Rapid Lateglacial tree population dynamics and ecosystem changes in the eastern Baltic region

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ABSTRACT: A growing body of evidence implies that the concept of 'treeless tundra' in eastern and northern Europe fails to explain the rapidity of Lateglacial and postglacial tree population dynamics of the region, yet the knowledge of the geographic locations and shifting of tree populations is fragmentary. Pollen, stomata and plant macrofossil stratigraphies from Lake Kurjanovas in the poorly studied eastern Baltic region provide improved knowledge of ranges of north-eastern European trees during the Lateglacial and subsequent plant population responses to the abrupt climatic changes of the Lateglacial/Holocene transition. The results prove the Lateglacial presence of tree populations (Betula, Pinus and Picea) in the eastern Baltic region. Particularly relevant is the stomatal and plant macrofossil evidence showing the local presence of reproductive Picea populations during the Younger Dryas stadial at 12 900–11 700 cal. a BP, a BP, occurring along with Dryas octopetala and arctic herbs, indicating semi-open vegetation. The spread of Pinus–Betula forest at ca. 14 400 cal. a BP, the rise of Picea at ca. 12 800 cal. a BP and the re-establishment of Pinus–Betula forest at ca. 11 700 cal. a BP within a span of centuries further suggest strikingly rapid, climate-driven ecosystem changes rather than gradual plant succession on a newly deglaciated land. Copyright © 2009 John Wiley & Sons, Ltd.

KEYWORDS: rapid climate change; vegetation dynamics; north European trees; Lateglacial; north-eastern Europe.

Introduction

The transition from the Last Glacial to the Holocene interglacial was characterised by abrupt and significant environmental changes in northern Europe. During the Last Glacial Maximum (LGM) ca. 21 000–18 000 cal. a BP the south-eastern sector of the Scandinavian Ice Sheet (SIS) extended south to central Poland, Lithuania and northern Belarus (Fig. 1(A)) and continuous permafrost was present to 45° N in Germany and Poland (Huijzer and Vandenberghe, 1998). The climate on the continent south of the SIS was dry and cold, reconstructed and modelled annual mean temperatures being 10–24°C lower than modern temperatures (Tarasov et al., 1999; Wu et al., 2007; Kim et al., 2008).

Deglaciation in the region started when the temperature rose, but the ice margin retreat was punctuated by oscillations in climate. Substantial warming occurred during the Bolling/ Allerød interstadial (B/A, Greenland Interstadial-1) ca. 14 700–12 900 cal. a BP (Rasmussen et al., 2006) and the SIS margin retreated across Estonia and southern Sweden. During the Younger Dryas stadial (YD, Greenland Stadial-1) ca. 12 900–11 700 cal. a BP (Rasmussen et al., 2006) the ice sheet margin was positioned over southern Scandinavia (Fig. 1(A)). The YD is probably the most well-studied abrupt climate event in the late Quaternary, as clear cooling is pronounced in glacial, marine and terrestrial records, centred in the North Atlantic region (Overpeck and Cole, 2006). The mean annual temperatures during the YD lowered 5–15°C (Severingham et al., 1998; Alley, 2000) and the seasonality was clearly strengthened (Denton et al., 2005; Broecker, 2006). Permafrost affected the land and soils as far south as ~54° N and evidence for periglacial phenomena is found to ~50° N (Isarin, 1997). At the end of the YD mean July temperatures rose 4–10°C (Birks and Ammann, 2000; Renssen and Isarin, 2001; Wohlfarth et al., 2004).

Fossil evidence of plant communities at the Lateglacial/Holocene transition shows distinct changes in tandem with the climatic changes. Pollen and plant macrofossil diagrams depict unique combinations of tundra and steppe plants colonising the deglaciated landscape of northern Europe following the LGM (Birks, 1986). The majority of the European temperate and boreal trees survived the Last Glacial cold phases in the favourable mid-altitude pockets of the mountain ranges in the Balkan, Italian and Iberian Peninsulas (Bennett et al., 1991; Hewitt, 1999; Tzedakis et al., 2002; Carrion et al., 2003). The nature of the glacial and Lateglacial vegetation, including the migration patterns and pathways of the trees and their
possible glacial ranges, are poorly known, especially in eastern Europe. A general view has been that the areas north and east of the southern mountain ranges were treeless, dominated by plants tolerant of harsh climatic conditions. Tree pollen has been found from the glacial deposits, but it has been considered to be reworked from previous interglacial layers or distantly transported. Recently, however, it has been suggested that sparse local tree populations also existed in central and eastern Europe during glacial times (Stewart and Lister, 2001; Willis and van Andel, 2004; Feurdean et al., 2007). Plant community response to Lateglacial climatic change is known to have been very rapid (Birks and Ammann, 2000; Post, 2003; Birks and Birks, 2008); hence potential small outlier populations could have played an important role in Lateglacial and postglacial plant population dynamics.

In order to investigate the Lateglacial plant communities and their response to the major climatic changes in the relatively unexplored south-eastern sector of the SIS, a sediment core was obtained from Lake Kurjanovas in eastern Latvia. Here we present pollen, stomata and plant macrofossil analyses of this core. The objectives of the paper are (1) to investigate the nature of the vegetation prior to the YD, including potential occurrence of tree taxa in the region, (2) to probe the response of plant communities to rapid environmental changes at the onset and the end of the YD, and (3) to contribute to understanding of the glacial distribution history and Lateglacial and postglacial migration patterns and pathways of north European trees.

