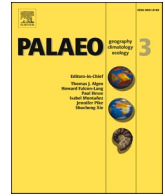




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Late- and postglacial vegetation and climate history of the central Kola Peninsula derived from a radiocarbon-dated pollen record of Lake Kamenistoe

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ABSTRACT

A radiocarbon-dated sediment core collected from the small freshwater Lake Kamenistoe, in the central part of the Kola Peninsula, provides a pollen record of vegetation and climate history of this part of Fennoscandia and the European Arctic during the past ca. 13,000 years. In contrast to existing Scandinavian Ice Sheet reconstructions, the record shows that the study site was ice-free at 13 cal. kyr BP, thus allows to improve our knowledge on deglaciation dynamics in North Europe. The biome reconstruction results together with other pollen records from the wider region suggest that forest-tundra surrounded Kamenistoe at the end of the Bølling-Allerød interstadial and that the reconstructed presence of trees is not determined by far-distance pollen transport. The spread of pine in the study region started ca. 9.3 cal. kyr BP, and maximum pollen percentages during 8.2–4.2 cal. kyr BP mark the Holocene thermal optimum. Progressive climate cooling accompanied by increasing moisture levels from 6 cal. kyr BP is indicated by the spread of spruce (boreal evergreen conifer), reflecting the expansion of taiga forests. In contrast to some previous interpretations, we argue that the spread of pine in the Early Holocene and spruce in the Middle Holocene did not follow zonal expansions, but rather originated from scattered small populations within the study region. Archaeological records from northern Fennoscandia suggest that postglacial human occupation on the Kola Peninsula began no later than 10,000 years ago. This northward expansion of hunter-gatherers was likely related to the continuous Early Holocene warming, which not only resulted in less harsh climatic conditions for human occupation, but may have also pushed reindeer populations to the study region. This game animal, which has been a major resource for humans, prefers July temperatures below 12–13 °C and thus may have migrated to cooler environments during the Early Holocene.

1. Introduction

The circumpolar regions are in the focus of political, scientific and

public organisations worldwide (e.g. Kotlyakov et al., 2017; Melles et al., 2012; Nicol et al., 2016; Pachauri and Meyer, 2014). The growing interest has many good reasons. Insights from remote sensing

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observations and model reanalysis (Kumar et al., 2020) demonstrate that the most pronounced temperature increase of recent years occurred in the Arctic regions. Global warming leads to alarming recession of the sea-ice cover, thus threatening the very fragile regional environments and various aspects of plant, animal and human life. Recent studies also indicate that the impacts of climate change in the Arctic will be not limited to this region but may influence other areas where great parts of the world population live (e.g. Pachauri and Meyer, 2014). Earth system modelling (ESM) experiments provide a powerful tool to assess the drastic changes in the climate and vegetation that will take place in the Eurasian Arctic over the next few decades and to evaluate the amplitude of changes in comparison to the recent and more distant past.

However, comparisons with palaeoenvironmental data suggest that the models considerably underestimate the magnitude of changes in these regions (e.g. Kageyama et al., 2001; Texier et al., 1997). Palaeoenvironmental research helps to reconstruct the impact of past climatic changes on vegetation, animal and human population dynamics and provides valuable data for testing ESM-simulated scenarios and improving the performance of climate models (Strandberg et al., 2022). Despite significant progress in generating new high-resolution and robustly dated records from the Arctic, some regions remain understudied and exhibit large uncertainties in the reconstructed climate and environments. Particularly challenging is the spatiotemporal reconstruction of the Lateglacial-Holocene transition (ca. 15–8 thousand calendar years before present = cal. kyr BP) on the Kola Peninsula, where the deglaciation began earlier and proceeded faster than in other parts of northern Fennoscandia (e.g. Hughes et al., 2016).

