Plant macrofossil evidence of changes in aquatic and terrestrial environments in north-eastern European Russia and Finnish Lapland since late Weichselian

Minna Väliranta

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Supervised by:
Dr. Heikki Seppä
Department of Geology
FIN-00014 University of Helsinki

Reviewed by:
Professor Hilary Birks
Botanical Institute
University of Bergen
N-5007 Bergen
and
Professor Marie-José Gaillard
Department of Biology and Environmental Sciences
SE-39182 Kalmar

Discussed with:
Dr. Ole Bennike
Geological Survey of Denmark and Greenland
DK-1350 Copenhagen

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Abstract

The long-term vegetation dynamics in north-eastern European Russia since the late Weichselian has until recent times been poorly studied. To produce multi-proxy evidence of changes in aquatic and terrestrial habitats, four lakes (Llet-Ti, Vankavad, Mezhgornoe and Tumbulovaty) and one permafrost peat profile (Ortino) were analysed for plant macrofossils. In addition, data from one lake in eastern Finnish Lapland (Njargajavri) were included. Supplementary proxy evidence was available from all sites: Lake Llet-Ti (pollen), Lake Vankavad (pollen, Cladocera and diatoms), Lake Mezhgornoe (pollen, Cladocera and diatoms), Lake Tumbulovaty (pollen), Lake Njargajavri (pollen, Cladocera, chironomids and diatoms) and Ortino peat plateau (pollen, paleosol). The study sites represent different vegetation zones, including alpine and arctic treelines, arctic and orohemiarctic tundra and taiga zone habitats.

Aquatic plant records show distinct changes in species diversity and abundances in all of the lakes over time. Despite the lakes being located in different vegetation and climate zones, the records reveal similar long-term patterns in early Holocene immigration of aquatics, subsequent maximum in aquatic species richness and a decline or disappearance of aquatics after the middle Holocene. Different factors possibly controlling the changes in aquatic plant communities are discussed. The warming temperature together with sufficient nutrient status likely enabled the immigration and establishment of aquatic plant communities during the early Holocene. Beyond this epoch the absence or presence of limnophytes was probably mainly controlled by the length of the open-water season, i.e. temperature related climatic parameters. This is supported by aquatic macrophytes often being absent from the lakes beyond treelines.

Plant macrofossil records of terrestrial and telmatic taxa showed a clear declining trend in species richness and the amount of finds during the mid to late Holocene. When these data are examined together with evidence provided by other proxies, it seems that the trend in addition to reflecting the general vegetation development (e.g shifts in treelines) also reflects a change in the distance between the sampling point and the shoreline. This phenomenon could be interpreted as being linked to the past lake-level changes. The assumption of fluctuating lake levels and their possible role in variations detected in the species richness record are discussed against previous climate reconstructions available from nearby areas.

Terrestrial plant macrofossil records revealed that tree birch and spruce were present at the modern extreme northern taiga zone throughout the Younger Dryas period. Tree birch had responded quickly to the warming climate, reaching modern treelines, both in Finnish and Russian sites, at the very beginning of the Holocene. The Russian treeline

sites were colonized by conifers during the early Holocene. A gradually cooling climate resulted in general withdrawal of forest lines ca. 5000-6000 years ago. A new period of permafrost initiation simultaneously took place in the modern tundra zone. A second cooling phase about 3000 years ago led to the final withdrawal of the treelines and to the establishment of the modern environments. Records from Lakes Mezhgornoe and Tumbulovaty showed some indication of a short-term warming about 1000 years ago. This time period corresponds with the so-called Medieval Warm Period. The terrestrial proxy records within the taiga zone revealed no significant changes in terrestrial species composition during the Holocene.

Contents

List of publications

This thesis is based on the following original articles referred to in the text by Roman numerals I-VI:

I Väliranta, M., Kultti, S. and Seppä H. Vegetation dynamics during the Younger Dryas - Holocene transition in the extreme northern taiga zone, north-eastern European Russia. Submitted to Boreas.

II Sarmaja-Korjonen,K, Kultti, S., Solovieva, N. and Väliranta, M. 2004. Mid-Holocene palaeoclimatic and palaeohydrological conditions in northeastern European Russia; a multi-proxy study of Lake Vankavad. Journal of Paleolimnology 30, 415-426.

III Kultti, S., Väliranta, M., Sarmaja-Korjonen, K., Solovieva, N., Virtanen, T., Kauppila, T. and Eronen, M. 2003. Palaeoecologial evidence of changes in vegetation and climate during the Holocene in the pre-Polar Urals, northeast European Russia. Journal of Quaternary Science 18, 503-520.

IV Kultti, S., Oksanen,P. and Väliranta, M. 2004. Multiproxy record of Holocene environmental change in the Nenets region, East-European Russian arctic. Journal of Canadian Earth Science 41, 1141-1158.

V Väliranta M., Kultti S., Nyman M. and Sarmaja-Korjonen K. 2005. Holocene development of aquatic vegetation in shallow Lake Njargajavri, Finnish Lapland, with evidence of water-level fluctuations and drying. Journal of Paleolimnology (in press).

VI Väliranta M., Kaakinen A. and Kuhry P. 2003. Holocene climate and landscape evolution East of the Pechora delta, East-European Russian arctic. Quaternary Research 59, 335-344.

The following persons contributed to this study:
Seija Kultti: pollen analyses (I-V)
Kaarina Sarmaja-Korjonen: Cladocera analyses (II and III)
Nadja Solovieva: diatom analyses (II and III)
Pirita Oksanen: plant macrofossil for Khosedayu peat plateau site (IV)
Anu Kaakinen: pollen analysis (VI)
Peter Kuhry: paleosol analyses (IV and VI)

1 Introduction

1.1 North-eastern European Russia – a paleoecologically nearly virgin research area

This summary presents evidence of changes in aquatic and terrestrial vegetation since the late glacial/early Holocene from one site in Finnish Lapland and five sites located in previously unstudied areas in north-eastern European Russia (Figure 1). The study sites represent different climate and vegetation zones, including records from and beyond the arctic treeline, from the alpine and orohemiarctic treeline and from the interior of the taiga zone. The long-term detailed dynamics of the vegetation in north-eastern European Russia since the late Weichselian has until recent times been poorly known. These data provide new paleoecological information from alpine treeline and taiga zones that have formerly been neglected, since treeline studies in the north-eastern European Russia have mainly concentrated on areas located beyond the arctic treeline (e.g. Kremenetski et al. 1998; Kaakinen and Eronen 2000; MacDonald et al. 2000a; Paus et al. 2003; Cremer et al. 2004). Previous studies have revealed a pattern of an early Holocene thermal maximum, resulting in expansion of treelines, and a post mid-Holocene cooling, leading to withdrawal of treelines. However, as demonstrated by the studies reviewed here, the chronology of the establishment of the first individuals of different trees species after the warming that started ca. 13 000 years ago is not yet fully resolved.

Few paleoecological records from north-eastern European Russia, mostly based on low-resolution pollen evidence, go beyond the Holocene, i.e. are older than 11 500 years (cf. Peteet 1995; Zelikson 1997). Longer records would be valuable because they would show how the vegetation has responded to changes in climate and growing conditions in areas deglaciated already during the early (or middle) Weichselian, some 90 000-60 000 years ago (Astakov et al. 1999, Henriksen et al. 2001; Mangerud et al. 2001; Hubberten et al. 2004; Svendsen et al. 2004). In general, the strong climatic forcing signal related to ocean-atmospheric circulation systems of the Atlantic Ocean, involved also in Younger Dryas climatic shifts, becomes weaker eastwards (Velichko et al. 1997; Wohlfarth et al. 2004). It has, however, become evident that great local and regional variations have occurred in climatic conditions during the Younger Dryas also around the North Atlantic (e.g. Birks et al. 1994; Isarin et al. 1998; Björck et al. 2002). Records that reach beyond the Holocene are needed to determinate whether the climatic changes at the late glacial/interglacial transition and their ecological impacts on areas around the North Atlantic (e.g. Birks and Mathewes 1978; Paus 1989; Birks et al. 1994; Mayle and Cwynar 1995; Rundgren 1995; Walker 1995; Taylor et al. 1997; Coope et al. 1998; Ammann et al. 2000; Birks et al. 2000; Seppä et al. 2002) can be detected in north-eastern European Russia as well.

The permafrost dynamics in northern Russia has long been inadequately understood, but recent studies have provided new insights into peatland development in subarctic areas (Oksanen et al. 2001; Oksanen 2002; Oksanen and Kuhry 2003; Oksanen et al., in press). Permafrost started to develop in mires of northern Russia ca. 3000 years ago, and permafrost aggradation has subsequently taken place during cold periods. Two especially active periods were approximately 2000 years ago and ca. 1300-1900 AD (the latter one corresponding to the so-called Little Ice Age) (Oksanen et al. 2001; Oksanen 2002; Oksanen et al., in press). The data provided by study VI is an interesting contribution to the discussion since the site is located beyond the modern arctic treeline, whereas the above-mentioned data is derived from more southern locations.

Paleoecological and paleolimnological studies with data and discussion about the dynamics of aquatic vegetation in European subarctic areas are relatively scarce, and are completely lacking for north-eastern European Russia. However, changes in aquatic and telmatic plant species assemblages have often been used to reconstruct past lake-level changes (e.g. Digerfeldt 1972; Gaillard 1984; Gaillard et al. 1991; Harrison and Digerfeldt 1993; Digerfeldt et al. 1997). Previous studies are usually from more southerly locations, and these records have often concentrated only on the late glacial/early Holocene transition, with many of them extending only to the middle Holocene (e.g. Birks and Mathewes 1978; Liedberg Jönsson 1988; Bennike and Böcher 1994; Gaillard and Lemdahl 1994; Birks 2000). However, some European studies covering the entire Holocene period are available from Greenland (e.g., Fredskild 1983, Fredskild 1992; Eisner et al. 1995; Bennike 2000). All of these studies show remarkable changes in aquatic plant species and communities. Since limnophytes are a fundamental element of aquatic ecosystems (Carpenter and Lodge 1986; Birks 2000; van Donk and van de Bund 2002, and references therein), providing habitats for several key components of subarctic food webs (Carvalho and Kirika 2003; Coops et al. 2003) and playing an essential role in carbon and nutrient cycling (Rooney and Kalff 2000), understanding the factors controlling the presence, abundance and species composition of aquatic plants is important. Consequently, the limnophyte data provided in studies I-V, covering the entire history of each lake, provide a significant contribution to the existing knowledge of the changes in aquatic plant communities during the Holocene. Since many internal and external factors may simultaneously be involved (Spence 1967; Pip 1989; Rørslett 1991; Fredskild 1992; Srivastava et al. 1995; Taylor and Helwig 1995; Hannon and Gaillard 1997; Middelboe and Markager 1997; Birks 2000; Birks et al. 2000; Murphy 2002), the interpretation of changes in aquatic plant records is a challenging task, especially when only one core, instead of a transect, is available (see for instance Hannon and Gaillard 1997).

