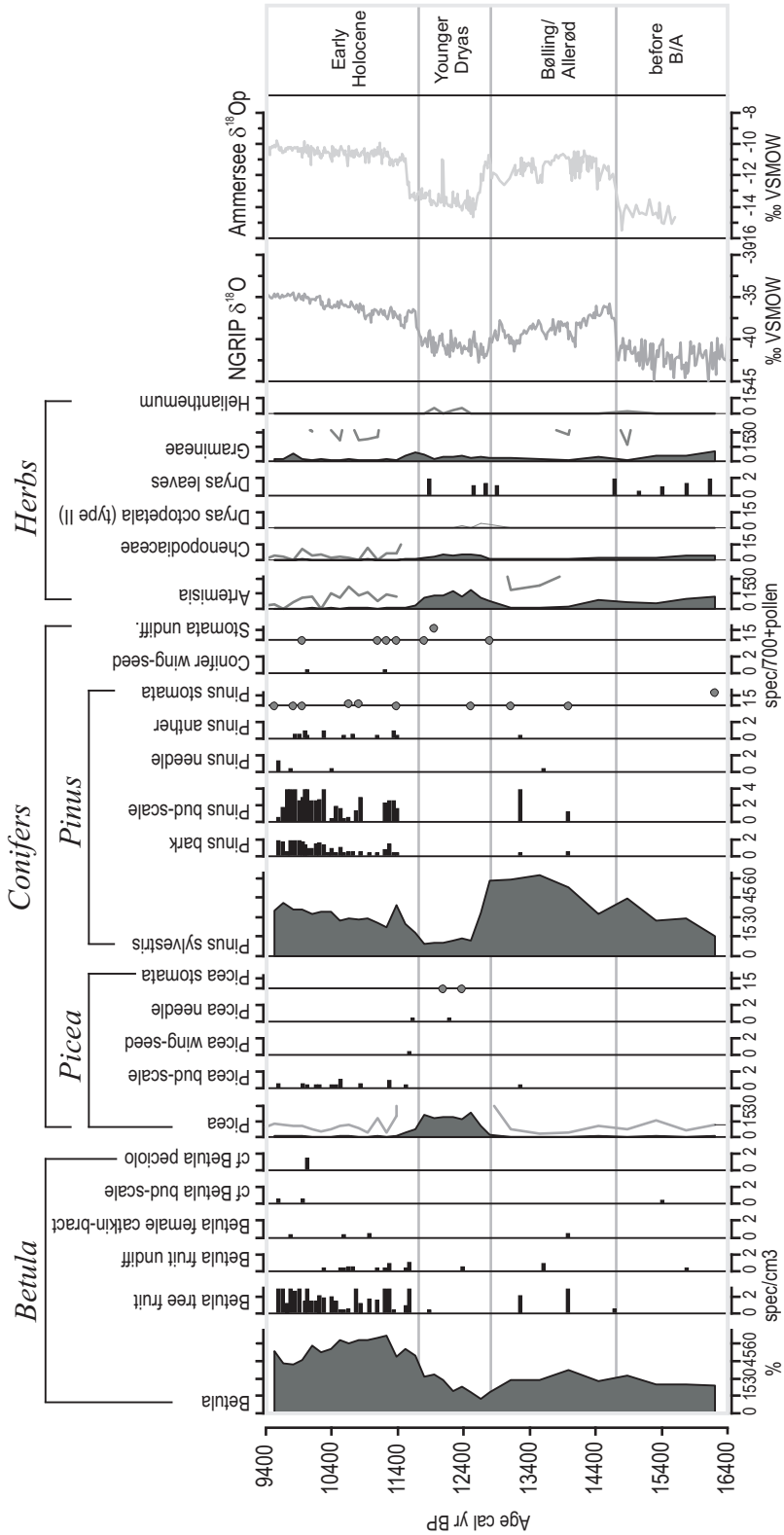
Figure 6. A diagram of Lateglacial vegetation changes in the eastern Baltic region similar to the Fig. 8 in Paper II, except that all macrofossil specimens of key tree taxa are shown here. References and explanations in text.

5 in Paper II) indicate that the vegetation community initially consisted of periglacial tundra plants, e.g., *Dryas octopetala*. Wind-dispersed pollen of steppe-taxa, such as *Artemisia* and Chenopodiaceae were abundant, but these taxa were not found in macrofossil samples, implying that steppe communities may have been located further south and east from the study site. The open tundra community was replaced by a dense *Pinus–Betula* forest during the B/A (~14,400-12,900 cal yr BP), demonstrated by high pollen proportions, stomata remains of *Pinus* and plentiful macrofossil specimens of both taxa. During the YD, ~12,900-11,700 cal yr BP, a peculiar semi-open, tundra-like herb and shrub community with localized *Picea* populations prevailed. At the boundary of the B/A and the YD, *Picea* pollen proportion increases in ~200 years from 0% to ~10–24%. Two stomata remains of *Picea*, a *Picea* needle and a conifer wing-seed were also recovered. Photographs of these specimens are presented in Fig. 6 of Paper II. At the start of the early Holocene, *Betula–Pinus* forest resembling that of the B/A quickly substituted the semi-open landscape of scattered stands of *Picea*.

Notably, the results of principal components analysis (PCA) reveal systematic aggregates of pollen sample scores in two-dimensional space (PCA axes 1 and 2)(see Fig. 7 in Paper II). Pollen assemblages from pre-B/A, the B/A, the YD and the early Holocene are each delimited in their own clusters, demonstrating the compositional divergence between the time intervals. The abrupt shifts in plant communities are also seen distinctly in the plant macrofossil stratigraphy. Instead of progressive plant succession on the recently deglaciated terrain (Birks 1986), the rapid ecosystem reshuffling was driven by substantial Lateglacial climate changes, illustrated in Fig. 6 by δ18O stratigraphy from the Greenland NGRIP ice core (North Greenland Ice Core Project (NGRIP) members 2004)(see also Fig. 8

in Paper II) and by precipitation δ18O record inferred from sediment biogenic calcite from Lake Ammersee, southern Germany (von Grafenstein *et al.* 1999a).

Rapid changes in temperature and moisture balance, and their seasonal distribution, are able to explain the striking vegetation patterns and the Lateglacial presence of boreal tree populations. *Pinus* is typically an abundant pollen taxon in the B/A of northern Europe (Berglund *et al.* 1994; Ralska-Jasieviczowa & Latałowa 1996; Saarse *et al.* 1996), which is considered as the interval of the initial postglacial warming. The local presence of *Pinus* forest near Lake Kurjanovas is indicative of summer temperatures higher than 12°C (Kultti *et al.* 2006), which is in accordance with proxy- and model-inferred July mean temperatures in central and western Europe (Renssen & Isarin 2001; Heiri & Millet 2005; Peyron *et al.* 2005; Heiri *et al.* 2007) In contrast, the abrupt cooling during the YD (12,900-11,700 cal. yr BP)(Rasmussen *et al.* 2006a), has been mostly attributed to the wintertime (Renssen *et al.* 2001; Denton *et al.* 2005; Broecker 2006; Brauer *et al.* 2008). The substantial intensification of seasonality, i.e., remarkably cold winters and mild summers, during the YD serves as a key explanation for anomalous assemblages of *Picea*-tundra in the Lake Kurjanovas sequence. Modern range of *Picea abies* in northern Europe is delimited by the highest temperature of the coldest month of -1.5 °C and the minimum of growing season degree days of 600 GDD, depicting the most continental range of European tree species (Prentice & Helmisaari 1991; Dahl 1998; Giesecke *et al.* 2008; Miller *et al.* 2008). *P. abies* has a greater tolerance of cold winters, and is more capable of growing in permafrost conditions than *Pinus sylvestris* and *Betula* (Hytteborn *et al.* 2005). Importantly, the shifts from *Pinus-Betula* dominance and *Picea* absence in the B/A to *Picea* presence in the YD, and again

to the disappearance of *Picea* pollen and readvance of *Betula-Pinus* forest in the early Holocene, are suggestive of changing continentality (Giesecke *et al.* 2008). Another feature of note is that the clearly defined changes in vegetation indicate immediate to rapid response times of plant associations to climate change, in agreement with the view of Post (2003), who argued that major climatic transitions induce vegetation changes "in the fast lane" (see also Birks & Ammann 2000; Williams *et al.* 2001; Williams *et al.* 2002; Yu 2003, 2007).