Studies of the Lateglacial and Holocene developments in Fennoscandia, including the Kola region, have focused on four major topics: (i) the history of deglaciation (e.g. Boyes et al., 2021; Hughes et al., 2016; Lunkka et al., 2018); (ii) postglacial vegetation development (e.g. Berglund and Ralska-Jasiewiczowa, 1986; Gervais et al., 2002; Giesecke and Bennett, 2004; Velichko et al., 2017); (iii) climate dynamics and sensitivity of pollen and other biological proxies to global and regional climate changes (e.g. Kremenetski et al., 2004a; Seppä et al., 2008); and (iv) human habitation in the region and human interactions with the postglacial environments (e.g. Manninen et al., 2018; Murashkin and Kolpakov, 2019; Rankama and Kankaanpää, 2011; Shumkin, 2017). In the current paper, we aim to discuss the implications of a new radiocarbon-dated pollen record from Lake Kamenistoe for addressing the aforementioned scientific issues.

2. Study site and regional environments

Lake Kamenistoe (205.3 m a.s.l.) is a small elongated lake with a surface area of ca. 0.15 km² (Fig. 1c) and an average depth of ca. 2.5 m. It is located about 6 km southeast of Umbozero (149 m a.s.l.) – one of the largest (ca. 422 km²) and deepest (maximum depth of 115 m) lakes of the Kola region (Fig. 1b). The two lakes are likely connected through a system of short temporary streams, including a small rivulet, which flows out of Lake Kamenistoe towards Umbozero. The area around Lake Kamenistoe is low-elevated and covered with boreal forests, wetlands and swamps.

The study area (Fig. 1c) in the central part of the Kola Peninsula (Fig. 1b) belongs to northeastern Fennoscandia (Fig. 1a). The entire region was covered by an extensive ice sheet during most of the Late Quaternary, and deglaciation of the Kola Peninsula did not start until ca. 15 cal. kyr BP (Stroeven et al., 2016; Svendsen et al., 2004;). Precambrian crystalline igneous rocks of the Baltic Shield, overlain by a relatively thin cover of glacial till, glaciofluvial and lacustrine deposits, including widely spread Holocene peats, are characteristic features of the regional geology (Alpat'ev et al., 1976; Gervais et al., 2002). Along with glacial and glaciofluvial processes, neotectonics and seismic activity processes played an important role in shaping the modern relief of the Kola Peninsula (Bungum and Lindholm, 1997). The highest elevations up to 1000–1200 m a.s.l. are registered in its central part, within

the Khibiny and Lovozero mountain massifs separated by Lake Umbozero, while most of the area is below 500 m (Fig. 1b).

The location of the Kola Peninsula almost entirely inside the Arctic Circle, proximity to the Barents and White seas (Fig. 1b) and the frequent alternation of North Atlantic and Arctic air masses throughout the year determine the regional climate (Alpat'ev et al., 1976). Mean temperatures range from –9 °C to –13 °C in January and +9 °C to +14 °C in July (Gervais et al., 2002). The recent years, however, have experienced warmer temperatures above the 20th century climatic averages. Meteorological records from the Kirovsk observatory (67.62°N, 33.67°E; 186 m a.s.l.) situated about 44 km west of Lake Kamenistoe reveal a mean January temperature of –8.2 °C in 2020 and a mean July temperature of +17.8 °C in 2018 and +14.1 °C in 2020 (<http://www.pogodaiklimat.ru/history/22224.htm>). Mean annual precipitation varies between 500 and 700 mm and falls primarily in the summer and autumn months (Gervais et al., 2002). Snow cover lasts about 200 days a year (Alpat'ev et al., 1976). The relatively high atmospheric precipitation and low evaporation determine the high humidity and abundance of lakes and rivers in the region.

The actual biome distribution in the Kola region (Atlas of the Murmansk region, 1971) reflects well the modern climate variability (Lee-mans and Cramer, 1991; Prentice et al., 1996), however, the local topography and hydrological conditions may strongly influence the microclimate and lead to mosaic vegetation (Alpat'ev et al., 1976; Fig. 1c). For example, islands of alpine tundra appear in the Khibiny and Lovozero mountains well within the forest zone (Atlas of the Murmansk region, 1971). Tundra and boreal coniferous forest (taiga) are the two major vegetation types in the region, separated by transitional woodland or forest-tundra (Fig. 1b), which some authors identify as a separate zone (Alpat'ev et al., 1976). In the forest-tundra, the main tree taxa are birch, more abundant in the northern part, and pine. In the biome classification adopted in climate-based vegetation modelling experiments (Prentice et al., 1992) and pollen-based vegetation reconstructions (Prentice et al., 1996), these tree taxa (together with larch and poplar) represent the cold deciduous forest biome that occupies the vast zone between arctic tundra and taiga in northern Eurasia.