**Study area**

**Study site description**

Our study site, Lake Kurjanovas (56° 31′ N, 27° 59′ E; 111 m a.s.l.), is located in south-eastern Latvia, near the borders of Russia and Belarus (Fig. 1). The basin lies on the lowland area east of the Latgale highlands. Lake Kurjanovas is a relatively small (~1.6 km²) and shallow (maximum depth 5.8 m) lake, surrounded by lush, broad-leaved and coniferous forest patches in addition to open fields and pastures. Mean annual temperature at the nearest meteorological station in Daugavpils (55° 52′ N, 26° 37′ E; 122 m a.s.l.) is +5.5°C with seasonal variability from −6.7°C in January to +16.8°C in July. The landscape in temperate Europe is largely agricultural and the largest patches of forest remain in the northern and eastern parts of the continent. The most common deciduous species are birches (Betula), alders (Alnus) and aspen (Populus tremula), but thermophilous trees are also common, such as elms (Ulmus), pedunculate oak (Quercus robur), ash (Fraxinus excelsior), small-leaved lime (Tilia cordata) and hazel (Corylus avellana).

Study area topography and deglaciation dynamics

The relief of Latvia is slightly undulating, with moderate absolute and relative variations in elevation. The average elevation is 87 m (Zelcs and Markots, 2004). The highest elevations, around 300 m, occur in the bedrock highlands of Vidzeme, Latgale and Aīfikste, where the glacialic overburden can be up to 160 m thick. The topography results mostly from the glacialic processes of the Pleistocene glaciations.

During the last (Weichselian) glaciation Lake Kurjanovas was located in the peripheral zone of the SIS. The ice marginal moraine marking the LGM extent of the SIS (Fig. 1(A)) lies ~100 km south-east of the study site. The SIS started to retreat north-west from its maximum position in Lithuania and Belarus ca. 20,000–18,000 cal. a BP (Velichko and Faustova, 1986; Raukas et al., 1995; Rinterknecht et al., 2006). The retreat was marked by stagnation and readvance, leaving behind several successive ice marginal moraines before the SIS margin reached its YD position in southern Scandinavia (Fig. 1(A)). Pomeranian, Middle Lithuanian and North Lithuanian moraines were deposited in the aforementioned order at ca. 18,000, ca. 17,000 and ca. 15,500 cal. a BP (Raukas et al., 1995; Ehlers et al., 2004; Zelcs and Markots, 2004).

Figure 1  Maps showing the location of Lake Kurjanovas and other sites mentioned in the text. (A) Location of Lake Kurjanovas in northern Europe. LGM ice extent (Svendsen et al., 2004) is shown in white and Younger Dryas ice extent (Donner, 1995) by a dotted line. (B) Three of the ice marginal moraines in the Baltic region that are discussed in the text (Raukas et al., 1995): A, the Pomeranian moraine; B, the Middle Lithuanian moraine; and C, the North Lithuanian (Luga, Haanja) moraine. Lakes (●) and moraine sediment sections (▲) mentioned in the text: 1, Lake Kurjanovas; 2, Lake Tamula; 3, the Kurenuma section; 4, Lake Kirkumäe in the Haanja Heights; 5, the Raunis section; 6, Lake Kausiala; 7, Lake Okono. See references in the text.
Lake Kurjanovas is situated between the Middle and the North Lithuanian (Luga, Haanja, Linkuva) moraines (Fig. 1(B)). The North Lithuanian moraine has conventionally been used as the marker of the last short ice stagnation before the final deglaciation of Latvia. The determination is based on the radiocarbon ages from the organic-bearing sediments of the Raunis beds in north-central Latvia (Fig. 1(B)), which centre around 13,000 ¹⁴C a BP (ca. 15,500 cal. a BP), i.e. just before the start of the B/A interstadial (Punning et al., 1968; Stelle et al., 1975; Cerina and Kalnina, 2000; Stelle and Savvaïtoï, 2002; Zelcs and Markots, 2004). Additional support for the B/A age of the final deglaciation of Latvia comes from the Estonian chronostratigraphy. The Kurenurme section on the proximal side of the Haanja moraine (Fig. 1(B)) has been dated by optically stimulated luminescence (OSL) to ca. 14,500 cal. a BP (Kalm, 2006), which is consistent with radiocarbon dates ca. 14,500–15,000 cal. a BP of the intermorainic plant remains from the same section (Liiva et al., 1966). Correlation of the clay varve magnetostratigraphy from the bottom sediments of Lake Tamula (Fig. 1(B)), about 20 km west of the Kurenurme section, yielded an age of 14,675 cal. a BP for deglaciation of the lake catchment (Sandgren et al., 1997; Kalm, 2006). Thus the age of the North Lithuanian moraine in Latvia and Estonia lies between ca. 14,500 and 15,500 cal. a BP. As the Middle Lithuanian moraine has an age of ca. 17,000 cal. a BP, the final deglaciation of Lake Kurjanovas took place well before the B/A warming.

The nine boulder exposure ages calculated from ⁹Be/⁸Be ratios, however, resulted in considerably younger ages than mentioned above. For the Middle Lithuanian and the North Lithuanian moraine the mean ages were 13,600 ± 300 and 13,100 ± 300 a, respectively (Rinterknecht et al., 2006). Thus the Middle and the North Lithuanian moraines would have been deposited during the B/A, suggesting a stagnation of the ice sheet during the period generally regarded as the turning point for substantial warming. These implications are contradictory to the established palearctic and palearce Tonight's description and constructing the chronology

Lake Kurjanovas was cored at the point of the greatest water depth while still ice covered in March 2005, using a Russian corer equipped with a barrel of 10 cm in diameter and 1 m in length. An 8 m sequence of sediment was recovered, in addition to a 2 m replicate sequence from the bottom sediments. Sediment cores were correlated visually and described in detail in the laboratory. Cores were subsampled at 1 cm intervals and stored in the cold room at +4°C. The long core (interval 1016–1148 cm) was used for pollen sample preparation and the bottom replicate (interval 1015–1147 cm) for macrofossil analysis.