3.1.2 Lateglacial populations of boreal trees

The SIS covered most of northern Europe during the Lateglacial (Fig. 4). Hence, pollen and plant macrofossil stratigraphies do not typically extend to the B/A or YD. The few Lateglacial records from the southeastern sector of the SIS indicate that *Betula* and *P. sylvestris* were the first colonizing tree taxa (Pirrus 1969; Saarse *et al.* 1996; Stančikaite *et al.* 2004). The low Lateglacial pollen values of *Picea*, *Alnus* and other temperate tree taxa, in contrast, have been attributed to long-distance transport or redeposition (Saarse *et al.* 1999).

Molecular evidence from organelle (chloroplastic and mitochondrial) and nuclear DNA of modern tree populations has recently shed new light on glacial histories and past colonization patterns of trees (McLachlan *et al.* 2005; Anderson *et al.* 2006; Petit *et al.* 2008; Hu *et al.* 2009). Studies of nuclear markers and organelle DNA from modern European populations have consistently revealed a clear distinction between northern and southern populations of *Betula pubescens, B. pendula*, *P. sylvestris* and *P. abies*, supporting the view of mid- and high-latitude survival of trees alongside with the southern refuge locations. Chloroplastic DNA haplotypes of *Betula* populations south of the Alps do not oc-

cur in northern Europe (Palmé *et al.* 2003; Palmé *et al.* 2004), whereas mitochondrial DNA haplotypes of central and northern *P. sylvestris* populations are absent in the southern peninsulas and vice versa (Cheddadi *et al.* 2006; Pyhäjärvi *et al.* 2008). The similar broad-scale genetic histories and concurrent timing of shifts in *Betula* and *P. sylvestris* populations suggests congruent responses of the two taxa to major climate changes of the Lateglacial/Holocene transition.

The current distribution of *P. abies* in Europe is divided into disjunct southern and northern ranges (Schmidt-Vogt 1977). The northern range covers almost the entire European Russia, the Baltic region and Fennoscandia, whereas the southern range is mainly restricted to mountain chains of central and east-central Europe. The geographically separated ranges are consistent with two divergent genetic lineages that have likely been separated over several glacial cycles (Vendramin *et al.* 2000; Heuertz *et al.* 2006; Tollefsrud *et al.* 2008).Latest genetic evidence suggests that the vast northern range of *P. abies* was colonized from a single refuge location in the East European Plain (Tollefsrud *et al.* 2008; Tollefsrud *et al.* 2009)Hence, the nucleus for the spread of the YD *P. abies* population in Latvia was most probably not far eastward from Lake Kurjanovas. Other paleoecological evidence, e.g., pollen stratigraphies from the Haanja heights in southeastern Estonia (Pirrus 1969; Ilves & Mäemets 1996; Saarse & Rajamäe 1997) and from northern Belarus (Makhnach *et al.* 2004) also demonstrate the YD peak in *Picea* pollen values. The challenge in assessing the Lateglacial presence of the species, however, has been the lack of evidence for populations *in situ*. The macrofossil evidence from Lake Kurjanovas, presented in Paper II, manifests the Lateglacial presence of *P. abies* in the Baltic region. In addition, Stančikaite *et al.* (2008) recently reported a finding of *Picea* needles dated to the YD

from Lithuania (see location in Fig. 1 of Paper II).

Bhagwat and Willis (2008) proposed that the full-glacial persistence of trees farther north in Europe was mostly restricted to small-seeded, wind-dispersed and coniferous species. Their suggestion is in line with results from species distribution modeling indicating that LGM conditions in northeastern Europe were sufficient for the presence of boreal tree species (Svenning *et al.* 2008). The Lake Kurjanovas record demonstrates that *P. sylvestris* was frequent in eastern Latvia during the B/A together with *Betula*, and *P. abies* was present during the YD, consistent with this argument. The proximity of glacial refuge locations of these boreal tree species to the receding ice sheet, as suggested by paleoecological and genetic evidence, evokes two final remarks. First, tree-migration rates may be lower than previously estimated (Huntley & Birks 1983), which may attest to the inadequate capacity of trees to adapt to predicted changes in future climate. Second, the strikingly rapid ecosystem shifts in response to major climatic changes suggested by the current study and other records from Europe and North America (e.g., Birks & Ammann 2000; Yu 2003, 2007; Tinner & Kaltenrieder 2005; Shuman *et al.* 2009; Williams *et al.* 2009) were likely facilitated by the proximity of glacial refuge locations to the study sites.

3.2 Holocene climate dynamics

3.2.1 Low-frequency trends in temperature

In general, changes in orbitally-driven insolation have been considered the dominant driver of low-frequency changes in temperature, shifts in arctic treeline and latitudinal ecotones during the Holocene (COHMAP members 1988; Texier *et al.* 1997; MacDonald *et al.* 2000; Brovkin *et al.* 2002; Wanner *et al.* 2008). The Holocene summer insolation in the Northern Hemisphere was at its highest 11,000-9000 cal yr BP (Berger 1978). Modeling experiments largely agree with the early Holocene insolation-driven temperature maximum (Weber 2001; Rimbu *et al.* 2004; Renssen *et al.* 2005; Timm & Timmermann 2007), but proxy data from Northern Hemisphere show spatial variation in the timing of peak warmth, commonly termed the Holocene Thermal Maximum (HTM). In western Canada, proxy-inferred maximum temperatures are roughly synchronous with the insolation maximum, whereas in eastern North America and Europe, the highest Holocene temperatures were attained some millennia later (Ritchie *et al.* 1983; Hu & Brubaker 1996; Seppä & Birks 2001; Korhola *et al.* 2002; Davis *et al.* 2003; Kaufman *et al.* 2004; Antonsson *et al.* 2006; Viau & Gajewski 2008).

The HTM has been identified in northern Europe since the beginning of the 20th century (Andersson 1902, 1909; von Post 1925; Iversen 1944), and the reconstructed temperature anomalies presented in Papers I and IV are roughly similar to their estimates of ~1.5-2.5°C. The pollen-based reconstructions from Lake Laihalampi (Paper I) and Lake Kurjanovas (Paper IV) illustrate similar millennial-scale trends (Fig. 5 and 7 in Paper I, Fig. 4 in Paper IV) during the Holocene. The early Holocene is characterized by steadily increasing temperatures, with peak warmth in the mid-Holocene ~8000-4000 cal yr BP, and subsequent gradual late Holocene cooling. These general trends are consistent with other proxy evidence from northern Europe, pinpointing the "delayed" timing of the HTM (Seppä & Birks 2001; Korhola *et al.* 2002; Davis *et al.* 2003; Seppä & Poska 2004; Bjune *et al.* 2005; Antonsson *et al.* 2006; Weckström *et al.* 2006; Ojala *et al.* 2008a; Nesje 2009; Seppä *et al.* 2009b). The gradual cooling of the late Holocene follows the declining Northern Hemisphere insolation, although there are fluctuations that

may reflect human influence on vegetation since ~2500 cal yr BP in Latvia and ~1000 cal yr BP in Finland. Some differences between the two reconstructions can be highlighted – the maximum warming was more pronounced in Lake Kurjanovas reconstruction (~3.0°C, T_{summer}) compared to Lake Laihalampi reconstruction (~1.5°C, T_{ann}). In addition, the highest inferred temperatures occurred slightly earlier (~8000-6000 cal yr BP) in the more southern, Latvian location than in the southern boreal zone of Finland (~6500-5500 cal yr BP).