The most representative landscapes and vegetation types (Alpat'ev et al., 1976) across the Kola Peninsula include tundra (Fig. 2a) with a dominance of shrubby birches, willows and species of the heath (Ericaceae) family and diverse herbaceous plants, mosses and lichens; forest-tundra (Fig. 2b–c) with birch trees (*Betula pubescens* ssp. *tortuosa*, *Betula pendula*), Scots pine (*Pinus sylvestris*) and patches of juniper shrubs (*Juniperus communis*) interspersed in the landscape; and northern boreal forests (Fig. 2d–f) with birch, pine and spruce (*Picea abies*) trees dominating in the canopy (Atlas of the Murmansk region, 1971). The Kola region has substantial resources of edible mushrooms and berries and is rich in terrestrial and aquatic fauna, which have been important food sources of prehistoric hunter-gatherers who came to this area in the Mesolithic (Shumkin, 2017). The regional fauna includes 26 species of land mammals, 90 species of nesting birds and 16 species of freshwater fish (<https://bigenc.ru/geography/text/2238756>). Forest species, including elk, reindeer, white hare, squirrel, fox and brown bear are common, while beaver and roe deer are rare. Sea coasts serve as wintering and nesting places for waterfowl and large bird colonies on the Murmansk coast. Seals and walrus live in the coastal waters of the Barents and White seas (Alpat'ev et al., 1976; Atlas of the Murmansk region, 1971).

3. Data and methods

3.1. Sediment coring and subsampling

For this study, we analysed a 135-cm-long sediment core from Lake Kamenistoe, recovered in July 2018 from a coring platform positioned in the deepest (ca. 4 m) and flat-bottomed central part of the lake (67°30'31.4'' N; 34°38'53.3'' E). The place for coring was chosen based