Organic matter and carbonate content of the sediment were estimated by loss on ignition (LOI). Samples of about 1–2 g of wet sediment were analysed at 2–4 cm intervals. Water content was estimated by oven-drying the samples for 24 h at 105°C. Samples were heated in a muffle furnace for 5 h, first at 500°C and then at 950°C. Following Heiri et al. (2001), results are expressed as percentages of weight loss of the sediment in each step in relation to the dry weight of the samples before combustion. Sediment colours were determined using Munsell soil colour charts.

Six samples of terrestrial and telmatic plant macrofossils were radiocarbon dated by accelerator mass spectrometry in the University of Uppsala Tandem Laboratory and Poznan Radiocarbon Laboratory. The resulting dates were calibrated using the IntCal04 curve (Reimer et al., 2004) and Oxcal 4.0 program (Bronk Ramsey, 1995, 2001) (Table 1). A Bayesian age–depth model was created using the deposition model implemented in Oxcal 4.0 (Bronk Ramsey, 2008), with a k parameter (increments per units of length) of 100 m⁻¹. Sample dates that clearly deviated from the overall age–depth relations were not included in the model. Rejection was based on the obvious incompatibility with the known biostratigraphic boundaries (see below), large uncertainty (>100 a), reversal in the stratigraphic order or a combination of these factors (Table 1).

Dating discrepancies do not attest to systematic behaviour. However, plant tissue type has commonly been reported as a source of dating error for various reasons. Among Lake Kurjanovas dating results, conifer bark (1046–1047 cm) and conifer wing-seed (1081–1082 cm) appear younger than their context, and mostly telmatic plant material (1089–1090 cm) older than its context, respectively (Table 1). The intrusive age of the conifer wing-seed, in turn, could result from high surface area/volume ratio that makes the sample susceptible to modern carbon contamination. In general, dating of filamentous or flat plant tissues can result in younger ages than dating of woody samples and seeds (Turney et al., 2000; Oswald et al., 2005). In addition, contamination by modern carbon usually leads to

### Table 1 AMS radiocarbon and calibrated dates for the Kurjanovas macrofossil samples. Calibration was performed with OxCal 4.0 program (Bronk Ramsey, 1995, 2001), using IntCal04 calibration curve (Reimer et al., 2004). The reasons of rejecting an age are specified, residual meaning an older age than the context, intrusive a younger age than the context and reversal a younger age than dated sample(s) above.

<table>
<thead>
<tr>
<th>Depth</th>
<th>Laboratory number</th>
<th>Material dated</th>
<th>Age ¹⁴C a BP</th>
<th>2σ age range</th>
<th>Median age (cal a BP)</th>
<th>Grounds for rejection</th>
</tr>
</thead>
<tbody>
<tr>
<td>1021–22</td>
<td>Poz-18408</td>
<td>Pinus bark, Pinus bud-scales, Betula pendula/parviflora, fruits, and female catkin bract</td>
<td>8 340 ± 40</td>
<td>9 470–9 260</td>
<td>9 363</td>
<td></td>
</tr>
<tr>
<td>1029–30</td>
<td>Poz-18410</td>
<td>Picea of cl. Betula</td>
<td>8 840 ± 50</td>
<td>10 159–9 705</td>
<td>9 928</td>
<td>Large uncertainty, reversal</td>
</tr>
<tr>
<td>1046–47</td>
<td>Un-32639</td>
<td>Conifer bark</td>
<td>8 035 ± 140</td>
<td>9 896–8 551</td>
<td>8 910</td>
<td></td>
</tr>
<tr>
<td>1081–82</td>
<td>Un-32640</td>
<td>Conifer wing-seed</td>
<td>9 205 ± 275</td>
<td>11 090–9 675</td>
<td>10 422</td>
<td>Large uncertainty, reversal</td>
</tr>
<tr>
<td>1089–90</td>
<td>Poz-18411</td>
<td>Plant material: mostly telmatic</td>
<td>10 600 ± 60</td>
<td>12 805–12 397</td>
<td>12 663</td>
<td>Residual: falls to the beginning of the Holocene in the biostratigraphy</td>
</tr>
<tr>
<td>1115–16</td>
<td>Un-32641</td>
<td>Telmatic plant leaves</td>
<td>10 930 ± 75</td>
<td>13 034–12 815</td>
<td>12 892</td>
<td></td>
</tr>
</tbody>
</table>
more significant dating errors due to higher $^{14}$C activity of young carbon compared to older carbon for equal amount of contaminant. Nevertheless, incorporation of hard-water derived old carbon in plant tissues of the telmatic vegetation at 1089–1090 cm is a probable explanation for the residual age, in contrast to the sample of telmatic leaves (1115–1116 cm) deposited during the time of carbonate deposition minimum (Fig. 3).