1.2 Plant macrofossil analysis as a means of reconstructing past vegetation and environments

Previous studies carried out in north-eastern European Russia as well as in Finnish Lapland have mainly utilized a single-proxy method. The reconstructions presented here have exploited evidence derived from several different paleoecological proxy records (plant macrofossils, pollen, chironomids, Cladocera, diatoms, paleosol and lithology). The main focus of this summary is, however, on discussing the information provided by macrofossil data. Nevertheless, in many cases, final conclusions would have remained more tentative had they been based solely on macrofossil evidence, without support from other proxies.

The plant macrofossil assemblage in lake sediments consists of two components: terrestrial macrofossils are exogenic originating from the catchment, whereas aquatic remains represent an endogenic compound derived from the lake itself (Birks and Birks 1980). However, in both cases, local vegetation dominates because macroscopic particles are seldom transported more than a few kilometres, and vegetative parts of aquatics are normally not transported at all (Birks and Birks 1980; Vance and Mathewes 1993; see, however, Glaser 1981). Macrofossil analysis reconstructs local development, but the method is not very good for regional reconstructions, in contrast to, for instance, the pollen method (Birks 2001). The macrofossil assemblages can also differ markedly in different parts of the same lake. Moreover, plant remains do not readily reach the centres of large and/or deep lakes diameter> 500 m, depth > 10 m (Wainman and Mathewes 1990; Birks 1973, 2001). Many aquatic plants either produce low quantities of pollen that do not disperse widely and are not preserved well in sediments or reproduce asexually (cf. Birks and Birks 1980; Cohen 2003). Hence, aquatic plant macrofossils are fundamental when reconstructing such changes in aquatic environments as past lake-level fluctuations (Hannon and Gaillard 1997; Yansa and Basinger 1999; Birks 2001). In addition, plant macrofossil analysis is an essential paleoecological tool in treeless environments, where low pollen production is overwhelmed by long-distance dispersed pollen i.e.

late glacial, arctic and alpine environments (see for instance Watts 1979; Dunwiddie 1987; Birks 1993, 2001, 2003).

1.3 Objectives of the studies

The main objectives of this work were to reconstruct changes in aquatic, terrestrial and permafrost environments in north-eastern European Russia and Finnish Lapland using the plant macrofossil method combined with other proxies (pollen, Cladocera, diatoms and chironomids), and to relate these changes to earlier climate reconstructions. Species richness data from all six study sites provides a new perspective for examining changes detected in plant macrofossil records. This thesis is part of to two large multidisciplinary projects, TUNDRA (funded by the European Commission) and ARCTICA (funded by the Academy of Finland). One assignment of both projects was to elucidate ongoing and past vegetation dynamics in tundra and taiga environments. The underlying aim was to confirm or contradict the scenarios devised by the Intergovernmental Panel on Climate Change (2001). The scenarios suggest that future warming will have the most dramatic consequences, involving several feedback mechanisms, in high-latitude regions (e.g. Betts 2000; Harding et al. 2002; ACIA 2004), and will subsequently lead to shifts in the location of the forest-tundra ecotone and the permafrost distribution (Skre et al. 2002; ACIA 2004; Virtanen et al. 2004a). The effect on aquatic ecosystems may be direct (e.g. an increase in water temperature) or indirect (e.g. changes in catchment hydrology and vegetation) (Carpenter et al. 1992; Duff et al. 1999; Birks et al. 2000; van der Linden et al. 2003; ACIA 2004). Climate reconstructions have testified that northern regions have experienced marked changes in temperature and humidity conditions since the end of the last glacial period (e.g. Ritchie et al. 1983; COHMAP members 1988; Hyvärinen and Alhonen 1994; Walker 1995; Davydova and Servant-Vildary 1996; Dahl-Jensen 1998; Last et al. 1998; Eronen et al. 1999; Rosén et al. 2001; Andreev et al. 2001, 2002; Seppä and Birks 2001; Bigler et al. 2003; Korhola and Weckström 2004). Paleoecological studies give baseline information on how these changes affect the subarctic and arctic ecosystems thus providing analogues for modern and future ecosystem changes.

2 Study areas and methods

Five of the study sites are located in the Pechora area, north-eastern European Russian and one in eastern Finnish Lapland (Figure 1). Lakes Llet-Ti, Vankavad, Mezhgornoe and Tumbulovaty (I-IV) are situated at the Usa River basin, the Usa River being a tributary of the Pechora River. The Ortino peat plateau (VI) belongs to the catchment of the small Ortino River, which merges with the Pechora River at the Pechora Delta.

The bedrock in the Pechora area mainly consists of a Lower Paleozoic platform, but Ordovician sedimentary rocks are also found (Khain 1985). At lowland areas, the bedrock is covered by thick Quaternary sediments, mainly fluvial and alluvial (Nalivkin 1973). According to Virtanen et al. (2004a), the mean annual temperature in the Usa basin declines from the south-west (-2.5°C) to the north-east (-6.1°C), and the climate is relatively continental. The mean annual precipitation ranges from 400 to 800 mm. Near the Ural Mountains, the limit of the Usa basin to the east, precipitation levels are higher, ca. 950 mm. All of the mean temperature values for the Usa basin region are based on the regional climate model developed by the Danish Meteorological Institute (Christensen and Kuhry 2000). Temperatures were downscaled to 1-km cell size using altitudinal, latitudinal and longitudinal gradients (for details, see Virtanen et al. 2004a). These values correspond well with the measured values (1961-1990) from several local meteorological stations. The precipitation values are according to Van der Linden and Christensen (2003) and were downscaled to 1-km cell size by

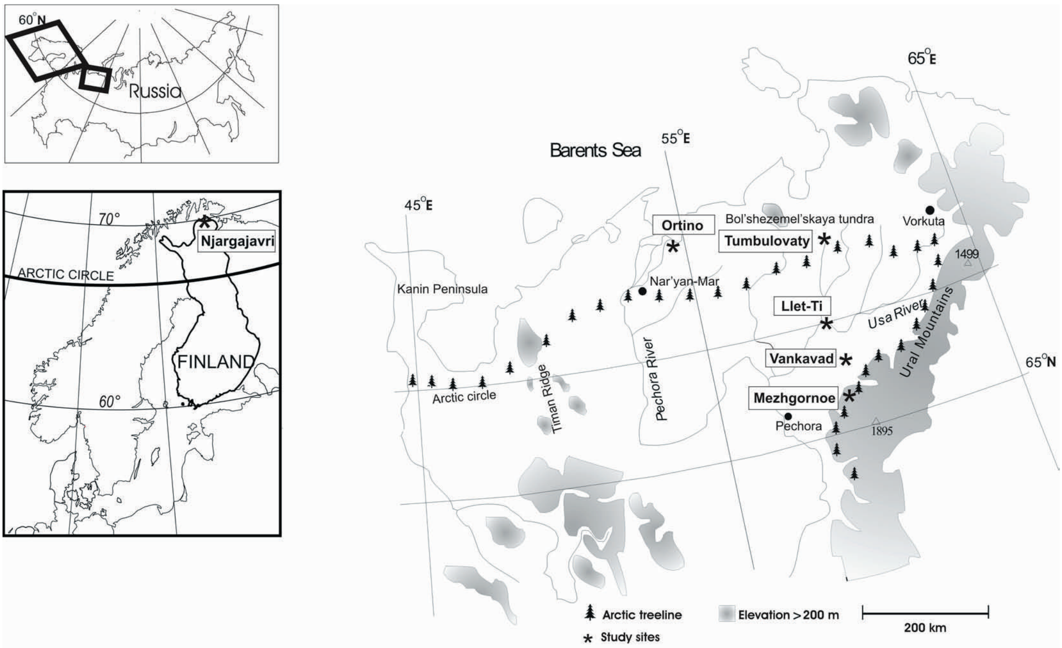

Figure 1. Study areas and sites

kriging interpolation.

Large open mires are common in the lowlands covering ca. 30% of the Usa Basin (Virtanen et al. 2004b). Permafrost, occurring only in mires in the central part of the Usa Basin, but also in mineral soils in the north, covers ca. 75% of the Usa Basin. Two permafrost layers of different ages can be found in north-eastern European Russia. The upper layer was formed during the late Holocene and is 50-100 m thick. Below this is an unfrozen layer, which melted during the early Holocene. The lower permafrost layer originating from early Weichselian (Valdai) glaciation, lies beneath this (Rozenbaum and Shpolyanskaya 1998).

The bedrock in eastern Finnish Lapland consists of Presvecokarelian granitic gneisses with some Svecokarelian micagneisses (Alalammi 1992). The terrain surrounding Lake Njargajavri is thinly covered by basal till. Near Njargajavri, the orohemiarctic treeline lies at ca. 300 m above sea level (a.s.l.) and is formed by mountain birch, whereas the conifer treeline is formed by pine and lies at approximately 220 m a.s.l. (Sihvo 2002).

The deglaciation histories of these two regions are different. According to recent studies, most of the land west of the Ural Mountains in Russia has been ice-free since the early Weicheselian (Astakov et al. 1999; Henriksen et al. 2001; Mangerud et al. 2001; Hubberten et al. 2004, and references therein). Eastern Finnish Lapland, by contrast, was deglaciated only after the onset of the Holocene, after 11 500 cal yr BP (Lundqvist 1986).