The spatial pattern of the magnitude of the HTM in northern Europe, reflected in pollen-based reconstructions, is illustrated as a map in Fig. 7 of Paper IV. It can be noted that the positive anomaly of the Holocene peak warmth increases eastward from the Atlantic coast towards the East European Plain and southward from the northernmost Fennoscandia to the Baltic Region. It can also be observed that July mean temperature (T_{jul}) has been reconstructed in arctic and alpine sites of northernmost Europe and the Atlantic coast, whereas in the lowland of forested northeastern Europe, annual mean temperatures (T_{ann}) have been used. The reason for this is that in arctic and alpine settings, growing season is restricted to summer months and summertime conditions are pivotal for plant growth and reproduction. In contrast, the growing season can be much longer in boreal and temperate zones and trees are dependent on wintertime conditions as well (Dahl 1998; Walther & Linderholm 2006; Giesecke *et al.* 2008). Lake Kurjanovas is currently the southernmost location where the north-European pollen-climate calibration set (Seppä *et al.* 2004) has been applied. Summer temperature estimates (May to August, T_{summer}) were reconstructed for Lake Kurjanovas, because many temperate tree species typical of the Baltic region are highly sensitive to changes in spring temperatures (Ahas *et al.* 2002) rather than mid-summer (July) temperatures. However, as demonstrated by the T_{ann} reconstruction performed for comparison with other records in Fig. 7 of Paper IV, the four-month summer temperature (T_{summer}) reconstruction and annual mean temperature (T_{ann}) reconstruction for Lake Kurjanovas are very similar. This is probably due to the seasonal distribution of the HTM warming, which has been mainly attributed to summer months (Davis *et al.* 2003; Antonsson *et al.* 2008). The more pronounced warming in the southern and eastern parts of northern Europe potentially reflects steeper than modern north-south gradient of increasing temperatures together with more effective warming of the Eurasian landmass compared to the Atlantic Ocean (Ganopolski *et al.* 1998).

The explanation for the commonly "delayed" and spatially varying timing of the proxy-inferred HTM in the Northern Hemisphere has been recently provided by transient model simulations in a coupled ocean-atmosphere-vegetation model, incorporating the influence of the Laurentide Ice Sheet (LIS) for the first time (Renssen *et al.* 2009)(Fig. 8A). Renssen *et al.* (2009) demonstrate that while the high surface albedo of the LIS had a cooling effect directly over eastern North America, the LIS meltwater flux led to weakening of meridional overturning circulation and reduced northward heat transport by the Atlantic Ocean. This cooled the climate on the northern Atlantic and on the Eurasian continent between 45 and 60°N until the disappearance of LIS at ~7000 cal yr BP. The more exact spatial pattern of the HTM suggested by the model experiments reveals a slightly earlier peak summer warmth ~7000-6000 cal yr BP along the Atlantic seaboard of Europe, whereas further inland and southward on the Eurasian continent, highest temperatures are attained ~8000-7000 cal yr BP. The reconstructions presented here are roughly consistent with this pattern: the peak of the HTM takes place ~1-2 millennia earlier in

Latvia (~8000-6000 cal yr BP) than in Finland (~6500-5500 cal yr BP). Also pollen-based T_{ann} reconstructions from Estonia, the Baltic region, show highest temperatures ~8000-7500 cal yr BP (Seppä & Poska 2004), whereas organic varve accumulation in Lake Nautajärvi, south-central Finland, indicates peak summer warmth ~6500-5500 cal yr BP (Ojala & Alenius 2005). The $\delta^{18}O_{carb}$-$\delta^{18}O_{lw}$ separation of the Lake Saarikko sequence was used to derive relative lake water temperature estimates (Paper V), based on differences in $\alpha_{cellulose-water}$ (constant) and $\alpha_{carbonate-water}$ (temperature-dependent) (Friedman & O'Neil 1977; Edwards 1993). Smaller $\delta^{18}O_{carb}$-$\delta^{18}O_{lw}$ separation indicates relatively higher lake water temperatures. The smallest $\delta^{18}O_{carb}$-$\delta^{18}O_{lw}$ separation ~6000-5000 cal yr BP is consistent with pollen-based reconstructions and other evidence for summer temperature maximum in Finland at this time (Paper V).

3.2.2 Low-frequency trends in moisture balance

The $\delta^{18}O$ stratigraphies of cellulose-inferred lake water ($\delta^{18}O_{lw}$) and authigenic carbonate ($\delta^{18}O_{carb}$) from small, hydrologically open Lake Saarikko reflect changes in the hydrological balance of the lake during the Holocene (Paper V). The modern isotope hydrology of the lake shows that at present, the lake water traces the isotopic composition of precipitation, modified by a slight summertime evaporative enrichment (~2‰) and a minor snowmelt signal (Fig. 3 in Paper V). However, stratigraphical changes in carbonate sedimentation (Fig. 4 in Paper V) and close correlation of carbonate $\delta^{18}O$ and $\delta^{13}C$ (Fig. 6 in Paper V), supported by other elemental and isotopic tracers (Fig. 5 in Paper V) indicate that the lake residence time was substantially longer during the Holocene than at present. Hence, the lake was probably more sensitive to summertime evaporative enrichment (Gat 1995; Gibson

& Edwards 2002; Edwards *et al.* 2004) and Holocene changes in $\delta^{18}O_{lw}$ and $\delta^{18}O_{carb}$ mainly reflect changes in lake hydrological balance, with additional signals from spring snowmelt, changing source moisture and variation in atmospheric circulation (Paper V).

Two periods of enriched $\delta^{18}O$ values, and hence, relatively dry conditions, are apparent: ~10,000-9000 cal yr BP and ~7500-3300 cal yr BP. The former period is not coupled with higher temperatures (see section 3.2.1), while the latter period coincides with the HTM. The phases of enriched $\delta^{18}O$ values of Lake Saarikko are also coupled with higher epilimnion productivity and lower lake levels, inferred from elemental and isotopic tracers from organic matter and higher carbonate sedimentation (Figs. 4 and 5 in Paper V). While temperatures in the earliest Holocene were low, dry climate may have been caused by reduced precipitation and snowmelt. Lower lake levels have been recorded from the Baltic region and Fennoscandia (Digerfeldt 1988; Saarse & Harrison 1992; Harrison *et al.* 1996; Fig. 5 in Sohar & Kalm 2008; Olsson & Lemdahl 2009), but the early Holocene dryness has not been demonstrated by all records (e.g., Hammarlund *et al.* 2003). The coupling of high mid-Holocene (~7500-4000 cal yr BP) temperatures, low effective humidity and dry conditions, on the other hand, has been extensively reported. Lake levels in northernmost Fennoscandia, Sweden and the Baltic region were low (Digerfeldt 1988; Almquist-Jacobsen 1995; Harrison *et al.* 1996; Korhola *et al.* 2005; Sohar & Kalm 2008), as was effective humidity, reflected by enriched carbonate $\delta^{18}O$ from Lake Igelsjön (Hammarlund *et al.* 2003) and reduced peatland initiation in Finland (Korhola 1995). In addition, Fennoscandian glaciers mostly melted away during the mid-Holocene; the most contracted phase was ~6600-6300 cal yr BP (Nesje 2009 and references therein).