In addition to the selected radiocarbon dates, the ages according to the GICC05 timescale, derived from the Greenland ice core records (Rasmussen et al., 2006), were used in the model for the following stratigraphic points of reference: the beginning of the B/A, the boundary between the YD and the B/A, the end of the YD and the 8200 cal. a BP cold event. These levels were assigned based on the typical features in pollen stratigraphies from the region (Ilves and Mäemets, 1996; Velichko et al., 1997; Kabai liene, 1998; Goslar et al., 1999; Latalowa and Boro´wka, 2006). Pinus and Artemisia curves being the key references. The beginning of the B/A (14 700 cal. a BP) was assigned a stratigraphic depth of 1128 cm, marked by the rise in the Pinus pollen curve coupled with the appearance of Pinus macrofossils, and the fall in Artemisia and Chenopodiaceae curves and disappearance of Dryas leaves. The boundary between the B/A and the YD (12 900 cal. a BP) was assigned to the level 1112 cm, characterised by the rising frequencies of herbaceous and shrub pollen, especially Artemisia, Chenopodiaceae and Juniperus, and the decreasing frequencies of Pinus pollen. The end of the YD (11 700 cal. a BP) was placed to 1084 cm, where (tree) Betula and Pinus curves rise, accompanied by the abundance of their macrofossils, at the same time as the decline of Artemisia, Chenopodiaceae and Juniperus. The 8200 cal. a BP event was assigned to the stratigraphic depth of 980 cm (not shown in the figures), where marked decline in temperate trees, particularly Corylus and Alnus, takes place. The abrupt decline of thermophilous trees during this cold climate event is a common feature in the pollen diagrams from the region (Veski et al., 2004; Seppä et al., 2007).

### Results

#### Chronology

Results and calibration of the radiocarbon ages are shown in Table 1. As explained above, several radiocarbon dates of macrofossils were not used for the age–depth model, but application of those considered reliable, together with the known ages of the biostratigraphic boundaries, supported development of a satisfactory age–depth model (Fig. 2).

However, the pre-B/A part of the chronology should be considered with caution, as the deposition rates in a newly formed, unstable glacial lake system may be highly variable (Cohen, 2003). The lowermost sediments of the Lake Kurjanovas core must be younger than the Middle Lithuanian moraine (ca. 17 000 cal. a BP (Fig. 1B)), and are probably substantially older than the age of the North Lithuanian moraine (ca. 14 500–15 500 cal. a BP (Fig. 1B)). It is difficult to determine the basal age of the sediments precisely based on the deglaciation history as the initiation of lacustrine sedimentation may be delayed by several hundred years (Warner et al., 1991). If the pace of the ice recession from the Middle Lithuanian moraine to the North Lithuanian moraine was fairly uniform.
and the lake formed without major delays, the basal age of the sediments, just north of the Middle Lithuanian moraine, would be ca. 16 000–17 000 cal. a BP. Our age–depth model gives a basal age of ca. 16 400 cal. a BP, which agrees with this interpretation.

Sediment stratigraphy

The Lake Kurjanovas sequence can be divided into clearly visible sedimentary units consisting of variable amounts of mineral and organic matter (Fig. 3). The lowermost horizon (1148–1123 cm; ca. 13 900–12 800 cal. a BP) is composed of sand, silt and clay, overlain by a unit of clayey organic matter with telmatic plant leaves (1123–1111 cm; ca. 13 900–12 800 cal. a BP). The overlying horizon (1111–1079 cm; 12 800–11 600 cal. a BP) is again mineral-rich, composed of clay, followed by a thin layer of organic matter with Sparganium seeds (1079–1072 cm; 11 600–11 300 cal. a BP), a carbonate-rich clay unit (1972–1039 cm; 11 300–10 200 cal. a BP), and then grading from clayey to highly organic-rich in the uppermost sedimentary units.

The above-mentioned units of organic and mineral matter are apparent in the LOI results as well (Fig. 3). Organic-rich (20–60%) horizons were deposited ca. 13 800–12 800 and ca. 11 700–11 200 cal. a BP and organic matter content increases up to 80% at ca. 9700 cal. a BP. In addition, a highly carbonaceous (20–28%) layer was deposited ca. 11 300–10 200 cal. a BP. These results are consistent with the biostratigraphic boundaries: mineral-rich sediment layer at 1148–1123 cm was deposited before the B/A, organic-rich layer at 1123–1111 cm during the B/A, mineral-rich layer at 1111–1079 cm during the YD and organic gyttja at 1079–1072 cm in the Holocene.

Biostratigraphy and vegetation changes

The ages for the biostratigraphic boundaries used as the input to the age–depth model (see above) are applied in the following text to stress the climatostratigraphic stages. The stages differ only slightly from optimal partitioning pollen assemblage zones (PAZ), except for the lowest boundary (between KU1 and KU2 PAZ or the beginning of the B/A climatostratigraphic stage). The optimal partitioning PAZ boundary is 500 a younger than the interpreted biostratigraphic marker point at the start of the B/A. This is due to the fact that pollen assemblage zonation does not take into account the macrofossil data used in assessing the biostratigraphic boundaries, in addition to gradual increase of Pinus pollen proportion that complicates the interpretation of the actual rise.

Before Bølling/Allerød > ca. 14 700 cal. a BP (= PAZ KU-1)

Pollen assemblages of the time before the B/A consist largely of herbaceous grassland and tundra plants such as Artemisia (~5–12%), Gramineae (~5–10%), Chenopodiaceae (~2–5%) and Rumex/Osyrus-type (Fig. 4). Remains of the leaves of Dryas octopetala, a light-demanding arctic-alpine tundra plant, are abundantly present in the macrofossil sequence (Fig. 5). Tundra shrubs are also present: Juniperus (~2–6%) and Salix (~5%), in addition to Betula pollen (~25%) and macroremains (fruit, bud-scale), which can reflect the presence of dwarf birch (Betula nana). The lake level was probably low, as remains of telmatic (Equisetum up to ~12%, Carex-type ~5–14%, Juncus seeds and a Phragmites fruit) and aquatic (Potamogeton subg. potamogelon and Myriophyllum spicatum pollen) flora are found.