2.1 Study sites and sampling

2.1.1 Lake Llet-Ti

The lake (ca. 75 ha) is situated at the northern boundary of the extreme northern taiga zone (66°31′N, 58°50′E, 50 m a.s.l.). The lake has one inlet that probably functions only seasonally. The northern limit of the forest-tundra lies less than 100 km north of Lake Llet-Ti. The vegetation in the area consists of mixed spruce forest and open mires. The mean July temperature is 14.5ºC, and the mean annual precipitation is 640 mm. The area belongs to the discontinuous permafrost zone. A 500-cm-long sediment sequence was collected through ice with a Russian peat corer in 1999, less than 100 m from the shore. The water depth at the sampling point was 1.5 m.

2.1.2 Lake Vankavad

The lake (ca. 46 ha) is situated inside the extreme northern taiga zone (65°N, 59°E, 56 m a.s.l.). The lake has no inlets or outlets. The surrounding vegetation consists mainly of spruce mixed with birch. The mean July temperature is 15ºC and the mean annual precipitation is 750 mm. The area belongs to the sporadic permafrost zone. A 220-cm-long sediment sequence was collected through ice from the middle of the lake (ca. 200 m from the shore) with a Russian peat corer in 1998. The water depth at the sampling point was 5.6 m.

2.1.3 Lake Mezhgornoe

The lake (ca. 6 ha) is situated at the alpine treeline on the western side of the Ural Mountains (65°N, 59°E, 550 m a.s.l.). The lake has one inlet and one outlet. The alpine treeline is formed mainly by larch, with some fir and birch (pubescent and mountain). The forestline runs ca. 100 m below the lake. Rich meadows occupy mesic terrestrial habitats, and shrubby tundra vegetation or bare rocks are found on drier sites. The mean July temperature is 12ºC, and the mean annual precipitation is 1200 mm. A 320-cm-long sediment sequence was collected in 1998 from a rubber boat with a Russian peat corer ca. 20 m from the shore, where the water depth was 2 m.

2.1.4 Lake Tumbulovaty

The lake (ca. 43 ha) is located on an upland plateau near the arctic treeline (67°N, 59°E, 115 m a.s.l.). The lake has one outlet. The area around the lake is characterized by dwarf-shrub tundra and some peat deposits. The mean July temperature is 13.4ºC, and the mean annual precipitation is 610 mm. The study area belongs to the discontinuous permafrost zone. A 280-m-long sediment sequence was collected through ice with a Russian peat corer in 2000, ca. 300 m from the shore. The water depth at the sampling point was 1.6 m.

2.1.5 Lake Njargajavri

The lake (ca. 14 ha) is located above the present treeline on a gently sloping mountain plateau in northernmost eastern Finnish Lapland (ca. 70ºN, 27ºE, 355 m a.s.l.). The lake has one, probably only seasonally functioning outlet. The surrounding vegetation consists of subarctic heath plants. In Utsjoki, the long-term (1962-1999) mean annual temperature is –1.9ºC, the mean July temperature is 13ºC and the mean annual precipitation is 400 mm (Kevo meteorological station, 107 m a.s.l. and ca. 10 km from the lake). The calculated mean July temperature at an altitude of 355 m a.s.l. was ca. 11ºC when a constant adiabatic lapse rate of 0.57 ºC 100 m^{-1} is applied (Laaksonen 1976). A 120-cm-long sediment sequence was collected with a Russian peat corer in 2001 through ice from the middle of the lake (ca. 150 m from the shore), where the water depth was 2 m.

2.1.6 Ortino peat plateau

The study site is located beyond the modern arctic treeline at ca. 68°N, 54°E. The prevailing vegetation types in the upland areas are shrub and lichen tundra. Open peatlands, lakes and thermokarst ponds dominate the lowlands. Present along the river valleys are meadows and sandy deflation fields. Only sporadic spruce individuals occur on mineral soils. Forest-tundra patches become more frequent ca. 50 km south of Ortino. The extrapolated mean July temperature for the Ortino area is ca. 12.5°C, and the mean annual precipitation is about 400 mm. The Pechora Delta corresponds to the discontinuous permafrost zone, but the regions to the east and west are underlain by continuous permafrost. Ortino peat samples were collected in 2000 from a 110-cm-thick exposed peat plateau margin.

2.2 Methods

All sites were analysed for plant macrofossil remains. Sample sizes and intervals varied as follows (the most common volume is bolded): Llet-Ti (20-**30** cm^3, 5-cm interval), Vankavad (20-**30** cm^3, 10-cm interval), Mezhgornoe (5-**20-30** cm^3, 5-cm interval), Tumbulovaty (25-**30-**50 cm^3, 5-cm interval), Njargajavri (10-**20** cm^3, 1-to 4-cm interval) and Ortino (5 cm^3, 1-to 5-to 10-cm interval). Pollen data are available from all study sites. In addition, diatom and Cladocera data are available from lakes Mezhgornoe, Vankavad and Njargajavri, and chironomid data also from Lake Njargajavri. All of the dates in the text are calibrated radiocarbon ages cal yr BP (Stuiver and Reimer 1993, version CALIB 4.4).

The species richness reconstruction (Figure 3) summarizes the historical changes in taxonomic quality and quantity of terrestrial (including telmatic) finds. To produce species richness data, each record was first divided into 1000-year intervals and the number of taxa present within these intervals was then calculated. The term “species richness” here is used to refer to the number of taxa representing any taxonomic level, not only remains identified to species level. For instance, birch bark considered to represent a taxonomic unit if no other birch remains were present. Accordingly, if birch finds included birch bark, tree-type and dwarf-type birch seeds and catkin scales, these were counted as representing two taxonomic units (tree birch and dwarf birch). To depict general historical trends, mean values of the number of species for 1000-years intervals were used (see Allen and Huntley 1999). Because of the variations in sample sizes and uncertainties in radiocarbon dates (see below), the species richness record is a rough estimation, and thus, merely tentative.

3 Results and discussion

3.1 Establishing chronological framework

All of the Russian lake sites were first dated using bulk sediment. However, pollen stratigraphical comparisons indicate that the obtained bottom ages of Lakes Mezhgornoe and Llet-Ti are too old, probably due to the influence of old carbon. This is possible since the bedrock in the area partly consists of Ordovician sedimentary rocks (Khain 1985), which are also the parent material for the Quaternary deposits covering the areas between the Ural Mountains and the Pechora River (Figure 1). To eliminate or at least minimize error caused by contamination, additional depths were dated using the AMS method and terrestrial material. The number of newly dated samples is low because of the scarcity of suitable terrestrial material available and the limited amount of funding. For instance, in the cases of Lake Tumbulovaty and Lake Llet-Ti, the bottom ages had to be dated using pieces of wood. Wood is not necessarily the best material for dating since it can remain on the ground in an un-decomposed state for a long time and then be transported to a lake.

Taking into account the methodological standard error ranges, the new dates for Lake Tumbulovaty and Lake Vankavad confirmed the chronology derived earlier using bulk sediments, suggesting that no contamination by old carbon had taken place. In Lakes Llet-Ti and Mezhgornoe, new age determinations yielded younger ages than the bulk dates, with the difference being about 1200 years in both cases. The Llet-Ti chronology was re-assessed by subtracting 1170 years from all bulk dates. Corrected dates were calibrated and an age-depth model was created. The new bottom age was also applied for Lake Mezhgornoe by subtracting 1200 years from the bulk derived date. However, the rest of the dates were corrected according to surface sample age. The surface sediment age was 980±65 ^{14}C years. Because of the industrial atomic activity that released excessive radiocarbon to the air during the 1950s and 1960s (e.g. Levin et al. 1985) the modern radiocarbon ages, in general, show ca. 800 radiocarbon years too young ages. This means that 800 years has to be added to the age 980 in order to get the real modern age. The derived age 1800 radiocarbon years for surface sediment shows that the sediment is influenced by old carbon. According to additional ^{210}Pb and ^{137}Cs dating, the surface sediment is of modern age (Solovieva et al. 2002). Thus, the rest of the sediment sequence was corrected by subtracting 1800 years from the bulk dates.

Because cross-checking was mostly done for the bottom sequences, the procedure improved trustworthiness of the chronology especially for these parts, making the estimations for the first immigrating tree individuals relatively reliable. According to re-assessed chronologies, Lake Llet-Ti was formed during the Younger Dryas period ca. 12 750 cal yr BP (not ca. 13 800 cal yr BP), and Lake Mezhgornoe formed at the onset of the Holocene ca. 11 440 cal yr BP (not during the Younger Dryas ca. 12 700 cal yr BP). These dates and related vegetation changes, such as altered proportions of different arboreal pollen, are in good agreement with earlier general climate and vegetation reconstructions (e.g. Kremenetski et al. 1998; Kaakinen and Eronen 2000; MacDonald et al. 2000a; Henriksen et al. 2001; Paus et al. 2003; Cremer et al. 2004).

However, it is known that the degree of hard-water effect may change over time depending on, for example, the amount of deposited terrestrial material (cf. Barnekow et al. 1998; Paus 2000). This variation could not be taken into account for the dates available, and thus, the late Holocene chronologies remain more tentative. However, some regional features in the pollen records can be used for correlation. For instance, earlier pollen/megafossil reconstructions (e.g. Kremenetski et al. 1998; Kaakinen and Eronen 2000; MacDonald et al. 2000a; Paus et al. 2003) have detected a decrease in the amount of arboreal pollen and a change in tree species composition ca. 3000 years ago. This phenomenon is related to the general climatic cooling. According to our revised chronologies, changes in arboreal pollen assemblages (an increase in *Betula* and/or *Pinus* pollen at the expense of *Picea*) and changes in proportions of arboreal/herb pollen and/or total concentrations occurred around 3000 cal yr BP. Although the corrections were done based on only a few new dates, the re-assessment provided conceivable chronologies, which are supported by pollen stratigraphy/age-depth model correspondence.