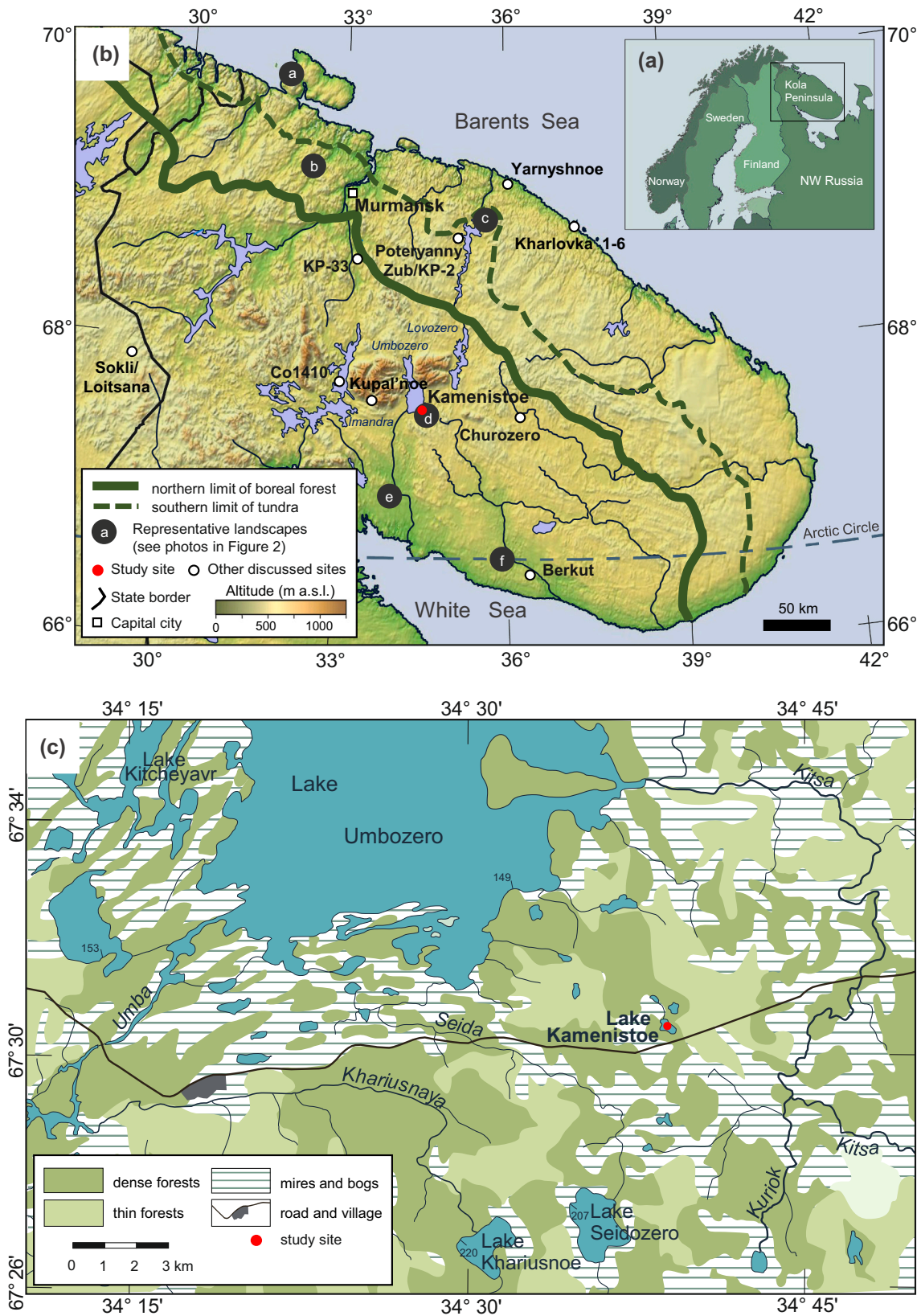


Fig. 1. (a) Location of the study region (black rectangle) in northern Europe and (b) topographic map of the Kola Peninsula showing key features of modern natural vegetation (simplified after Atlas, 1971) and hydrology. Lake Kamenistoe study site is indicated by a red dot and the white dots indicate the sites with environmental records discussed in the text. (c) Topographic map of the area around Lake Kamenistoe. Dense forests around the lake are dominated by pine, birch and spruce, while birch and pine dominate in the sparse forests. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