Relatively depleted $\delta^{18}O$ values ~9000-7500

cal yr BP and after ~3300 cal yr BP are indicative of higher effective humidity. During these time intervals, lake level was higher (Fig. 4 in Paper V), nitrogen limitation in the lake was alleviated, presumably due to higher lake levels, lower lake productivity and/or higher precipitation allowing nitrogen recharge from the catchment (Fig. 5 in Paper V). The depleted early Holocene fingerprint probably resulted from several processes: 1) cool summers (see section 3.2.1) with reduced evaporative enrichment, 2) moisture derived from the Ancylus Lake/early Littorina Sea influenced by the SIS meltwater, 3) heavier winter snowfall and hence, ample spring snowmelt, and 4) the well-reported 8.2 ka cold event in southern Fennoscandia (Veski *et al.* 2004; Seppä *et al.* 2007; Ojala *et al.* 2008b; Zillén & Snowball 2009) (see section 3.2.3). Almost complete cessation of carbonate sedimentation since ~3300 cal yr BP refers to higher lake levels and/or lower productivity in the late Holocene, consistent with low $\delta^{18}O_{lw}$ values and lower summer temperatures. A significant drop to values comparable to modern minimum $\delta^{18}O$ of snowfall takes place during the latest millennium, indicating a drastic change in the lake hydrological mode and probably the activation of its present outlet. This may have been related to the large-scale climatic changes of the Little Ice Age (LIA) and related accumulation of deeper snowpacks. Rising $\delta^{15}N$- and C/N-values of the sediment organic matter indicate increased nitrogen limitation that could have been caused by rapid hydrological flushing due to severe spring flooding (Bergström *et al.* 2008).

3.2.3 High-frequency variation and the "8.2 ka event"

The temporal resolution of the records presented here is ~60-80 years per sample, and age-depth models contain additional uncertainty. Hence, the records are not reliable recorders of fine-scale variation unless it is represented by several successive samples and exceeds error estimates in magnitude (e.g., the prediction error of 0.91°C for Lake Laihalampi and 0.74°C for Lake Kurjanovas WA-PLS-models (Table 2), or the analytical reproducibility of ±0.4‰ for Lake Saarikko cellulose $\delta^{18}O$ measurements). Even though the materials and methods of this study are not ideally suited for probing high-frequency climate variation, there is one feature that is notable and highly interesting: the 8.2 ka cold event (Alley *et al.* 1997).

An abrupt climate anomaly around 8200 cal yr BP in the Northern Hemisphere, often termed the 8.2 ka (cold) event, is commonly related to weakened Atlantic meridional overturning circulation triggered by freshwater drainage from glacial Lake Agassiz and Ojibway (Alley & Ágústsdóttir 2005; LeGrande *et al.* 2006; Kleiven *et al.* 2008; Li *et al.* 2009). It is seen e.g., as lower $\delta^{18}O$ values and increased wind-blown dust in Greenland ice cores (Alley *et al.* 1997), as colder temperatures reflected in terrestrial and marine records from northern and central Europe (von Grafenstein *et al.* 1998; Rohling & Pälike 2005; Nesje *et al.* 2006; Marshall *et al.* 2007; Ojala *et al.* 2008b; Zillén & Snowball 2009). The proxy-inferred and modeled temperature drop on the European continent is about 1-2°C (Tinner & Lotter 2001; LeGrande *et al.* 2006; Wiersma & Renssen 2006; Seppä *et al.* 2007). Lake sediment and speleothem $\delta^{18}O$ records show a depletion of ~1‰ in central Europe (von Grafenstein *et al.* 1998; Boch *et al.* 2009) and ~2‰ in Sweden (Hammarlund *et al.* 2003); however, one has to bear in mind that $\delta^{18}O$ records reflect source moisture, rainout histories and atmospheric conditions, not merely temperature.

In the records presented in this work, the 8.2 ka cooling is seen as an abrupt cooling in pollen-based temperature records (Figs. 5, 7 and 8 in Paper I and Figs. 4 and 5 in Paper III), and de-

pleted $\delta^{18}O_{lw}$ and $\delta^{18}O_{carb}$ in Lake Saarikko moisture balance record (Fig. 6 in Paper V). In the Lake Laihalampi T_{ann} reconstruction, the cooling is not particularly pronounced, but deviations from the warming trend in several samples can be noted. The Lake Kurjanovas T_{summer} reconstruction, on the other hand, demonstrates a clear cooling of more than -1.8ºC compared to temperatures after the event and -0.9ºC compared to those before the event. Examination of the pollen diagrams during the time period 8500-8000 cal yr BP reveals that the cooling in pollen-based temperature records is a result of a drop in temperate tree species, particularly *Corylus* and *Alnus* that flower early in the spring (Fig. 5 in Paper IV; see more discussion in section 3.4.2). In the Lake Saarikko record, the 8.2 ka event coincides with generally depleted $\delta^{18}O$ values 9000-7500 cal yr BP, however, particularly in the $\delta^{18}O_{lw}$ record the longer period of depleted values culminates ~8200-8100 cal yr BP (Fig. 6 in Paper V). These results are consistent with the general view of the 8.2 ka event as a primarily wintertime fluctuation, recorded as expansions in west-Norwegian glaciers, increased mineral matter accumulation in varved lakes in southern Fennoscandia and reduced abundance of early-flowering taxa in pollen diagrams from northern Europe.

The smaller magnitude of reconstructed cooling in Finland compared to Latvia is consistent with the spatial pattern 8.2 ka event demonstrated by Seppä *et al.* (2007). Based on a regional set of pollen-based temperature reconstructions, they suggest that the event was weaker in central Fennoscandia and absent in northernmost Fennoscandia. However, Lake Saarikko and Lake Igelsjön $\delta^{18}O$ records (Hammarlund *et al.* 2003; Hammarlund *et al.* 2005) together with records of mineral matter accumulation in varved lakes from Sweden and Finland (Ojala *et al.* 2008b; Zillén & Snowball 2009) suggest that the 8.2 ka event may have been clearly experienced in central Fennoscandia. These records are physical proxy records, and suggest that weaker cooling seen in pollen-based reconstructions from Fennoscandian sites may be biased by differences in forest composition compared to the Baltic region, namely, a smaller proportion of sensitive temperate tree taxa. Increased effective humidity and spring flooding inferred from $\delta^{18}O$ and varve records from Finland and Sweden indicate deeper snowpacks and colder/longer winters in central Fennoscandia during the 8.2 ka event. It can therefore be noted that the 8.2 ka event is recorded in the Baltic region and in central Fennoscandia most clearly by proxies sensitive to changes in winter/spring temperatures. In contrast, to date, there is not much evidence for a clear 8.2 ka event in northernmost Fennoscandia (Seppä *et al.* 2007).

3.2.4 The role of atmospheric circulation and seasonality

Dominant atmospheric circulation patterns have a marked influence on the spatial and seasonal distribution of patterns in temperature and moisture balance as explained above (section 2.1). The $\delta^{18}O$ records together with temperature reconstructions and changes in the abundances of indicator trees in pollen assemblages, give insight into Holocene changes in atmospheric circulation modes.

According to the results presented above, the early Holocene (11,500–8000 cal yr BP) was characterized by cool temperatures and overall positive moisture balance in northern Europe. The first temperate tree taxa that proliferated after *Betula* and *Pinus* were *Corylus* and *Ulmus* (Fig. 4 in Paper I and Fig. 3 in Paper IV). Corresponding tree species, *Corylus avellana* and *Ulmus glabra*, have oceanic distributions in northern Europe (Hintikka 1963; Dahl 1998; Giesecke *et al.* 2008), which means they tolerate cool sum-

Table 3. Limiting bioclimatological measures for the modern ranges of some key tree species (Prentice & Helmisaari 1991; Miller *et al.* 2008). Species are listed from the most oceanic (top row) to the most continental (bottom row) according to Giesecke *et al.* (2008). Flowering months are reported for northern Europe.