The terrestrial plant communities were probably more tundra-like than steppe-like, as Dryas octopetala is present throughout the whole period, in addition to the other tundra shrubs. The pollen of Artemisia and Chenopodiaceae can be carried vast distances aerially in an open landscape (Liu et al., 2008). On the other hand, their macrofossils are rarely present, and thus it is hard to assess their local presence or absence. The abundance of these taxa probably demonstrates windiness, dryness and soil disturbance further south and east in the Russian plain.

The landscape after deglaciation was certainly open, but whether the landscape was treeless is more difficult to judge. If trees were present, they must have been sparse. Betula pollen (~25%) and macrofossils can represent either dwarf or tree birches. The Betula pollen proportion is probably too low to represent local populations in an open landscape setting, as are Pinus pollen values (~15–30%). The Pinus curve rises steadily towards the beginning of the B/A, probably reflecting the approaching Pinus populations from the neighbouring
regions. Pinus macrofossils are absent, but stomata were found in one sample. These can represent a local stand of trees, but it is also possible that the stomata were redeposited and washed in from the overburden in the catchment. Redeposition is very probable in the case of the pollen grains of thermophilic tree taxa (Alnus, Corylus, Ulmus, Tilia), which appear clearly degraded compared to other concurrently occurring grains.

Figure 4 Percentage diagram of main pollen taxa (above) and selected herbaceous and aquatic taxa, Sphagnum and Pediastrum (below) against age (cal. a BP). Pollen assemblage zones (PAZ) KU1–4 based on optimal partitioning are shown on the right-hand side.

Bolling/Allerød ca. 14 700–12 900 cal. a BP (= PAZ KU1 until 14 200 cal. a BP and PAZ KU2)

A clear change in the plant communities took place in the beginning of the B/A. The B/A seems to have been a rather lush and moist phase in comparison with the earlier glacial vegetation. Assemblages are characterised by the suppression of tundra and steppe taxa and the growing dominance of Pinus...
Aquatic and telmatic plants (e.g., *Sphagnum*, *Equisetum* and *Potamogeton subg. potamogeton*) are reduced, suggesting higher lake levels.

The change from an open landscape to a relatively dense forest appears to have been fairly rapid. The prevalent role of *Pinus* both in pollen (30–60%), stomatal and macrofossil (bark, bud-scales, needle, anther) assemblages attest to its dominance in the local and regional landscape. The rapid decline in dry- and cold-favouring taxa (*Artemisia*, Chenopodiaceae, *Juniperus*) and the absence of the light-demanding *Dryas octopetala* is consistent with the development of closed or at least semi-closed *Pinus* forest. However, deducing the timing of the establishment of the relatively dense forest is not straightforward, as *Pinus* pollen values rise gradually, possibly indicating ongoing processes of forest closure and population invasion. Coupling the pollen data with the appearance of *Pinus* macrofossils and stomata (Fig. 5) indicates that the closure of the *Pinus* forest took place ~14 400 cal. a BP. *Betula* also seems to have been a common element in the B/A forests: *Betula* pollen proportion is around 30% and tree *Betula* fruits are present in the macrofossil assemblages.

Younger Dryas ca. 12 900–11 700 cal. a BP (= PAZ KU-3)

The change in vegetation was abrupt at the transition between the B/A and the YD. Open communities occupied the land and the *Pinus–Betula* woodland was reduced. *Pinus* values drop to ~10% and remain at that level (Fig. 4). *Betula*, instead, rises from ~15% to ~45% towards the Holocene and its fruits are found in the latter part of the YD (Fig. 5).

The shrubs and herbaceous taxa indicate openness and tundra-like conditions, with light-demanding *Dryas octopetala* (leaves, also a few pollen grains) and *Helianthemum* (~0.2%), *Juniperus* (~5–20%), *Salix* (~1.5–4%), various fossils from the families Caryophyllaceae (*Lychnis viscaria*-type and *Dianthus*-type, Caryophyllaceae seed) and Asteraceae (*Achillea*-type, *Solidago*-type) (Figs. 4 and 5). Also grasses (Gramineae ~4–10%) and steppe elements (*Artemisia* values ~8–19%, Chenopodiaceae ~3–6%) are abundant, but it is difficult to assess their importance in the local landscape.

A striking feature is the presence of *Picea* both in the pollen and macrofossil assemblages. *Picea* pollen values increase over ~200 a from 0% to ~10–20%, reaching 24% at its highest (Fig. 4). The pollen grains were well preserved, showing no signs of redeposition (Fig. 6(E)). Two *Picea* stomata (Fig. 6(C) and (D)) and two unidentified conifer stomata were noted on the pollen slides. A *Picea* needle and a conifer wing-seed were recovered (Fig. 6(A) and (B)). Other *Picea* macrofossils (a needle, a bud-scale and a wing-seed) occur at the boundary of the YD and the early Holocene.