In Lake Njargajavri, the four radiocarbon dates from the bottom sequence showed relatively similar ages. Based on radiocarbon dates only, it could be argued that the lowermost sediment was mixed. However, the pollen stratigraphy shows features typical of early Holocene vegetation development in Finnish Lapland, suggesting that the sediment was not mixed. Therefore, to establish the chronology and the age-depth model, the dates and certain pollen stratigraphical features were compared with regional vegetation reconstructions (Hyvärinen 1975; Mäkelä et al. 1994; Seppä 1996; Mäkelä 1998). Based on these comparisons, two dates were omitted from the chronology, and the interpretation relied on the remaining radiocarbon dates and pollen stratigraphical age approximations. One of the omitted dates, representing the bottom age, was derived from aquatic moss species *Warnstorfia procera*. Mosses, in general, are considered a reliable material for dating (Nilsson et al. 2001), and aquatic bryophytes have also successfully been used to date lake sediments, especially in places where there is no risk of a hard-water effect (e.g. Abbot and Stafford 1996; Miller et al. 1999; Gervais et. al. 2002; Wolfe et al. 2003). In the case of Lake Njargajavri, contamination by old carbon is out of the question because the age proved to be too young when compared with the general deglaciation history of northern Finland (Lundqvist 1986) and the subsequent vegetation dynamics (Hyvärinen 1975; Mäkelä et al. 1994; Seppä 1996; Mäkelä 1998). Unfortunately, the reason for the too young age remains unknown. The other omitted date was derived from terrestrial plant remains. This date seemed to be too old when compared to the known regional vegetation history.

The reason for the excessively old age could be re-deposition of the older terrestrial material, for example, in circumstances where the lake level lowered and the former lake bottom was exposed to erosion. However, despite the lack of a completely satisfactory level of accuracy in the dating for the lower part of the sediment sequence in Lake Njargajavri, the chronology nonetheless indicates that the lake initiated during the early Holocene and dried out for an unknown period of time during the middle Holocene, and that the sediment accumulation re-started ca. 5000 years ago.

The chronology of the Ortino peat plateau profile was based on three radiocarbon dates. The bottom age was derived from plant remains (*Andromeda polifolia* seeds), and two dates were derived from bulk peat. In general, pure peat is considered reliable material for dating (Nilsson et al. 2001). Seeds were probably also deposited *in situ*. Even though the dated depths were few, the established chronology can be assumed to be reliable. It was also based on stratigraphical comparison with an adjacent peat profile (Kaakinen and Eronen 2000), which shows, for instance, a similar age for sand layers within both peat sequences.

3.2 Long-term changes in aquatic environment and aquatic plant species composition - possible driving factors

The following elodeid and rooted floating aquatic plant genera/species occurred in historical records: *Callitriche (hermaphroditica)*, *Potamogeton*, *Ranunculus* sect. *Batrachium*, *Myriophyllum, Nuphar, Sparganium* and Characeae. In addition, isoetids *Elatine hydropiper*, and *Subularia aquatica* and aquatic/semi-aquatic moss species were detected infrequently. The current aquatic plant assemblages in north-eastern European Russia correspond (at genus level) with fossil ones (NB *Nuphar* currently thriving only in taiga lakes) (Teteryuk 2004). The records of aquatic plants show distinct changes in diversity and abundance in each lake's history (Figure 2). Despite being located in different climate and vegetation zones, the records reveal similar patterns of the early Holocene immigration of aquatics, a subsequent maximum in species richness, and a decline or disappearance after the middle Holocene. All sampling points are today located within a water depth of 1.5-5.6 m, the range in which littoral plants typically occur, and therefore, any absence of remains is not the result of the sampling point lying outside the littoral zone.

Figure 2 summarizes the variations in aquatic plant remains, and the simultaneous presence of terrestrial (+ telmatic) remains by tripartite scale. Because vegetative parts of aquatics are seldom transported, fossil finds conclusively indicate the presence of the taxon (Birks 1973; Vance and Mathewes 1993). Also seeds of obligate aquatics tend to sink rapidly (Birks 1973; Dieffenbacher-Krall and Halteman 2000). In contrast, many emergent plants thriving in shoreline habitats have buoyant seeds that are readily transported over long distances (Glaser 1981; Dieffenbacher-Krall and Halteman 2000).

The high abundance and relative diversity of remains of aquatic macrophytes in northern lakes during the early Holocene are frequently reported phenomena (e.g. Birks and Mathewes 1978; Fredskild 1992; Birks 2000; see also Iversen 1954). Furthermore, Holocene records often show a change in aquatic species assemblages towards the late Holocene, with the remains becoming scarce or only vegetative remains persisting; alternatively the remains may disappear entirely (Fredskild 1992; Bennike 2000). The question then arises that what is the driving mechanism behind these changes. Many factors may be involved; including changes in climate (especially temperature) water level, nutrient supply, pH, light conditions, competition, and exposure to wave action (Spence 1967; Pip 1989; Rørslett 1991; Fredskild 1992; Srivastava et al. 1995; Taylor and Helwig 1995; Hannon and Gaillard 1997; Middelboe and Markager 1997; Birks 2000; Birks et al. 2000; Vestergaard and Sand-Jensen 2000; Engelhardt and Richie 2001; Murphy 2002). The following discussion mainly concentrates on the first four factors.

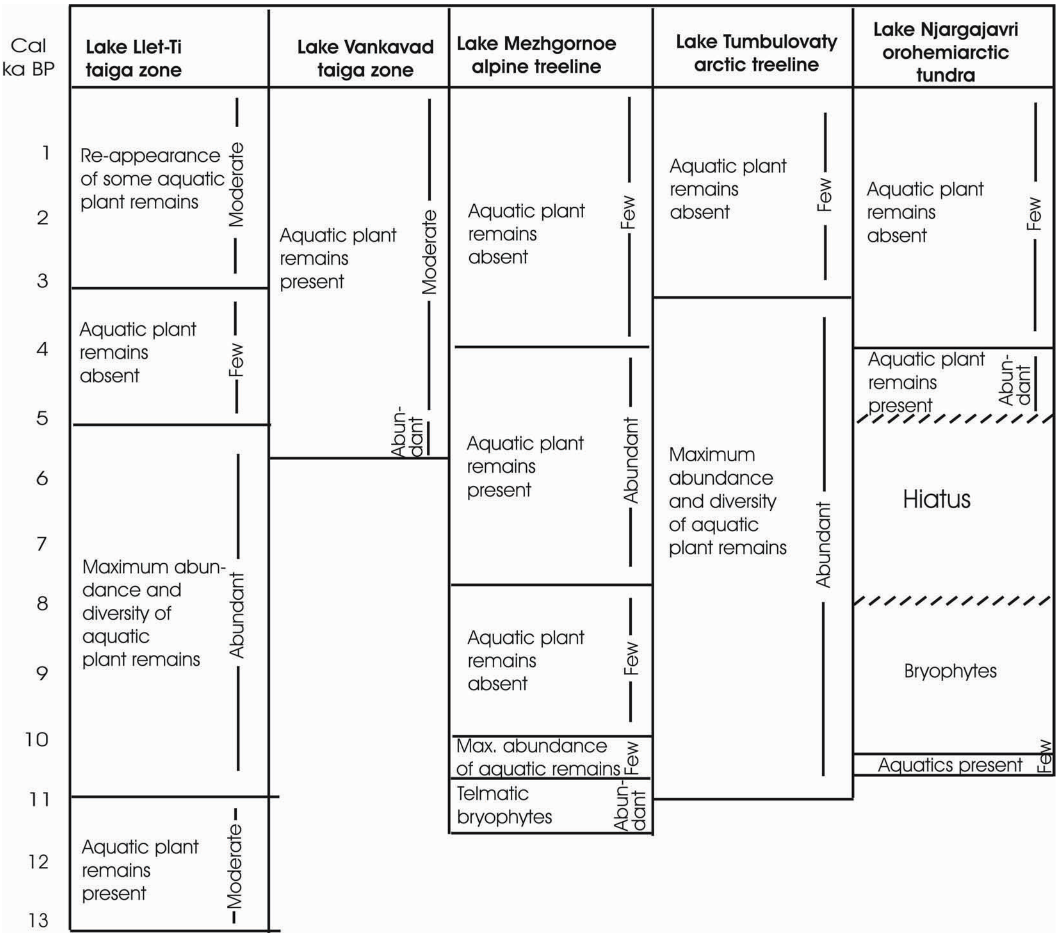

Figure 2. A summary of the changes in aquatic plant remains. Finds of terrestrial plant remains within the same zone are indicated by a relative tripartite scale: few, moderate and abundant.

3.2.1 Temperature as a controlling factor in variation of aquatic plant species communities

Modern ecological studies show that temperature is a major external driving factor for a lake's biota. Although water temperature *per se* seems to be relatively unimportant to aquatic species richness (Pip 1989), most physiological processes, such as nutrient cycling (at the catchment and the lake itself), are temperature-dependent (Rooney and Kalff 2000; see also Birks et al. 2000). Probably the most important way that temperature in northern areas affects aquatic communities, including aquatic plants, is through ice conditions, that is, through the length of the open-water season (Spence 1967). The length of the open-water season (i.e. the growing season) controls vascular aquatic plant communities and their reproduction regardless of the lake's nutrient status (Rørslett 1991).

The abundance (but also presence/absence) and richness of the modern aquatic plants in north-eastern European Russia follow temperature (and thus major vegetation) gradients, both of these declining with increasing latitude and altitude (Teteryuk 2004). In alpine and arctic lakes, vascular macrophytes are often absent, since surface water temperatures colder in lakes beyond the treeline, than in forest lakes (Weckström et al. 1997; Duff et al. 1999). The higher nutrient status in forest lakes than in tundra lakes is also related to temperature. Terrestrial vegetation is often temperature-dependent and forest litter provides continuous input of nutrients (Duff et al. 1999; see, however, Wardle et al. 2004). Thus, warmer temperature promotes higher primary production and more rapid nutrient cycling in forest lakes and in the catchment. Various earlier studies of arctic lake ecosystems from different continents have shown that the productivity in arctic treeline lakes is indeed strongly related to vegetation biomes, thus indicating climatic (primarily temperature) control (MacDonald et al. 1993; Rühland and Smol 1998; Korhola et al. 2002; see also Engstrom et al. 2000).