	$T_{c\text{-max}}$	$T_{c\text{-min}}$	$GDD_{5\text{-min}}$	$GDD_{5\text{-max}}$	Flowering
Wych elm (*Ulmus glabra*)	6	-10.5	1150	3000	IV-V
Hazel (*Corylus avellana*)	10	-13	1100	3600	III-IV
Pedunculate oak (*Quercus robur*)	7	-10	1200	4000	V
Small-leaved lime (*Tilia cordata*)	5	-11	1050	3400	VII

mers but require generally mild winters (Table 3). Overall, the inferred early Holocene climate was characterized by reduced seasonality, increased oceanicity and high effective humidity. These features are coherent with zonal, westerly air-flow, often postulated as the dominant early Holocene atmospheric circulation mode in northern Europe (Seppä *et al.* 2005; Jonsson *et al.* 2009a; St. Amour *et al.* 2010). In northernmost Fennoscandia, vigorous westerly air-flow likely led to reduced precipitation distillation, recorded as relatively enriched $\delta^{18}O$ values, and an anomalous 'non-Dansgaard' $\delta^{18}O$-temperature relation in lake sediments and speleothems (Hammarlund *et al.* 2002; Rosqvist *et al.* 2007; Linge *et al.* 2009; St. Amour 2009), although moisture derived from the Baltic Sea may also have had an influence (St. Amour *et al.* 2010).

The north-Fennoscandian "non-Dansgaard" signal is manifested as an early Holocene $\delta^{18}O$ maximum, and is followed by a subsequent trend of decreasing $\delta^{18}O$ toward the present. This pattern is normally not seen in $\delta^{18}O$ stratigraphies from more southern sites (Hammarlund *et al.* 2003; Hammarlund & Edwards 2008; Jonsson *et al.* 2009a; St. Amour 2009). Interestingly, however, Lake Saarikko $\delta^{18}O$ records clearly demonstrate relatively enriched lake water in the immediate postglacial, ~10,000-9000 cal yr BP, even though the record does not otherwise resemble

the north-Fennoscandian "non-Dansgaard" sequences. Wolfe *et al.* (2003) also reported enriched $\delta^{18}O$ values ~10,000-8500 cal yr BP from the Kola Peninsula. Similar to eastern Finland, the low effective humidity was probably not induced by high temperatures. Pollen-based temperature reconstructions from the Kola Peninsula show the beginning of the HTM not earlier than ~7500 cal yr BP (Seppä *et al.* 2008). At the same time, the population of *Pinus*, a taxon limited by summer temperatures in the northern part of its range, expanded in northernmost Fennoscandia (MacDonald *et al.* 2000; Gervais *et al.* 2002; Kultti *et al.* 2006). If the high early Holocene $\delta^{18}O$ values of the Lake Saarikko record do portray a "non-Dansgaard" signal, then a deep penetration of northwesterly winds across the northern Scandes Mountains (Hammarlund *et al.* 2002) to southeastern Finland may have taken place, and this circulation pattern would have switched rapidly ~9000 cal yr BP. An alternative explanation for the relatively enriched earliest Holocene $\delta^{18}O$ is a circulation pattern that could have led to scant precipitation even though temperatures were low, possibly reflecting influence of dry easterly air-masses that extended to eastern parts of Fennoscandia. However, as discussed above (section 3.2.2), many lake level records from southern Fennoscandia and the Baltic region also suggest dry condi-

tions, which may imply that the earliest Holocene dryness was spatially more extensive. In any case, it is postulated that the atmospheric circulation regime of the immediate postglacial in southern and eastern Fennoscandia differed from the pattern experienced in northernmost Sweden and Norway.

The HTM peak warmth coupled with the low effective humidity has been attributed to summertime anticyclonic circulation (e.g., Antonsson *et al.* 2008), which is a typical circulation giving rise to warm, dry spells of summer weather in the modern climate regime (see section 2.1). The results presented in this work are in harmony with this view: high temperatures, low effective humidity, lower lake levels, higher lake productivity and the maximum population densities of continentally distributed *Tilia* (*T. cordata*) and *Quercus* (*Q. robur*) (latter predominantly in Latvia) (Fig. 4 in Paper I; Figs. 3 and 8 in Paper IV; Fig. 2 in Paper III). The early- and mid-Holocene climate forcings differ essentially in that the effects of vanishing continental ice sheets (the LIS and the SIS) had attenuated by ~8000-7000 cal yr BP (Renssen *et al.* 2009). Hence, higher summer insolation was no longer suppressed by ice-sheet feedbacks in the mid-Holocene. The faster heating of the Eurasian landmass compared to the Atlantic Ocean could have induced the formation of strong anticyclones over the Scandinavian Peninsula, creating the typical June-August SNAO pattern: a strong positive pressure node located over northern Europe instead of the Azores region and a smaller-scale negative pressure node located in the Arctic (Hurrell *et al.* 2003; Folland *et al.* 2009). The stationary SNAO anticyclone is related to clear skies and high temperatures in northern Europe (Folland *et al.* 2009), consistent with the inferred climate of the HTM.

The late Holocene was characterized by steadily lowering temperatures and higher ef-fective humidity, both attributable to gradually weakening Northern Hemisphere summer insolation. The populations of warmth-demanding, temperate trees were reduced and *Picea* (*P. abies*) gained dominance that has prevailed until today (Fig. 4 in Paper I and Fig. 3 in Paper IV). Presumably, low temperatures and high lake levels reflect predominantly zonal circulation, particularly in summer. However, increased frequency of negative winter NAO and hence, reduced zonal air-flow, has also been postulated (Wanner *et al.* 2008). Negative winter NAO would have led to cold winters, increased ice-cover times and accumulation of deeper snowpacks, culminating in the cold spell of the LIA. In general, the mid- to late Holocene boundary has been depicted as a transition to a highly variable climate regime (Jessen *et al.* 2005; Väliranta *et al.* 2007; Wanner *et al.* 2008; De Jong *et al.* 2009; St. Amour *et al.* 2010), possibly due to more transient influence of different atmospheric circulation modes in the late Holocene compared to the stable circulation regime of the mid-Holocene.

3.3 Holocene vegetation responses

3.3.1 Mechanisms of long-term establishment and expansion of forest trees

The Holocene temperature reconstructions discussed above illustrate a clear low-frequency pattern of rise, maxima and fall in temperatures, with the general peak warmth ~8000-4000 cal yr BP. These features are broadly apparent in the rise, maxima and fall of broad-leaved deciduous trees depicted in pollen diagrams (Fig. 5 in Paper I, Fig. 4 in Paper IV), predominantly *Corylus*, *Ulmus*, *Alnus*, *Tilia* and *Quercus*, in addition to changes in the prime taxa of boreal forest: *Picea*, *Pinus* and *Betula*. As mentioned earlier, tree species diversity is fairly low in northern Europe and pollen types can be commonly assigned to

specific tree species, which aids ecological interpretations. However, temperature records based on pollen, or vegetation, are hampered by the fact that reshuffling of vegetation may have been driven by other than climatic constraints, such as postglacial migration, disturbances and inter-specific competition (Tinner *et al.* 1999; Bradshaw & Lindbladh 2005; Gavin & Hu 2006; Svenning & Skov 2007; Gillson *et al.* 2008). Therefore, physical proxy records are fundamental to the validation of pollen-based climate reconstructions and to the understanding of vegetation responses to climatic change.