To indicate the local presence of *Picea*, the pollen threshold of 1–5% (Huntley and Birks, 1983; Hicks, 1994; Giesecke and Bennett, 2004; Latalowa and van der Knaap, 2006) or the rise in the continuous pollen curve (Hafsten, 1992) has been used. Both criteria are satisfied in the Kurjanovas data, and the macrofossil and stomatal evidence confirm that *Picea* was a significant component in the local vegetation. Yet the proportion of herbs, grasses and shrubs shows that the landscape was mostly open and that *Picea* trees formed local stands or forest patches.

*Sphagnum* mosses and *Pediastrum* algae also appear during the YD, and telmatic and aquatic flora are more abundant (*Juncus* sp. seeds, *Typha* sp. seeds, *Nymphaea* sp. seed, *Myriophyllum spicatum*-type pollen). This could indicate subsiding lake levels, or a change in the substrate or nutrient conditions of the lake. Particularly interesting is the presence of *Typha* seeds, as at present the plant needs above 12–15° C July mean temperatures (Isarin and Bohncke, 1999; Yu, 2000).

Early Holocene >11 700 cal. a BP (= PAZ KU4)

In the beginning of the Holocene, the open landscape quickly became forested. The forest closure took place rapidly, as

![Figure 5 Diagram of plant macrofossils (number of specimens per cm³) and stomata (number of specimens per 700 counted pollen grains) against age (cal. a BP). Pollen assemblage zones (PAZ) KU1–4 of Fig. 3 are shown on the right-hand side.](image-url)
tundra shrubs and herbs such as Juniperus and Dryas octopetala and steppe taxa (Artemisia, Chenopodiaceae) were replaced by Pinus (~25–50%) and Betula (~35–65%) (Fig. 4). A variety of macrofossils of both of these trees occur abundantly, tree Betula fruits being remarkably plentiful (Fig. 5).

Picea pollen values fall back to the background level of <1%, but fossil Picea bud-scales are present continuously. Picea was probably present locally, but its abundance in the newly formed forests of the region is more difficult to assess. Picea pollen is underrepresented in modern boreal forests, especially when Betula and Pinus are dominant, the relative pollen representation being ~0.3 of that of Pinus and ~0.2 of Betula (Parsons et al., 1980; Sugita et al., 1999). The pronounced decline in the Picea curve may be a result of both the decrease of its proportion in the regional vegetation and reduced sexual regeneration and pollen productivity in the more oceanic climate of the early Holocene.

Populus macrofossils are present together with Populus pollen (Figs. 4 and 5). Populus may have been a common element in the early Holocene Betula–Pinus forests, as well as Sorbus aucuparia, whose pollen occurs occasionally. Temperate and broad-leaved tree taxa are also apparent in the pollen assemblages, Corylus and Ulmus curves rising first at ca. 11 000 cal. a BP, Alnus, Quercus and Fraxinus becoming frequent at ca. 10 100 cal. a BP and Tilia later at ca. 9400 cal. a BP (Fig. 4).

Pollen and fossil hair of the light-demanding Hippophaë rhamnoides occur (Figs. 4 and 5), a common feature in the records of the newly deglaciated terrain in northern Europe. This implies that the landscape was not yet fully covered by forests, as postglacial reforestation in Europe led to range fragmentation and suppression of Hippophaë rhamnoides populations (Bartish et al., 2006). On the other hand, Lake Kurjanovas pollen and macrofossil evidence shows that herbaceous taxa are greatly reduced from their Lateglacial frequencies. Spores of various ferns are present (Dryopteris-type, Dryopteris filix-mas-type, Athyrium filix-femina, Athyrium distentifolium-type, Thelypteris palustris and Gymnocar-
pium dryopteris) (Fig. 4), demonstrating a change in the type of undergrowth in the early Holocene forests.

Aquatic plants became increasingly frequent. Warmth-demanding taxa such as Nymphaea, Typha and Najas were present instead of more cold-tolerant species like Myriophyllum. The beginning of the Holocene was commonly the time when aquatic plants rapidly colonised lakes, but responses to the climatological and hydroecological changes seem to have been lake-specific (Birks, 2000; Sawada et al., 2003; Välimäki, 2006).

Discussion and conclusions

Abrupt and stepwise nature of ecosystem changes

Lake Kurjanovas was established on recently deglaciated terrain at ~16 400 cal. a BP. The vegetation initially comprised typical periglacial tundra plants. The open tundra community was replaced by a dense Pinus–Betula forest during the B/A at ca. 14 400 cal. a BP, the B/A forest by a tundra-like herb and shrub vegetation with localised Picea populations in the YD at ca. 12 900 cal. a BP, and finally the YD community by the early Holocene Betula–Pinus forest at ca. 11 700 cal. a BP. The systematic clustering of the pollen sample scores on PCA axes 1 and 2 plotted in Fig. 7 demonstrates the compositional divergence between the time periods. Pre-B/A, B/A, YD and early Holocene samples each have their own separated clusters in two-dimensional space, but a directional change in time is also observed inside each phase, with the exception of the oscillation in the early Holocene. In fact, the early Holocene samples from ca. 9800–9400 cal. a BP plot close to the B/A cluster, showing the similarity of the Pinus–Betula forests dominating at both times. The abrupt shifts in local plant communities are also clearly apparent in the macrofossil...
sequence, which shows virtually immediate transitions at the climatostratigraphic boundaries (Figs. 5 and 8).