Fossil records (I, III, IV, V) show evidence relatively diverse early Holocene aquatic plant communities, but the disappearance of limnophytes from lakes beyond the treeline and diminished species richness in forest lakes after the middle Holocene. Chronologically, this development correlates with climate reconstructions, indicating a warmer than present early Holocene and a cooling late Holocene from ca. 5000 years onwards (e.g. from Fennoscandia: Rosén et al. 2001; Seppä and Birks 2001; Bigler et al. 2003, and from north European Russia: Kremenetski et al. 1998; Kaakinen and Eronen 2000; MacDonald et al. 2000a; Oksanen et al. 2001; Andreev et al. 2002; Paus et al. 2003; I-VI). Apparently, the aquatics were capable of rapidly taking advantage of the warming early Holocene climate (see Iversen 1954; Fredskild 1992; Birks 2000). Besides its direct warming effect, the warm climate also resulted in changes in the terrestrial environment that probably led to increased nutrient input from the catchment (MacDonald et al. 1993; Rühland and Smol 1998; Duff et al. 1999; Birks et al. 2000; Engstrom et al. 2000; Korhola et al. 2002).

The treeline lakes (Mezhgornoe, Tumbulovaty and Njargajavri) show a disappearance of aquatic remains after the middle Holocene (Figure 2). In taiga lakes, by contrast, modern samples show the presence of aquatics (macroscopic remains and pollen). A recent reconstruction from the polar Ural region suggests that the late Holocene cooling climate resulted in longer winters with thicker ice covers (Cremer et al. 2004). Thus, an excessively short open-water season is a plausible explanation for the concomitant disappearance of aquatic plant communities from subarctic and alpine lakes.

Some further support for temperature dependency is derived from Lake Mezhgornoe, where a brief appearance of *Nuphar* and *Nymphaea* pollen took place about 1000 cal yr BP, probably indicating the actual presence of the species (Edwards et al. 2000). This appearance coincides with the so-called Medieval Warm Period. Today, *Nuphar* and *Nymphaea* do not occur in lakes beyond treelines (Teteryuk 2004), and Wohlfarth et al. (2004) interpreted the presence of these genera as evidence of a mean summer temperature ≥ 10°C. The modern mean summer (Jun-Aug) temperature for the Lake Mezhgornoe area has been calculated to be 9.2°C. The biological records from the arctic treeline site of Lake Tumbulovaty also revealed a corresponding warmer period ca. 1000 years ago. However, the Mezhgornoe record showed no other evidence of warming at that time.

Thus, according to the current fossil aquatic plant records, changing temperature has apparently played a major role in the variations detected in historical aquatic plant communities.

3.2.2 The effect of changes in chemical conditions

In general, mesotrophic (small and shallow) lakes support more aquatic plant species than oligotrophic (large and deep) lakes (Rørslett 1991). However, the nutrient status of the water is not crucial since many macrophytes are also able to take up nutrients from the sediment (Moss 1982; van Donk and van de Bund 2002). This alternative nutrient source enables macrophytes to grow in nutrient-poor waters as well. A common feature of arctic lakes is that they have over time become more oligotrophic and acidic (e.g. Engstrom et al. 2000; Korhola and Weckstöm 2004). In theory, therefore, Lakes Mezhgornoe, Tumbulovaty and Njargajavri should have experienced a long-term impoverishment in nutrient status. Yet, a diatom-based total phosphorus (TP) reconstruction for Lake Mezhgornoe from the alpine treeline shows no dramatic change TP level (III). Unfortunately, no proxy data exist from Lake Tumbulovaty. According to Duff et al. (1999), tundra lakes in the Pechora area are commonly oligotrophic, but not ultra-oligotrophic (cf. Wetzel 2001), with TP ranging between 3.4 $\mu g\ l^{-1}$ and 31.5 $\mu g\ l^{-1}$ (median 8.2 $\mu g\ l^{-1}$). The authors concluded that the productivity is not limited by P, but by other nutrients. This is a somewhat controversial statement since, in general, the P storage in organic soil is considered to become increasingly exhausted within a few thousands of years after the onset of natural development of the virgin landscape, for instance, after a deglaciation (Birks and Birks 2004; Wardle et al. 2004). This is because P, unlike e.g. nitrogen (N), is not a renewable nutrient, but leaches effectively out from soils (Wardle et al. 2004). It is possible that even though the deglaciation took place in the Pechora area several tens of thousands of years ago, P storage may not have yet completely run out because of the very thick layers (hundreds of metres) of Quaternary sediments originating from the Ordovician sedimentary rocks, which provide a P source (see Wetzel 2001). In any case, mountain lakes, such as Lake Mezhgornoe, probably continuously receive supplemental nutrient loads from the eroding mountain slopes.

Unlike tundra lakes, forest lakes in the Pechora area are relatively nutrient–rich and productive today (high POC, TP, PON, chlorophyll α) (Duff et al. 1999). Moreover, P reconstruction for Lake Vankavad shows stable values over time. Accordingly, even though no such data exist for Lake Llet-Ti, it could be argued that, as both of these lakes have always been located within the taiga zone, they both have probably been relatively productive throughout their histories. Therefore, there is no deficiency in elemental nutrients, nor has there likely ever been (cf. Srivastava et al. 1995; Wetzel 2001), in Russian forest lakes. The late Holocene disappearance of the aquatics and/or decline in aquatic species richness may thus not be “nutrient-derived”, with other factors instead being more important. In contrast to the Russian sites, the changes in different aquatic organisms in Lake Njargajavri testify to a significant drop in nutrient status (from mesotrophic to oligotrophic conditions) (Sarmaja-Korjonen et al., accepted). This may be due to the catchment being only thinly covered by till (originating from nutrient-poor granite-gneiss bedrock), with this thin soil layer rapidly losing its nutrient storage when exposed to leaching after deglaciation (cf. Birks and Birks 2004). In the case of Njargajavri, the dry-out during the middle Holocene complicates the interpretation of the history of the aquatic plant community. The role of nutrient depletion for missing late Holocene limnophytes therefore remains tentative (see also pH discussion below).

A diatom-based pH reconstruction for Lake Mezhgornoe shows that pH has varied between 7.4 and 7.6, and that in Lake Vankavad the pH has consistently been ca. 6.5. No historical data exist for Lakes Llet-Ti and Tumbulovaty. The reconstructed pH values roughly correspond to modern measurements from the Pechora River catchment, the median being 6.8 (Duff et al. 1999). Again, the Njargajavri record shows a divergent development, indicating a significant drop in pH (from 7.5 to 5.3) (Sarmaja-Korjonen et al., accepted). Nevertheless, pH is thought to have no direct impact on aquatic plant communities, instead acting indirectly, having an effect on the form in which different nutrients (N, P, C) occur and thus become available for plants (Srivastava et al. 1995). The historical pH values in the studied lakes have never reached very acidic or alkaline levels. Thus, from the limnophytes’ point of view, the role of changes in pH is relatively unimportant.

3.2.3 Macrofossil records as possible indicators of fluctuating lake levels

Because only one core per site was examined it is not possible to reliably reconstruct or quantify past water level changes (Digerfeldt 1972; Digerfeldt 1986; Gaillard 1984; Gaillard et al. 1991; Harrison and Digerfeldt 1993; Digerfeldt et al. 1997; Hannon and Gaillard 1997). However, since additional aquatic proxy evidence is available for Lakes Mezhgornoe, Vankavad and Njargajavri, it is worthwhile discussing whether the declining trend in terrestrial (including telmatic taxa) remains through the Holocene is due to factors other than changes in vegetation composition and density, for instance, the past lake-level changes (i.e. changes in the distances between the sampling points and the shoreline). When the macrofossil data derived from all lake sites are examined together with the other proxy records, it can be speculated that the historical variations in the abundances of (especially) terrestrial remains reflect the position of the sampling point in relation to the shoreline. A high abundance of terrestrial remains implies close proximity to the shoreline, whereas abrupt disappearance of terrestrial remains (sometimes with a concurrent increase in aquatic remains) implies rising/higher water level at the sampling point (and development of the littoral zone). Similarly, disappearance of terrestrial remains and concurrent disappearance of limnophyte remains suggest deep water and a remote location from the shoreline (Birks 1973; Birks and Birks 1980; Vance and Mathewes 1993; Hannon and Gaillard 1997; Last et al. 1998; Dieffenbacher-Krall and Halteman 2000; Cohen 2003, and references therein).

Macrofossil records show that a maximum in the abundances of remains often corresponds to the initial situation where the sampling points, which at present have a mid-lake position (except Lake Mezhgornoe), were situated close to the shoreline (Figure 3). The macrofossil data suggest that the sampling points were situated near the shore in Lakes Llet-Ti and Vankavad until ca. 5000 cal yr BP, in Lake Mezhgornoe only until ca. 10 000 cal yr BP, in Lake Tumbulovaty maybe until 3000 cal yr BP and in Lake Njargajavri until the lake dried out possibly around 8000 cal yr BP. The macrofossil-based interpretation in terms of the low water levels during the early to middle Holocene, Lake Mezhgornoe being an exception in this pattern, receives support from other available proxies: Lake Mezhgornoe (Cladocera, diatoms), Lake Vankavad (Cladocera, diatoms) and Lake Njargajavri (Cladocera, diatoms, chironomids). Macrofossil and Cladocera assemblages from Lake Mezhgornoe show that the lake level was relatively high between 10 000 and 8000 cal yr BP), i.e. the sampling point situated further from the shoreline than before 10 000 and after 8000 cal yr BP. After ca. 8000 cal yr BP, the shoreline seems to have located nearer to the sampling point, i.e. the water level probably dropped. Figure 4 illustrates a possible interpretation in terms of shifts in the position of the sampling point in relation to the shoreline based on several proxy records.