The Lake Saarikko $\delta^{18}O$ records (Fig. 6 in Paper V) reflect moisture balance that is mainly controlled by evaporation during the open-water season, which in turn, is often a function of summer temperatures (see section 3.2.3). In addition, $\delta^{18}O$ can help untangling seasonal signals related to e.g., deeper snowpacks and ample spring snowmelt. The early Holocene spread of oceanic tree taxa (*Corylus avellana* and *Ulmus glabra*) ~9000-7000 cal yr BP is consistent with $\delta^{18}O$-inferred high effective humidity and reduced seasonality, whereas the maxima of *Tilia cordata* that spread later ~7000-5000 cal yr BP occur with $\delta^{18}O$-inferred negative moisture balance and high summer temperatures reflected by reduced $\delta^{18}O_{carb}$-$\delta^{18}O_{lw}$ separation. Hence, the late spread of *T. cordata* in Fennoscandia can be attributed to its requirement for high mid-summer temperatures (Pigott 1991; Dahl 1998; Giesecke *et al.* 2008), rather than lagged postglacial migration. Moreover, pollen data indicate that scattered *T. cordata* populations were established locally at favorable sites a couple of millennia before its mid-Holocene expansion in Fennoscandia (Fig. 4 in Paper I, Fig. 2 in Paper III). Fruits of *T. cordata* are heavy and rarely present in plant macrofossil assemblages, and it is therefore difficult to unambiguously assess the presence of these early populations. However, the $\delta^{18}O$ records suggest that at the time of *T. cordata* population expansion, the conditions were climatically optimal for its growth and reproduction. The history of *T. cordata* is not entirely similar further south in southern Sweden and the Baltic region. There, the species expanded 1-2 millennia before its maxima (Fig. 3 and 8 in Paper IV), which may be related to varying ecological requirements of *T. cordata* inside its range (Pigott 1991; Diekmann 1996).

Another temperate species that spread later in the mid-Holocene (~5000-3000 cal yr BP), *Quercus robur*, is also dependent on warm mid-summer temperatures. The late expansion is particularly notable in the southern part of the temperate-boreal zone (Fig. 8 in Paper IV). Ecological requirements of *Q. robur* contrast in many aspects with those of other common thermophilic trees. *Q. robur* is not discriminating when it comes to nutrients and moisture, but it is very light-demanding (Diekmann 1996). Hence, in addition to high summer temperatures, the late maxima of *Q. robur* in Latvia (Paper IV) and in southern Sweden (e.g., Giesecke 2005) may be related to the late Holocene transition from a closed-canopy temperate forest to a patchier mixed boreal forest. In contrast, *Q. robur* populations in central Fennoscandia do not show a clear species expansion phase (Fig. 4 in Paper I, Fig. 8 in Paper IV). This could be due to the fact that favorable climatic conditions were never established in the more northern part of its historical range. Another proposition is that the spread of *P. abies* never enabled the expansion light-demanding *Q. robur*. This is plausible since *P. abies* seems to have spread as a dense front in Fennoscandia, suggested by the lack of charcoal peaks and open-landscape plants at the time of its invasion (Fig. 4 in Paper I, Fig. 3 in Paper III). Furthermore, mitochondrial DNA diversity of *P. abies* has been maintained across its vast northern range, indicating that *P. abies*
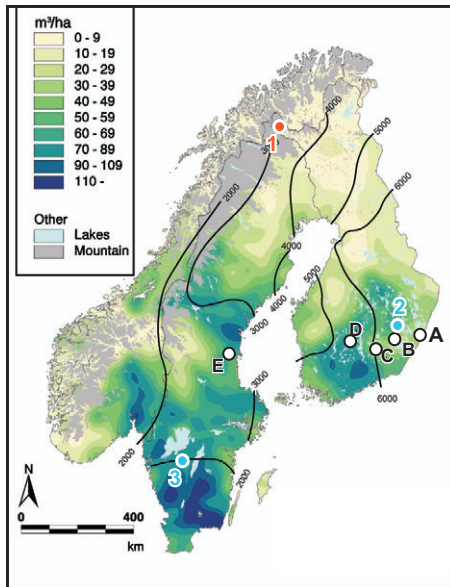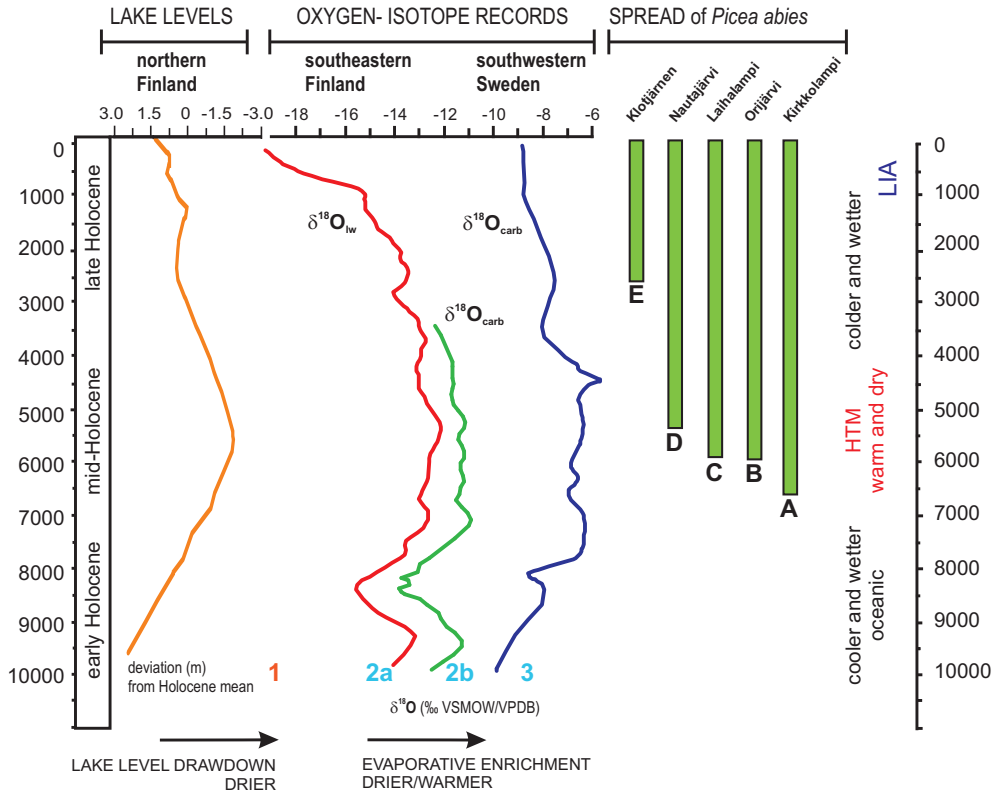
Figure 7. Holocene hydroclimate and the invasion of *Picea abies* in Fennoscandia. Stacked lake-level curve for northern Fennoscandia based on three records portrays low lake levels in the mid-Holocene (1) (Weckström *et al.* 2010). In the middle, Lake Saarikko cellulose-inferred lake water δ18O (2a), Lake Saarikko carbonate δ18O (2b) (Paper V), and Lake Igelsjön carbonate δ18O (3) (Hammarlund *et al.* 2003). On the right (green bars), the spread of *P. abies* population front and related rise of the boreal ecosystem demonstrated by pollen data from five study lakes (A-E) (Paper III). Numbers and letters refer to sites, plotted as dots on the map of modern *P. abies* abundance (volume m3/ha). Black isolines show the east-to-west spread *P. abies* according to Giesecke and Bennett (2004). The figure highlights that the invasion of *P. abies* started in eastern Fennoscandia when conditions were still seemingly climatically unfavourable for the species (see Table 3).

invaded at high population densities (Tollefsrud *et al.* 2008).