Comparison of the rapid ecosystem changes with the climatostratigraphic stages illustrated in the $^{18}$O stratigraphy from the Greenland NGRIP ice core (Fig. 8) suggests that the ecosystem development does not reflect gradual plant succession on the deglaciated terrain (Iversen, 1958; Birks, 1986) but is predominantly driven by rapid Lateglacial climate changes. During the ca. 1700 a of the B/A interstadial, the inferred presence of $Pinus$ forest suggests that summer temperatures were higher than 12°C (Kultti et al., 2006), which is consistent with the reconstructed and modelled July mean temperatures of 13–20°C in western and central Europe (Renssen and Isarin, 2001; Peyron et al., 2005; Heiri et al., 2007). The summer temperature decrease of 2–10°C at the onset of the YD (Birks and Ammann, 2000; Marshall et al., 2002; Peyron et al., 2005; Larocque and Finsinger, 2008) is apparent in the decline of $Pinus$–$Betula$ forest and its replacement by predominantly open tundra-like landscape with local presence of $Picea$ for the following ca. 1200 a.

How was $Picea$ able to reproduce and advance to new regions during the cold YD stadial, when other forest elements were replaced by cold-adapted tundra and steppe flora? The most common $Picea$ species in Europe is Norway spruce, $Picea abies$ (L.) Karst. $Picea abies$ is a boreal tree with more

Figure 7  PCA plot showing the sample scores on the first (PC1) and second (PC2) axes. Samples of each climatostratigraphic stage are connected in stratigraphic order and shaded in grey (except for the YD). Sample depths are not shown for every sample of the early Holocene cluster due to label crowding.

Figure 8  Summary diagram of the environmental stages and associated ecological patterns in the study region. The records of key pollen (%) and macrofossil (specimens per cm$^3$) taxa, $Pinus$ and $Picea$ stomata (specimens per pollen sample) are shown. The NGRIP ice core $^{18}$O (with respect to Vienna Standard Mean Ocean Water) record provides a general climate background, indicating the rapid climatic shifts during the Lateglacial (North Greenland Ice Core Project (NGRIP) members, 2004; Rasmussen et al., 2006). The proportion of organic matter determined by LOI at 500°C shows mostly inorganic deposition during the cold climatic stages, except for the low percentages in the early Holocene due to carbonate deposition (see Fig. 3). Interpretations of the stages shown on the right-hand side: (1) before B/A, open tundra characterised by $Dryas octopetala$, a light-demanding arctic herb; (2) B/A, $Pinus$–$Betula$ forests, probably a closed or semi-closed forest as the light-demanding taxa disappear; (3) YD, semi-open tundra characterised by the reappearance of $Dryas$, possibly by light-demanding steppe taxa $Artemisia$ and $Helianthemum$, and by the replacement of $Pinus$ and $Betula$ forest by scattered $Picea$ stands, suggesting permafrost conditions and extremely continental climate; (4) rapid early Holocene warming with re-establishment of the $Betula$–$Pinus$ forest and disappearance of the arctic taxa.
continental distribution than Pinus sylvestris or the two tree Betula species (Dahl, 1998; Gervais et al., 2002). In the present range of Picea in Fennoscandia the mean temperature of the coldest month is lower than -1.5° C and the sum of growing degree days is over 600 GDD (Prentice and Helmisaari, 1991; Miller et al., 2008), which is higher than for boreal tree species in general. Climate reconstructions of the YD indicate a drop in summer temperatures of only 2–10° C on the European continent (see references above). Also the presence of Typha in our record during the YD suggests that the summer temperature decline was moderate in the region. Winters were, however, drastically colder. The amplification of seasonality by 10–20° C compared to the B/A (Renssen et al., 2001; Denton et al., 2005; Lie and Paasche, 2006), as well as the permafrost conditions, favoured Picea and prevented the growth of Pinus and Betula, which are less tolerant of cold winters and permafrost. In addition, the high Picea pollen values during the YD can be explained by the dryness of the YD (Goslar et al., 1999; Magny et al., 2001), as seed and pollen production of Picea abies is correlated with dry, warm summers, while wet summers encourage vegetative growth (Selás et al., 2002). The disappearance of Picea pollen in the beginning of the Holocene and the readvance of Betula–Pinus forest may indicate that the shift from the YD was foremost a shift in winter temperatures and from a continental climate during the YD to a more oceanic climate in the early Holocene (Gießekke et al., 2008).

The rapid climate-driven vegetation changes in the Lake Kurjanovas record are in accordance with recent arguments for immediate to rapid response times of plant associations to climate change (Birks and Ammann, 2000; Post, 2003), as opposed to delayed, gradual spread (Davis and Botkin, 1985; Payette, 2007). It has been argued that the rapid response potential is a typical feature of ecotonal regions (Loehle, 2000; Payette et al., 2001). This is well demonstrated in the past and recent dynamics of the Northern Hemisphere ecotonal ecosystems, for example the altitudinal vegetation belts in northern Fennoscandia (Seppl et al., 2002) and the Swiss Alps (Ammann et al., 2000; Tinner and Kaltenrieder, 2007), the treeline in eastern and northern Canada (Williams et al., 2002; Danby and Hik, 2007) and the outermost coast of western Norway (Birks and Birks, 2008). Lake Kurjanovas is situated on the flat forested terrain of the eastern Baltic region, yet the stratigraphy suggests rapid ecosystem responses to changing climate. This implies that during the Lateglacial the lake may have been located ecotonally within the latitudinal vegetation zones south of the retreating SIS.

Climate influences on multiple biotic processes and the inherently complex character of ecosystems can create nonlinearity and threshold-type responses (Burkett et al., 2005; Morin et al., 2008). Vegetation shifts may not be simply forced by rapid changes in temperature, but by more complex climate-controlled changes in the environment. Apparently the Lateglacial to Holocene transition near the south-eastern margin of the receding SIS involved active landscape restructuring, pedogenesis and permafrost fluctuations. Based on current data these interactions are challenging to disen- tangle, but clearly the ecosystem changes in the vicinity of Lake Kurjanovas were rapid and predominantly climate-driven.