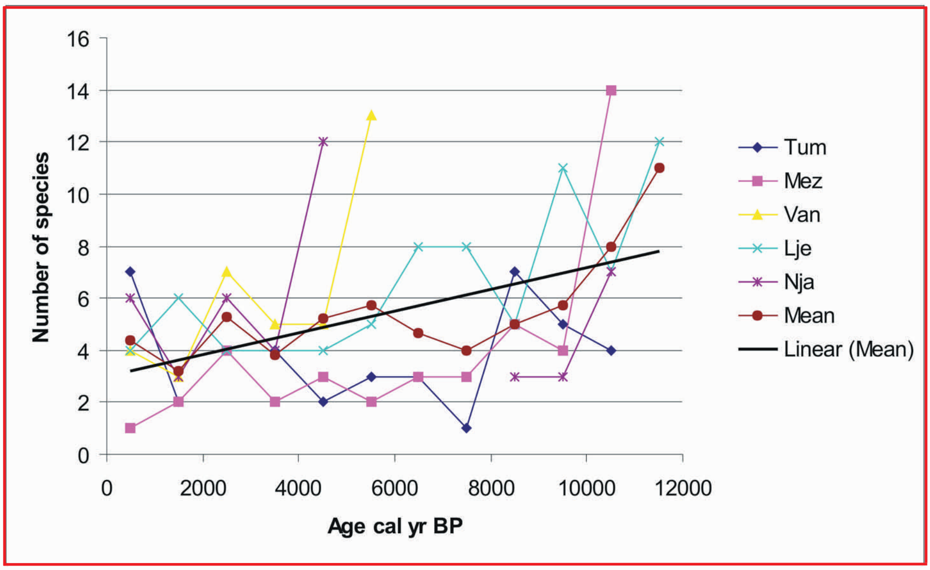

Figure 3. Past changes in species richness of terrestrial and telmatic taxa. A mean value of number of taxon within 1000 year periods was used to illustrate the long-term trend.

The rise in water level, resulting in an increase in distance between sampling points and the shoreline, seems to have occurred in Russian taiga lakes and in Njargajavri around 5000 cal yr BP, in Lake Tumbulovaty around 3000 cal yr BP and in Lake Mezhgornoe around 2000 cal yr BP. Some (even though weak) indication of a water-level lowering about 1000 years ago also exists. In Lake Mezhgornoe, this subtle shallowing is suggested by a decrease in the proportion of planktonic Cladocera, and in Lake Tumbulovaty by an increase in the proportion of telmatic plant pollen. Also in Lake Llet-Ti, a late Holocene lake-level change emerged by an increase in the amount of terrestrial and telmatic plant remains and in the proportions of telmatic pollen, suggesting a closer position of the sampling point, but this change occurred earlier, ca. 2500 cal yr BP.

In all cases, modern samples were characterized by scarcity of macroscopic remains. This may be because the sampling points are currently located relatively far from the shoreline (100-300 m), with the exception of Lake Mezhgornoe, where the distance is ca. 20 m.

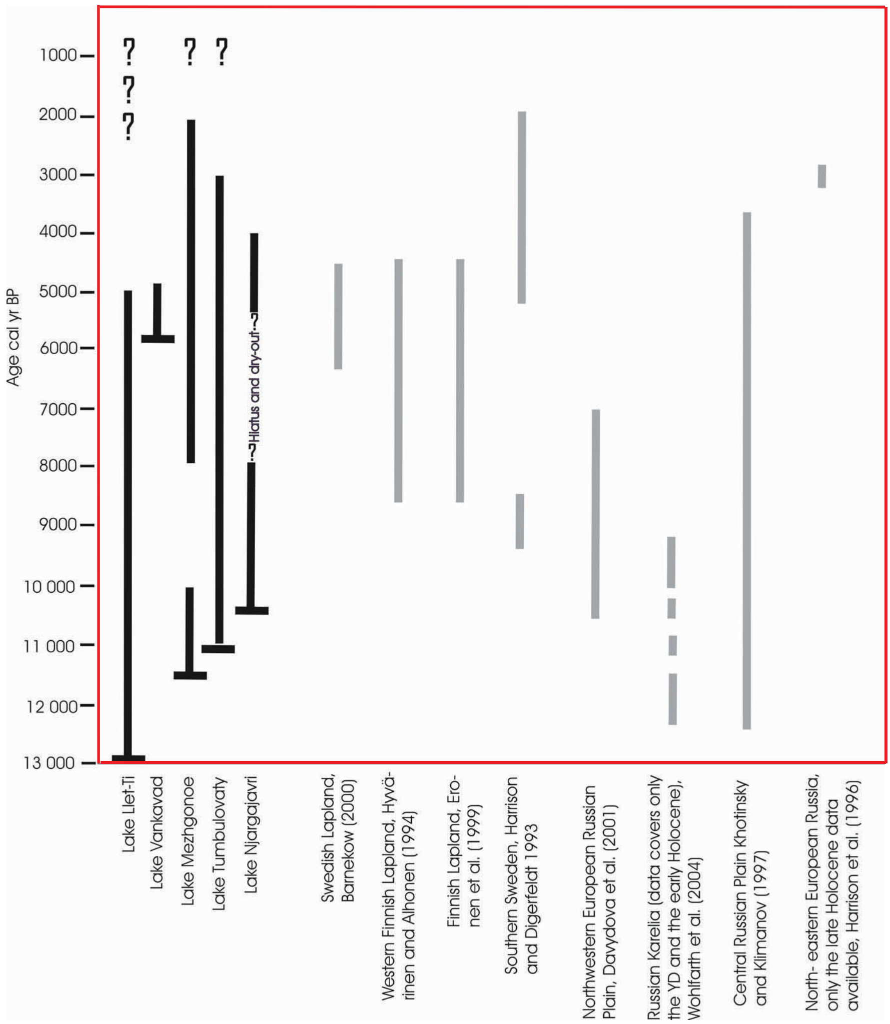

Figure 4. A plant macrofossil-based interpretation of the time periods when the sampling point probably located near the shore (i.e. low water level). For comparison some examples of the reconstructed periods with dry climate and/or low lake levels in northern Fennoscandia, northern European Russia and southern Sweden are shown. For question marks see discussion in Chapter 3.2.3.

3.2.4 Potential mechanisms underlying local/regional water-level fluctuations

The water balance of a lake is dependent on such factors as precipitation, evaporation and evapotranspiration, the area of the lake and catchment, runoff from the catchment, outflow from the lake, and groundwater flow (Street-Perrott and Harrison 1985; Dearing and Foster 1986). However, models developed by Vassilev and Harrison (1998) suggest that especially changes in precipitation are needed to cause significant lake-level changes; shifts in temperature alone are not sufficient. Changes in permafrost conditions affect soil permeability and moisture retention capacity, complicating historical water-balance interpretations in arctic and subarctic areas (MacDonald et al. 2000b; van den Linden et al. 2003). The natural infilling process leads to the shallowing of lakes and shorelines and to an increase in the extent of littoral habitats (Hannon and Gaillard 1997). Regional differences in historical moisture balances also depend on the past geographical position in relation to, for instance, i) the melting Scandinavian ice-sheet, which maintained regional climate conditions along the edge of the ice-sheet (e.g. Subetto et al. 2002; Wohlfarth et al. 2002), ii) the historical Barents Sea coastline, which affected the oceanic/continentality rate (e.g. Andreev and Klimanov 2000), and iii) the Atlantic Ocean, the climatic influence weakening eastwards (e.g. Velichko et al. 1997; Wohlfarth et al. 2004). Ina ddition, the early Holocene changes in insolation (COHMAP members 1988) may have had a strong regional impact on moisture regimes (MacDonald et al. 2000b; Mioussa et al. 2003).

In general, the initiation of the lakes in north-eastern European Russia is linked to the warming that started ca. 13 000 cal yr BP, leading to a gradual melting of the permafrost (Sidoruk et al. 2001; Henriksen et al. 2003). Earlier studies on long-term changes in lake-levels are not available from the north-eastern part of European Russia. Yet, some reconstructions exist for north-western Russia and Russian Karelia. Harrison et al. (1996) synthesized data derived from various proxy records and applied a rough lake-level reconstruction to the western part of the north European Russia. The reconstruction shows a somewhat contradictory pattern to the one indicated by current data. It suggests that in north-western Russia higher-than-present lake levels prevailed around 10 500 cal yr BP, and higher or similar lake levels were present ca. 8000 and 3000 cal yr BP. In addition, according to Harrison et al. (1996) lake levels were lower than present in the north-eastern European Russia ca. 3000 years ago. The records presented here indicate that after the initial phase the lake levels were not high, in fact remaining relatively low (except in Lake Mezhgornoe). Wohlfarth et al. (2004) report more congruent results from Russian Karelia and conclude that during the early Holocene several periods of negative effective moisture occurred. Moreover, these results are in fairly good agreement with some previously published paleoecological studies from northern Russia (Khotinsky 1984; Khotinsky and Klimanov 1997; Arslanov et al. 1999), suggesting intermittent warm and cool periods during the early Holocene. In addition, Davydova et al. (2001) report low lake levels for the Russian Karelian area during the early Holocene.

In the light of these reconstructions, the suggestion of low lake levels until the middle Holocene, based on plant macrofossil records of four Russian lakes, is reasonable. Additional support can be found in regional vegetation and climate reconstructions for north-eastern European Russia. These reconstructions show that a warming early Holocene climate led to the rapid immigration of different trees to previously treeless areas as well as to denser vegetation in areas formerly occupied by sparse vegetation (Kremenetski et al. 1998; Andreev and Klimanov 2000; Kaakinen and Eronen 2000; MacDonald et al. 2000a; Paus et al. 2003; I, III-V). Such a succession must have resulted in an increase in the evapotranspiration rate and had a negative effect on the catchment's moisture balance (Lockwood 1979; Bosch and Hewlett 1982; Yu and McAndrews 1994; Zhang et al. 2001). This was also interpreted to be the case in Njargajavri. The Njargajavri record, which indicated that the water level had started to lower already around 10 000 cal yr BP, was not in total harmony with earlier records from Fennoscandia, which reported higher-than-present lake levels during 10 000-8000 cal yr BP (Korhola and Weckström 2004). Apparently, the drying effect resulting from immigration of tree birch was enhanced because of a small lake/catchment relation (1:5). The middle Holocene dry-out of the lake is, however, in accordance with other historical Fennoscandian lake-level data (Hyvärinen and Alhonen 1994; Eronen et al. 1999; Sarmaja-Korjonen and Hyvärinen 1999; Barnekow 2000; Korhola and Weckström 2004).