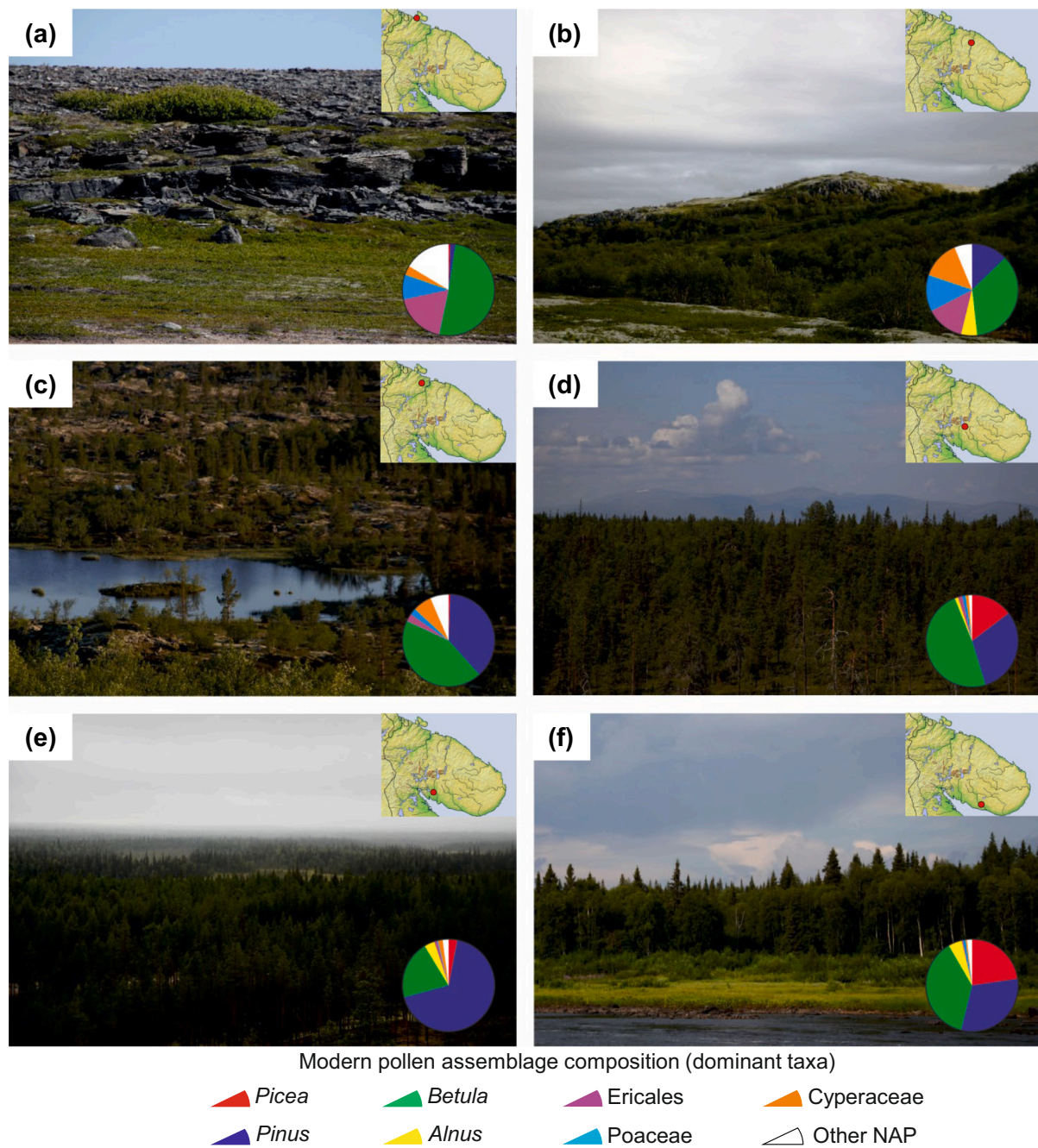


Fig. 2. Photos of representative landscapes, vegetation types and modern pollen assemblage composition across the Kola Peninsula (red dots show respective site locations on the regional map): (a) tundra with a dominance of dwarf shrubs (birch, polar willow, Ericaceae species), higher shrubs (birch, willow) and diverse herbaceous plants on the Sredny Peninsula (July 2021); (b) birch forest-tundra landscape in the Voronya River basin with a predominance of birch, willow and members of the heath family among the tundra shrubs (August 2018); (c) forest-tundra landscape in the Ura River basin with birch, pine and juniper at higher elevations (June 2018); (d) birch and pine-dominated forest in the Umba River basin (August 2018); (e) pine-dominated forest south of Umbozero (July 2018); (f) pine and spruce-dominated forest in the Varzuga River basin (July 2018). All photos taken by N. Kostromina. Pollen assemblage composition diagrams are based on (a) Davis et al. (2020), (b, d, f) Kostromina (unpublished data) and (c, e) Tarasov et al. (2005). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

on the results of water depth measurements with an echo sounder. Visual description of the core lithology was carried out in the field. Considering the lithological boundaries, 30 samples were taken from the composite sediment core for loss on ignition (LOI) and palynological analyses. Each sample from the depth interval 0–129 cm represented a 1 cm layer of sediment, and two samples from the lowest, sandy-clayey unit were 2 cm thick.

3.2. Loss on ignition analysis

The LOI analysis is generally considered to be a simple method to estimate organic matter and carbonate contents of sediments (Beaudoin, 2003; Bendell-Young et al., 2002; Boyle, 2004; Dean, 1974). In this study, the sample preparation and analysis were carried out following the standard procedure (Heiri et al., 2001). All samples were dried in the oven at 100 °C to determine the dry weight of the sediment. After that,

they were placed in a muffle furnace and heated at 550 °C for 2 (samples with a very high organic matter content) or 4 h (for the 'mixed sediment') to combust the organic matter, as recommended in Heiri et al. (2001).