Eastern Baltic Lateglacial populations of tree Betula, Pinus sylvestris and Picea abies

The prevailing concept has been that as the climate became gradually warmer during the Lateglacial, more warmth-demanding species spread over the European continent (Birks, 1986). These species are known to have moved back and forth from their southern locations during Quaternary climatic fluctuations (Willis and van Andel, 2004). The established picture of the Lateglacial spread of trees in Europe from their southern refugia in Italian, Iberian and Balkan peninsulas (Bennett et al., 1991) has recently become complicated by accumulating evidence based on well-dated pollen stratigraphies and plant charcoal material indicating the presence of several tree species in the Lateglacial environments of central, eastern and northern Europe (Gießekke and Bennett, 2004; Willis and van Andel, 2004; Latalowa and van der Knaap, 2006; Feurdean et al., 2007; Wohlfarth et al., 2007).

In the south-eastern sector of the SIS, pollen and plant macrofossil stratigraphies do not often extend back to the Lateglacial, as the continental ice sheet covered most of northern Europe. Where the Lateglacial records are available, tree Betula and Pinus have normally been reported as the first colonising tree taxa (Pirrus, 1969; Stancikaite et al., 2004; Latalowa and Borówka, 2006), as in Lake Kurjanovas. There is also evidence of the presence of Alnus and Picea (Ilves and Mäemets, 1996; Saarse and Rajamäe, 1997; Latalowa and van der Knaap, 2006; Stancikaite et al., 2008), although the low Lateglacial pollen percentages of Picea, Alnus and other temperate tree taxa are most often attributed to long-distance transport or redeposition (Saarse et al., 1999), as pollen is usually present sparsely and the grains are often somewhat degraded.

Genetic analyses have recently provided new evidence of the glacial history of European tree species. It is shown that the most common chloroplastic DNA (cpDNA) haplotypes of modern European Betula (B. pendula Roth, B. pubescens Ehrh.), populations are clearly separated in north-eastern and north-western geographical domains, and that the southern haplo- types of the Balkan, Italian and Iberian peninsulas do not occur north of the Alps (Palmé et al., 2003, 2004; Maliouchenko et al., 2007). A similar situation is suspected for modern Pinus sylvestris L. populations, as the mitochondrial DNA (mtDNA) haplotypes of this tree in the Iberian and Italian peninsulas are restricted to northern Europe (Sinclair et al., 1999; Chedaddi et al., 2006; Pyhäjärvi et al., 2008). There is also evidence of full-glacial and Lateglacial core populations in the Danubian plain in eastern central Europe (Willis and van Andel, 2004; Chedaddi et al., 2006) and mtDNA indications of population origins in north-eastern Europe (Sinclair et al., 1999; Pyhäjärvi et al., 2008). Our study supports this view, as the rapidity of the vigorous Pinus colonisation during the B/A implies a nearby origin. It is unclear, however, how much of the histories of the first colonising tree Betula and Pinus populations in the eastern Baltic region resemble each other. The timings of their proliferation and decline seem to reflect similar responses to Lateglacial and early Holocene environmental changes. Several regions have been suggested as the potential glacial ranges for Picea, e.g. the Alpine forelands, the Danubian plain and the Russian plain (Terhümre-Berson, 2005). Our record confirms the YD presence of Picea in the eastern Baltic region. Numerous other pollen diagrams from the Baltic region and adjacent areas show Picea pollen curves rising in the YD and declining in the early Holocene. For example, the high-resolution pollen stratigraphy from Lake Kiirikumäe (Saarse and Rajamäe, 1997) and other pollen diagrams from the Haanja heights in south-eastern Estonia (Pirrus, 1969; Ilves and Mäemets, 1996) show the YD peak of Picea pollen values (Fig. 1(B)). Similar patterns are typical in Belarus, as clearly apparent in the stratigraphy of Lake Okono in the northern part of the country (Makhnach et al., 2004) (Fig. 1(B)). The difficulty in assessing the Lateglacial presence of Picea arises from the
lack of direct evidence for its existence in situ, such as stomata or macrofossil remains. A recent study from Lake Kašučiai in western Lithuania (Stancikaite et al., 2008) reported Picea needles dated to the YD. Although Stancikaite et al. (2008) do not elaborate on this feature, it is important for clarifying the Lateglacial dynamics of Picea in the region. It appears that the local populations of Picea survived in the Baltic region and adjacent areas, but the more detailed patterns remain to be untangled. The core populations for spread may have been located east of the region, potentially in western Russia, where Picea was commonly prevalent during the B/A instead of Pinus (Zelikson, 1997; Velichko et al., 2002).

In general, our results are in accordance with the pattern of persistence suggested by Bhagwat and Willis (2008), who argued that the tree species that survived farther north in Europe during the full-glacial were mostly small-seeded, wind-dispersed and coniferous. The Lake Kurjanovas record demonstrates that Pinus occurred densely in eastern Latvia during the B/A together with Betula, which was possibly present even earlier. Our evidence also demonstrates the presence of Picea in Latvia during the YD. We therefore suggest that the full-glacial locations of Pinus, Betula and Picea populations were in the regions south and south-east of Lake Kurjanovas, possibly as far north as 55–60° N (see Fig. 1A for LGM ice extent).

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