The reason for the higher water level period detected between 10 000 and 8000 cal yr BP for Lake Mezhgornoe remains unclear. It might, for instance, be related to dynamics of local cirque glaciers. In any case, the almost concurrent post mid-Holocene rise in lake levels (and the initiation of Lake Vankavad) coincides with climate reconstructions indicating widespread cooling and a more humid climate after the middle Holocene (Fennoscandia: Rosén et al. 2001; Seppä and Birks 2001; Bigler et al. 2003; Korhola and Weckström 2004 and Northern Russia: Davydova and Servant-Vildary 1996; Kremenetski et al. 1998; Arslanov et al. 1999; MacDonald et al. 2000a; Kaakinen and Eronen 2000; Oksanen et al. 2001; Andreev et al. 2002; Paus et al. 2003; III-V).

In conclusion, the plant macrofossil records seem to reflect past changes in aquatic environment in the following ways:

1)The **immigration** and **establishment** of aquatic plant communities during the early Holocene were possible due to rising **temperatures** and sufficient **nutrient status.**

2)The **absence** or **presence** of limnophytes in lakes beyond treelines after the middle Holocene was mainly controlled by **temperature.**

3)The variation in the **amount** of terrestrial and in some cases also aquatic macroscopic remains is strongly linked to the **position of the sampling point** in relation to the shoreline; fluctuations in water level being the main driving factor behind such changes.

3.3 Changes in terrestrial plant communities in relation to past climate conditions

3.3.1 Degrading and aggrading permafrost

The initiation of Lake Llet-Ti after 13 000 cal yr BP coincides with the recorded enhanced melting of the permafrost in north-eastern European Russia. Recent studies have shown that although the deglaciation in the area took place already during the early to middle Weichselian (90 000-60 000 years ago), the intensive melting of the mineral soils did not occur until ca. 20 000-15 000 years ago (Henriksen et al. 2003; Paus et al. 2003; see also Velichko and Nechayev 1984).

The paludification at Ortino I and II sites (Paper VI) started approximately. 10 300 and ca. 8700 cal yr BP, respectively. The Ortino II macrofossil record indicates a moist minerotrophic phase with a rich bryophyte flora until ca. 7000 cal yr BP. The species assemblage indicates permafrost-free conditions. After that, the establishment of species thriving in drier conditions started while the amount of vascular plant remains declined. The time period between 5500 cal yr BP and present-day is characterized by a sharp increase in Ericales remains and declines in the amount of moss remains and moss species. As a whole, this succession can be linked to permafrost aggradation and the establishment of the present-day peat plateau environment.

The inception age of ca. 5000 cal yr BP for permafrost aggradation is markedly older than that obtained in other permafrost studies from north-eastern European Russia (Oksanen et al. 2001, in press). However, too few dates are available to enable a large-scale interpretation of the permafrost initiation history in north European Russia. Even earlier onsets for permafrost aggradation, before 6000 cal yr BP, are reported from arctic Canada (Vardy et al. 1997), where the aggradation was associated with regional deterioration in climatic conditions and consequent withdrawal of treelines. Two significant periods of intensive permafrost aggradation have been detected so far for north-eastern European Russia (Oksanen et al. 2001; Oksanen 2002; Oksanen et al., in press): from 3400 to 1900 cal yr BP, and from 600 to 100 cal yr BP. When the Ortino age is combined, all three periods of permafrost initiation correspond roughly to the reconstructed regional cooling periods: ca. 5000 and 3000 years ago and 1500-1850 AD (i.e. the Little Ice Age) (Andreev and Klimanov 2000; Kaakinen and Eronen 2000; MacDonald et al. 2000a; Oksanen 2002; III, IV). Recent studies from subarctic areas east of the Ural Mountains show that the climatic cooling led to an increase in permafrost aggradation around 4000 cal yr BP (Kremenetski et al. 2003), whereas in Fennoscandia the permafrost development seems to have started somewhat later, ca. 2500 cal yr BP (Oksanen, unpublished PhD thesis). Thus, relatively large regional variations appear to have existed in the late Holocene initiation of permafrost. Permafrost aggradation and degradation are basically climate-driven phenomena, but soil properties and prevailing vegetation also play an important role (e.g. Seppälä 1986). More studies are required to investigate the reasons behind variations in permafrost development and to predict regional variations in future degradation (ACIA 2004).

3.3.2 Immigrating and withdrawing trees

Plant macrofossils from Lake Llet-Ti yielded new information about the growing conditions that had prevailed during the Younger Dryas in the present taiga zone in north-eastern European Russia. The record (Figure 5) testifies that throughout the Younger Dryas period tree birch and conifers grew in the vicinity of Lake Llet-Ti, suggesting that the mean July temperature was approximately the same as at the present treeline i.e. 13.4°C (1961-1990) (Virtanen et al. 2004a), meaning that at least the July temperature was not more than one degree cooler than today. A minimum mean July temperature of 13°C is also indicated by the pre-Holocene presence of *Typha* seed (cf. Kolstrup 1979; Andreev et al. 2001, see also Isarin and Bohncke 1999). Unfortunately, limited data are available for comparison since adequately dated paleovegetation studies from the European part of northern Russia, reaching beyond the Holocene, have been scanty. Growing conditions nearly as warm as today are suggested by Borisova (1997), who claimed that January temperatures were not more than ca. 1°C cooler and July temperatures were about the same as current temperatures. The results showing Younger Dryas presence of spruce are similar to those reported by Khotinsky and Klimanov (1997). According to them spruce was continuously present in the central Russian Plain during the Younger Dryas period. Their climate reconstruction also indicates that warm but short summers prevailed during the Younger Dryas around the central Russian Plain. Paus et al. (2003) suggest that in Timan Ridge area (ca. 67°N, 48°E, ca. 500 km west of Llet-Ti (Figure 1)) treeless tundra habitat prevailed and that a mean July temperature was similar to present (10°C) during the late Weichselian. This suggests that the currently prevailing phytogeographical gradient across the taiga to tundra zones also existed throughout the Younger Dryas period. This interpretation coincide with Borisova (1997), who suggests that the northern part of Russia did not experience the same cold spell as western Europe but that the mean July and January temperatures resembled modern temperatures. However, too few sufficiently long reconstructions exist to establish a geographically extensive picture of the late Weichselian environments in northern European Russia.

The plant macrofossil records indicate that within the Usa basin tree birch was already present at the alpine and arctic treelines at the time of the early Holocene initiation of the lakes (Figure 5). The age of tree birch finds 11 500 cal yr BP from Mezhgornoe and 11 200 cal yr BP from Tumbulovaty, are about one thousand years older than earlier finds derived from the European Russian arctic treeline (Kremenetski et al. 1998; MacDonald et al. 2000a; Oksanen et al. 2001). No previous data exist from the European Russian alpine treeline. The needle and stomata records from the alpine tree-line (Lake Mezhgornoe) show a successive invasion of different conifer species; with larch immigrating first (ca. 10 500 cal yr BP), then fir (ca. 10 200 cal yr BP) and finally spruce (ca. 10 100 cal yr BP). The relatively rapid early Holocene immigration was possible because the Ural Mountain valleys probably provided a late glacial refugium for conifers (O. Lavrinenko, pers. comm.). The immigration of spruce to and beyond the modern arctic treeline took place between ca. 10 200 and 9600 cal yr BP (IV and VI). Current records thus reveal an earlier presence of conifers at the treeline areas than recorded in previous research (9500 cal yr BP) (Kremenetski et al. 1998; McDonald et al. 2000a). Based on the modern climate/treeline relationship, the establishment of the mixed taiga forest in Russian arctic and alpine treeline areas implies that the early Holocene mean annual and July temperatures were ca. 2°C warmer than today. Finds of *Typha latifolia* seeds between 9000 and 8000 cal yr BP from Lake Tumbulovaty also suggest warmer than modern temperature. The modern distribution of *Typha latifolia* in European Russia mainly follows the latitude 60°N, i.e. ca. 15°C July isotherm (Isarin and Bohncke 1999), indicating a 1.6°C warmer early Holocene July temperature for Lake Tumbulovaty.

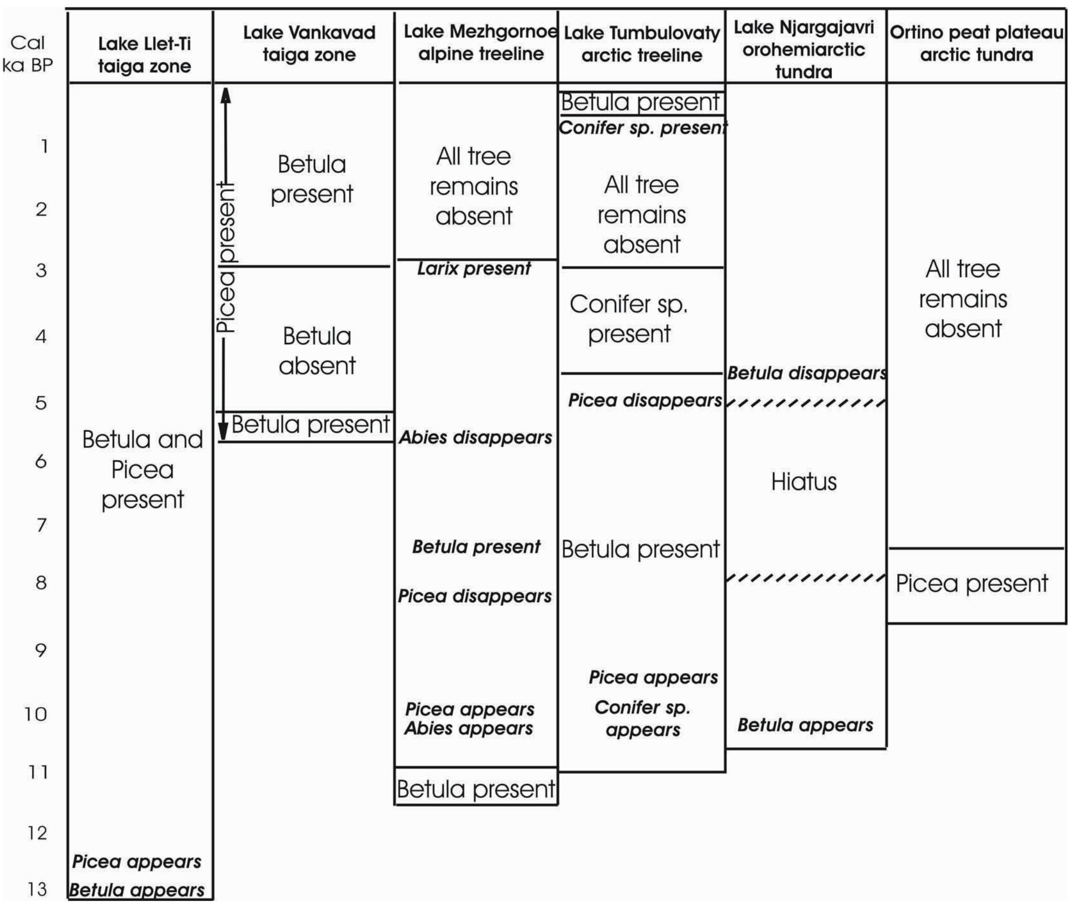

Figure 5. A summary of the appearance, presence and disappearance of different tree remains according to macrofossil records. *Italicized text* **indicates the precise depth of the find, whereas non-italicized text refers to the whole zone, separated by crossbars. Betula refers to tree-type birch finds.**