The long-debated postglacial equilibrium vs. disequilibrium between climate and vegetation (Davis 1976; Webb 1986; Bennett & Lamb 1988; Prentice *et al.* 1991) is a topical issue, as understanding the species range shifts and ecosystem responses under the predicted climate change scenarios (IPCC 2007) will be a crucial future undertaking (Thuiller *et al.* 2008; Hu *et al.* 2009). The results of this work suggest that the population expansions of tree species in northern Europe were in dynamic equilibrium (sensu Webb 1986) with climate and that migration delays, competition and disturbances did not play a significant role at the spatial and temporal scales examined here. A remarkable exception to this pattern may be the postglacial spread of *P. abies* (Paper III), a strong competitor that favors continental climates with cold winters and thrives on moist substrates. Paleoecological evidence clearly shows that in Fennoscandia, *P. abies* spread gradually from east to west (Hafsten 1992; Giesecke & Bennett 2004; Giesecke 2005)(Fig. 7), which led to great population reductions in temperate taxa, particularly *T. cordata* (Fig. 2 and 3 in Paper III). *P. abies* expanded in eastern Finland already ~6500 cal yr BP during the dry and warm HTM (Giesecke & Bennett 2004; Alenius & Laakso 2006; Alenius *et al.* 2008)(Fig. 7 and Fig.2 and 3, Paper III), seemingly a climatically unfavorable phase for the species. Two explanations are postulated: 1) winter conditions were pivotal for *P. abies*, or 2) *P. abies* invaded in disequilibrium with climate.

As discussed in Paper II, *P. abies* was established in the Baltic region and possibly in the adjacent areas during the YD and earliest Holocene, but these populations were suppressed for millennia preceding the late-Holocene colonization that completely reshaped the forest ecosystem of northern Europe (Giesecke & Bennett 2004; Kullman 2008). Indeed, the early Holocene suppression of *P. abies* may be ascribed to mild winters related to the intensification of westerly circulation (see section 3.2.4). It is possible that warm early- to mid-Holocene winters hindered earlier advancement of *P. abies* (see also Miller *et al.* 2008), but that later ~6500 cal yr BP winters in eastern Fennoscandia were sufficiently cold for its population expansion. Due to the lack of explicit winter-temperature proxies, it is currently difficult to explore the influence of winter temperatures on *P. abies* in any detail. Hence, this hypothesis remains inconclusive and independent proxy evidence is needed to disentangle the role of climatic control on the postglacial spread of *P. abies*. Finally, it is noted that shade-tolerance could have provided a superior competitive advantage for *P. abies* that enabled its invasion to the mid-Holocene closed-canopy temperate forest. In fact, recent studies in invasion ecology show that shade-tolerance is a key characteristic of species that invade undisturbed forests, indicating that deeply shaded closed-canopy forests may not be as resistant to plant invasions as generally believed (Martin *et al.* 2009).

Fig. 8 presents a summary of the Holocene

Figure 8 (on p. 39). A summary of Holocene climate changes and vegetation responses in northern Europe. **(A)** Modeled timing of the Holocene Thermal Maximum (HTM) around the Atlantic Ocean (Renssen *et al.* 2009); **(B)** 1. NGRIP δ^{18}O record (Johnsen *et al.* 2001) from Greenland in GICC05 timescale (Rasmussen *et al.* 2006a; Vinther *et al.* 2006), reflecting general temperature changes in the North Atlantic realm, 2. Incoming insolation in the Northern Hemisphere summer (MJJA) at 60°N (Berger 1978); **(C)** 1. Ostracod-inferred relative water level changes in Lake Sinijärv, Estonia (Sohar & Kalm 2008), 2. Pollen-based T_{summer} reconstruction and pollen percentage diagrams for key tree taxa from Lake Kurjanovas (Paper IV), Latvia; **(D)** 1. Annual organic varve accumulation (relative units) in Lake Nautajärvi (Ojala & Alenius 2005), 2. Lake water δ^{18}O changes in Lake Saarikko (Paper V), 3. Pollen-based T_{ann} reconstruction and pollen percentage diagrams for key tree taxa from Lake Laihalampi (Papers I, III)..
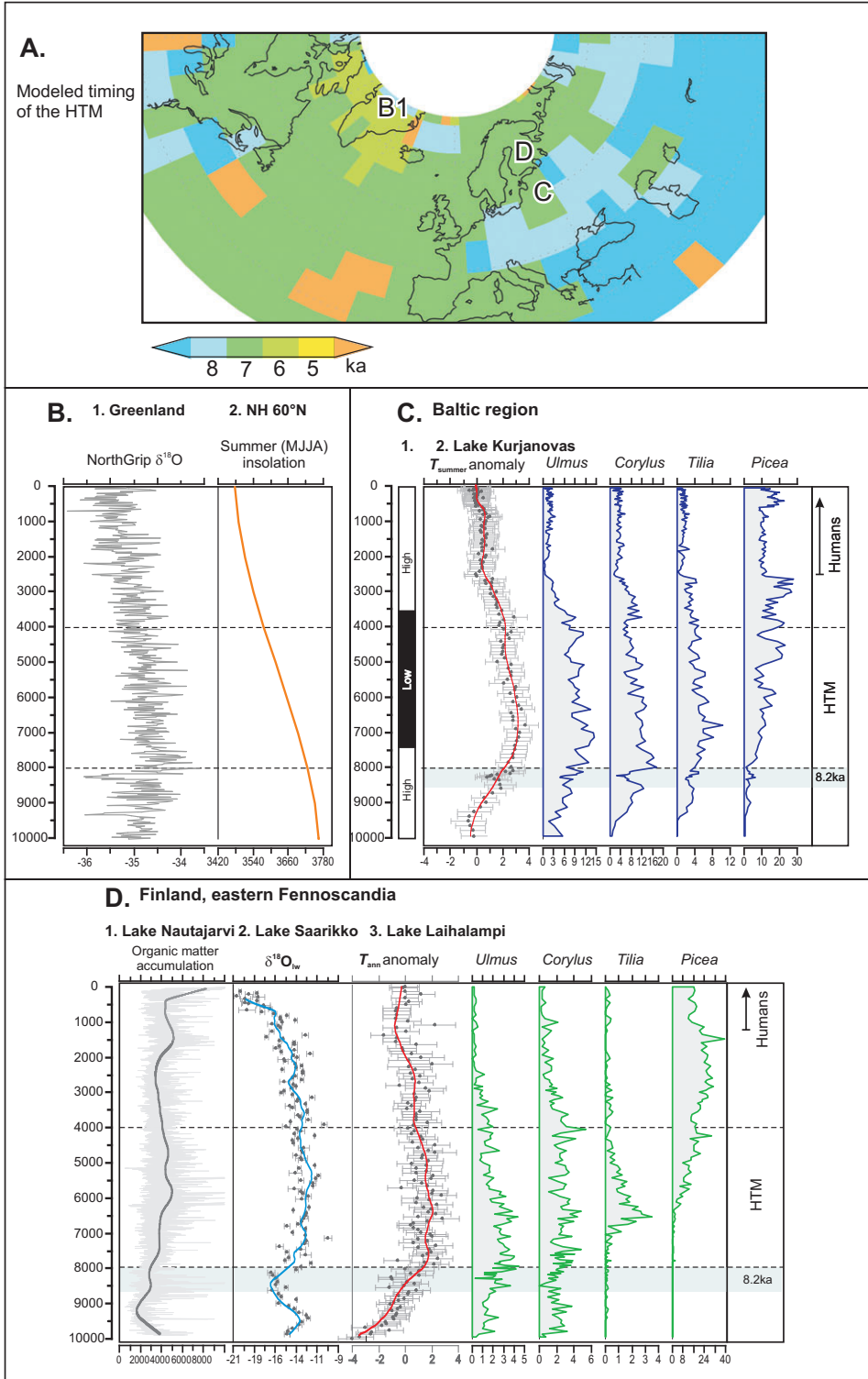
Figure 8. See caption on facing p. 38.