An early to middle Holocene thermal maximum in northern European Russia with summer temperatures from 2°C to 7°C warmer than present-day, has also been reported by previous studies (Kremenetski et al. 1998; Andreev and Klimanov 2000; Kaakinen and Eronen 2000; MacDonald et al. 2000a; Oksanen et al. 2001; Paus et al. 2003; Oksanen et al., in press). The early Holocene thermal maximum, apart from being caused by the higher summer insolation (COHMAP members 1988), may also have been due to the different location of the Barents Sea coastline. The coastline lay about 100-300 km further north during the early Holocene, contributing to a more continental climate and warmer summers in northern Russia (Andreev and Klimanov 2000). In addition, the sea-surface temperature reconstruction for the Barents Sea shows a warming trend starting at ca. 10 000 cal yr BP, culminating as a temperature maximum between 7800 and 6800 cal yr BP (Duplessy et al. 2001).

The current results (especially those derived from pollen records) from the treeline sites suggest that the mixed spruce-birch forest started to withdraw southwards between 6000 and 5000 cal yr BP. This middle Holocene withdrawal concurs with findings of earlier studies carried out in northern Russia (Davydova and Servant-Vildary 1996; Kremenetski et al., 1997, 1998; MacDonald et al. 2000a; Gervais et al., 2002; Paus et al. 2003). The wide-ranging withdrawal is related to the general climatic cooling detected in, for instance, Greenland ice cores (e.g. Dahl-Jensen et al. 1998). However, sites within the modern taiga zone, Lakes Llet-Ti and Vankavad, show no change in species composition during that time.

A cooling phase around 3000 cal yr BP, recorded earlier by e.g. Davydova and Servant-Vildary (1996), Arslanov et al. (1999), Kaakinen and Eronen (2000) and MacDonald et al. (2000a), can be detected from the present macrofossil data from treeline sites (Figure 5). Lower-than-today temperatures may also have prevailed at the arctic treeline between 3000 and 2100 cal yr BP. This is supported by the historical temperature reconstructions derived from the ice cores, which indicate cooler-than-present conditions about 2000 years ago (Dahl–Jensen et al. 1998). According to for instance MacDonald et al. (2000a), the late Holocene degradation in growing conditions in north European Russia is connected to a decrease in summer insolation, cooling of arctic waters and possible extension of sea ice.

Both pollen and macrofossil records from Lake Tumbolovaty as well as a paleosol horizon from the adjacent Khosedayu peat plateau, containing wood fragments, indicate a temporal warming about 1000 years ago, corresponding to the Medieval Warm Period. This warmer period is also detected, for instance, as an upward shift of the alpine treeline in the Ural Mountains (Shiatov 1993).

The macrofossil record from Njargajavri, although discontinuous due to a dry-out, follows roughly the same Holocene climatic pattern. Tree birch immigrated to the area during the early Holocene (ca. 10 200 cal yr BP), and the last tree birch remains were detected ca. 4500 cal yr BP. No evidence of local presence of conifers was found. Overall, the macrofossil and pollen records correspond to previous Fennoscandian treeline studies, in which the shifts in treelines have been related to the regional climate history (e.g. Hyvärinen 1975; Seppä 1996; Mäkelä 1998).

In conclusion, the terrestrial plant macrofossil records demonstrate that:

1) Tree birch and conifers were present at the modern taiga zone throughout the Younger Dryas period.

2) Tree birch was present beyond the modern treeline areas already at the very beginning of the Holocene.

3) The Russian treeline areas were colonized by conifers during the early Holocene.

4) The general withdrawal of the treelines started gradually ca. 5000-6000 years ago.

5) Permafrost initiation took place at the modern tundra zone after 5500 cal yr BP.

6) A second cooling phase around 3000 years ago led to the final withdrawal of treelines.

7) The Medieval Warm Period was possibly detected from the Lake Tumbulovaty record.

8) Within the taiga zone no big changes in species composition occurred during the Holocene.

4 Conclusions and a glance to future prospects

Macrofossil data indicated that conditions comparable with modern treeline conditions prevailed in the Usa basin taiga zone during the Younger Dryas. With the climatic warming, a rich flora rapidly established to aquatic and terrestrial habitats. The immigration phase was followed by a maximum in species richness and abundances generally corresponding to the early Holocene thermal maximum. The middle Holocene cooling resulted in withdrawal of treelines and degradation of aquatic plant communities, leading to new permafrost aggradation in areas beyond the arctic treeline. A simultaneous rise in water levels led to an increase in distances between the sampling points and the shoreline. This development is detected as a decline in number of finds of terrestrial plant macrofossils and in species richness. The second cooling phase, which started around 3000 cal yr BP, resulted in the modern kind of environment. However, some indication exists from sites beyond current treelines that a short warming took place about 1000 year ago, corresponding to the so-called Medieval Warm Period.

This paleoecological study has evidenced that rather moderate changes (ca. 2°C) in temperature in the past have had significant impacts on subarctic environments. Climate change models (IPCC 2001) predict a rise in mean annual surface temperatures of 1.4-5.8°C within the next centuries and an even more pronounced warming at high latitudes (ACIA 2004). This would lead to shorter winters and an earlier onset of the growing season. Moreover, lake-ice models suggest that the ice-off-date is more sensitive than the ice-on-date to changes in air temperature, and that both dates are more sensitive to warming than cooling (Vavrus et al. 1996). Since an increase of 1°C in temperature may correspond to a 7 to 9 day increase in the duration of the open-water period (Magnuson et al. 2000), a future increase in the length of the open-water season might be of an order of several weeks. According to presented results, warming might result in a greater distribution of submerged macrophytes in northern lakes (see also Rooney and Kalff 2000). This will have a marked effect on arctic freshwater habitats. The increase in number and/or density of macrophytes will have a direct impact on light, temperature and biochemical conditions (Carpenter and Lodge 1986). In addition, aquatic macrophyte communities are involved in several biotic interactions, providing a substrate for different micro–organisms; phytoplankton and zooplankton (Carpenter and Lodge 1986; van Donk and van de Bund 2002). Productivity probably increases due to shifts in treelines (cf. Weckström et al. 1997; Rühland and Smol 1998; Duff et al. 1999; Korhola et al. 2002), and changes in the terrestrial environment will also have an effect on pH and transparency in northern lakes (MacDonald et al. 1993; Carvalho and Kirika, 2003; Coops et al. 2003). These changes will in turn have a significant influence on micro-organisms. Further studies investigating in detail the historical factors that have controlled aquatic plant assemblages (see Carpenter and Lodge 1986; Duff et al. 1999) are, however, needed to answer the question of whether a longer open-water season will in fact lead to the establishment of vascular aquatic plant communities in shallow subarctic lakes.

As lake-level reconstructions have shown (e.g. Hyvärinen and Alhonen 1994; Eronen et al. 1999;

Barnekow 2000; Korhola et al. 2005), considerable water-level fluctuations have taken place in the northern treeline regions during the Holocene, and they are related to the changes in temperature and precipitation conditions. The amount of summer and winter precipitation is projected to increase at high latitudes (IPCC 2001; ACIA 2004). Depending on the future level of effective humidity, including a possible increase in evapotranspiration (Zhang et al. 2001), lakes may experience either rising or lowering water tables, although according to Vassiljev (1998), lake levels are more sensitive to a decrease than an increase in precipitation. The data presented here, especially that derived from Lake Njargajavri, suggest that should there be a decline in effective humidity, the shallowest lakes with small catchments would experience a marked decline in water level, possibly leading to overgrowth or drying.

Terrestrial environments will probably also face considerable changes, such as degrading permafrost and shifting treelines (Anisimov and Nelson 1996; Harding et al. 2002; Skre et al. 2002). According to recent calculations (Kultti et al., accepted), an increase in mean July temperature of only 1°C would result in an expansion of pine to the catchment area of Lake Njargajavri in Finnish Lapland. Virtanen et al. (2004a) calculated that a 1°C increase in mean July and minimum temperatures would lead to 70-km northward shift of the forest line in the Usa basin. This means that 77%, instead of the current 26%, of the lowland area of the Usa basin would be covered by forests. Such a development would trigger a complicated chain of feedback effects in subarctic/arctic areas, having an increasing or decreasing effect on the climate forcing mechanism (Harding et al. 2002). Young spruce individuals observed growing in the modern shrub tundra of the Usa basin indicate that spruce has in the past decades already spread northwards (Virtanen et al. 2004a, T. Virtanen, pers. comm.). On the other hand, relict spruce "islands" originating from the earlier warmer periods of the Holocene and occurring beyond the treeline are still unable to produce new seedlings (Lavrinenko and Lavrinenko 1999).

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