climate-vegetation relations demonstrated in this work. Upper panel (Fig. 8A) displays a map of the modeled timing of the HTM around the Atlantic Ocean, taking into account the effects of the LIS (Renssen *et al.* 2009). Fig. 8 illustrates the slightly earlier occurrence of the HTM in central and eastern Europe compared to western Europe and Fennoscandia. The middle and bottom panels display a general climate framework for the Northern Hemisphere (Fig. 8B), physical proxy records, pollen-based climatic reconstructions and percentage diagrams of key pollen taxa from the Baltic region (Fig. 8C) and eastern Fennoscandia (Fig. 8D), respectively. It can be noted that the warmest summertime temperatures indicated in the physical proxy records prevailed ~6500-5500 cal yr BP in Finland, concurrent with the expansion of *T. cordata* (Fig. 8D). Moister and cooler conditions of the late Holocene were coupled with the dominance of *P. abies*. However, *P. abies* started to invade in eastern Fennoscandia already during the warm and dry HTM. The scheme for the Baltic region displays the same broad-scale patterns; however, it can be noted that both populations of *T. cordata* and *P. abies* expanded slightly earlier (Fig. 8C). The differing dynamics and interactions of these two species in the Baltic region and Fennoscandia may be attributed to varying ecological characteristics and competitive abilities inside their geographical distribution ranges (Schmidt-Vogt 1977; Pigott 1991; Diekmann 1996; Latałowa & van der Knaap 2006). Another possibility is that the climate histories were somewhat divergent as well, e.g., the HTM took place earlier in the Baltic as suggested by the model experiment in the top panel of Fig. 8 (Renssen *et al.* 2009). To elaborate on the spatial diversity of climate-vegetation relations, independent, high-resolution proxy records of winter climate and moisture balance records particularly from the Baltic region, are needed.

3.3.2 Responses of vegetation to short-term climatic events

The 8.2 ka event is manifested in the pollen diagrams as century-scale reductions in temperate tree taxa, particularly by the declining values of *Alnus* and *Corylus*, the first trees to flower in the spring, but also by reductions in *Ulmus* (flowers late April) and *Tilia* (flowers late July) (Table 3, Fig. 5 in Paper IV). Similar responses are reported by other records from northern and central Europe (Tinner & Lotter 2001; Veski *et al.* 2004; Antonsson & Seppä 2007). The responses of tree species support the postulate of the 8.2 ka cooling distributed primarily to the winter-half of the year (Hammarlund *et al.* 2005; Ojala *et al.* 2008b; Zillén & Snowball 2009). The pollen records also suggest that plant reproductive mechanisms can respond virtually simultaneously to changes in climate, also demonstrated by studies on changing plant phenology as a response to recent warming (Menzel *et al.* 2006; Delbart *et al.* 2008).

An important aspect highlighted by the 8.2 ka cold event is the role of seasonal change and climate extremes to species ranges. Climatic 'envelopes' (Dahl 1998; Pearson & Dawson 2003) explain species distributions along climatic gradients limited by their optima and tolerances, determined either by their present ranges or physiological responses. However, interannual and seasonal variation around the mean values, abrupt deviations from the trend, and combined major shifts in temperature and moisture balance, exert an influence on species reshuffling in addition to climatic means (Tinner *et al.* 2008; Walther 2009). Whereas the most severely affected, early flowering tree species recovered relatively quickly from abrupt winter cooling (Fig. 5 in Paper IV)(Veski *et al.* 2004; Seppä *et al.* 2007), other paleoecological evidence suggests that extreme events may lead to severe and long-term changes in populations and ecosystems (e.g., Foster *et al.*

2006). Based on tests that incorporate measures of drastic climate variation to predict tree species distributions in Switzerland, Zimmerman *et al.* (2009) suggested that climatic extremes are crucial for plant populations particularly if climate means are shifting or climate variability is increasing. Indeed, paleoecological evidence from northeastern United States suggests that abrupt events can accelerate, delay or reverse vegetation responses to long-term trends in climate (Shuman *et al.* 2009). Records of vegetation responses to high-frequency climate variation may be of great value to the understanding of potential future changes in species ranges. The 8.2 ka event offers a prime retrospective experiment, since other recognized high-frequency events, such as the Medieval Warm Period (MWP) and the LIA, took place later in the Holocene when human influence on vegetation was already substantial in many regions.

4   Concluding remarks

The work summarized above sheds light on the low-frequency trends, rapid shifts and abrupt events in postglacial temperature and moisture balance histories of northern Europe. In addition, the studies elucidate vegetation responses to climate change, particularly taking up the common boreal and temperate tree species.

Pollen and plant macrofossil stratigraphies shed light on Lateglacial plant population response rates, particularly concerning the main boreal tree species *Picea abies, Pinus sylvestris* and *Betula pubescens/pendula*, as well as provide improved knowledge of tree population refuge locations and ranges during the Lateglacial. Pollen-based climate reconstructions expanded and employed a carefully designed north-European pollen-climate calibration set (Seppä & Birks 2001; Seppä *et al.* 2004; Antonsson 2006). They demonstrate centennial- to millennial-scale climate patterns and their spatial variability in northern Europe during the Holocene. Stable oxygen isotopes from authigenic carbonate and aquatic cellulose support the conclusions of temperature changes drawn from pollen-based climate reconstructions and give insight into changes in moisture balance. Other geochemical and isotopic analyses facilitated the interpretation of pollen and oxygen-isotopic records. Pollen percentage and pollen accumulation rate values were used to study the responses of thermophilic, deciduous trees (*Corylus avellana, Ulmus glabra, Tilia cordata, Quercus robur*) and the most common boreal tree of Europe, *Picea abies*, to changes in climate and other abiotic and biotic factors.

The main results and implications of this work can be summarized as follows:

- Contrary to the traditional view of species refuge locations in the south-European peninsulas during the glacial-interglacial oscillations (Bennett *et al.* 1991), it is shown that common boreal trees (*Betula sp., P. sylvestris, P. abies*) were present in the Baltic region during the Lateglacial. The results are in harmony with recent paleoecological and genetic evidence (Maliouchenko *et al.* 2007; Bhagwat & Willis 2008; Pyhäjärvi *et al.* 2008; Tollefsrud *et al.* 2008; Binney *et al.* 2009) and species distribution modeling (Svenning *et al.* 2008) suggesting that tree species persistence in northern latitudes of Europe during the LGM was mainly restricted to boreal taxa.

- Postglacial climate patterns in northern Europe were characterized by generally cool, moist and oceanic early Holocene, warm and dry mid-Holocene, and cool and variable late Holocene. The peak warmth (HTM) was attained ~8000-4000 cal yr BP, a few millennia later than the Northern Hemisphere summer insolation maximum. Spatial differences in temperature and moisture balance were not-

ed along the north-south and west-east gradients, tentatively attributed to the differential heating of land masses and ocean, changes in atmospheric circulation and position of sites and regions with respect to large water bodies and topographic boundaries.

- The δ^{18}O records from Finland, supported by physical characteristics of lake varves (Ojala & Alenius 2005), manifest that postglacial climate changes were the main driver of the establishment and expansion of temperate and boreal tree populations, and hence, Holocene vegetation patterns in northern Europe were in "dynamic equilibrium" with climate. However, climatic control on vegetation may have been locally overridden by edaphic conditions, disturbance and competitive interactions, particularly on the edges of species distribution ranges. Moreover, a remarkable exception to the general rule of vegetation-climate equilibrium may exist: the postglacial spread of *P. abies* and the development of the modern boreal ecosystem cannot be explicitly explained by current evidence of postglacial climate changes.

- The records of both the Lateglacial/Holocene transition and the Holocene suggest that vegetation responses to climate change, including long-lived tree species, can be strikingly rapid. This contrasts with the traditional view of weak or delayed responses of temperate and boreal tree species to climate change (Davis & Botkin 1985). Even though continental-scale spread of species from far-away dispersal loci may be relatively slow, species presence as scattered refuge populations or diffuse local stands may have been sufficient to account for rapid invasions and population expansions in concert with climate changes. However, if scattered populations are not present, tree populations may not be responsive to predicted rates of future climate change.

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