3.3. Palynological analysis and visualisation of results

Extraction of pollen, cryptogam spores and non-pollen palynomorphs (NPPs) from the sediment matrix followed the hydrofluoric acid (HF) approach (Berglund and Ralska-Jasiewiczowa, 1986). To each sample, one tablet with a known number of *Lycopodium* spores was added prior to chemical treatment in order to calculate the concentration of palynomorphs (Stockmarr, 1971). Pollen and non-pollen palynomorphs (NPPs) were counted using a light microscope at $\times 400$ magnification and identified with the help of published regional atlases and reference collections (Bobrov et al., 1983; Kupriyanova and Aleshina, 1972; Kupriyanova and Aleshina, 1978; Moore et al., 1991; Savelieva et al., 2013; van Geel, 2001). Pollen preservation was good for identification and sufficiently high concentration allowed counting of at least 300 terrestrial pollen grains in most of the samples.

Tilia version 1.7.16 software (Grimm, 2011) was used for calculating relative taxa percentages and for drawing the pollen diagram. Percentages for all terrestrial pollen taxa were calculated based on the sum of arboreal pollen (AP) and non-arboreal pollen (NAP) taken as 100%. Percentages for aquatic plants, terrestrial cryptogams and other NPPs were calculated based on the terrestrial pollen sum plus the sum of palynomorphs in the corresponding group. The CONISS program for stratigraphically constrained cluster analysis by the method of incremental sum of squares (Grimm, 1987) was used to draw pollen zone boundaries.

3.4. Radiocarbon dating and chronological control

To determine the age of the Kamenistoe core, four bulk samples (Table 1) were taken from the sediment sequence and radiocarbon-dated in the Radiocarbon Laboratory of St. Petersburg State University following techniques described in Arslanov et al. (1993) and Muraki et al. (2001). We calibrated the radiocarbon dates using the most up-to-date IntCal20 calibration curve (Reimer et al., 2020) in OxCal v.4.4 (Bronk Ramsey, 1995). The age-depth relationship of the sequence was modelled using the rbacon software package v.2.5.7 (Blaauw and Christen, 2011) on the R v.4.1.2 platform (R Core Team, 2016). The model was run with default configurations. One tie point at the top (i.e. 0 cm depth) of the core was assigned to the model with an age of -68 cal. yr BP, the year when the core was recovered. The dates were modelled using the longer-tailed student's t-distribution instead of the Gaussian distribution as suggested for the dating results with large uncertainties (Peti et al., 2020) and their modelled interval estimates were presented in 99.7% ranges. In the bottommost (undated) part of the Kamenistoe core, the modelling results (i.e. medians) were revised based on pollen-stratigraphic correlation with the northern hemisphere ice-core data (Svensson et al., 2008) and with the Lateglacial-Holocene pollen record from Lake Imandra (Fig. 1b) supported by several

Table 1

Radiocarbon dating results obtained on bulk sediments from the Lake Kamenistoe sediment sequence. The radiocarbon dates (in ^{14}C yr BP) were calibrated and modelled in OxCal v.4.4 software (Bronk Ramsey, 1995) using the IntCal20 calibration curve (Reimer et al., 2020).

Laboratory code	Core depth (cm)	Radiocarbon date (^{14}C yr BP)	Modelled age, 99.7% range (cal. yr BP)	Modelled age, point estimate (cal. yr BP)
LU-9195	50–55	5470 \pm 190	6852–4189	6073
LU-9196	85–88	6960 \pm 130	8880–7353	7856
LU-9193	102–105	8830 \pm 200	10,723–8808	10,377
LU-9194	110–112	9180 \pm 290	11,895–9492	11,587

accelerator mass spectrometry (AMS) radiocarbon dates (Lenz et al., 2021). This age-depth model was then applied to the pollen and sedimentary records and used in the discussion.

3.5. Pollen-based vegetation reconstruction

Pollen records rank very highly in a wide range of proxies, which are used for reconstructing the environmental setting, vegetation and climate histories and the way of life of past human cultures (Berglund and Ralska-Jasiewiczowa, 1986; Beug, 2004; Dumbleby, 1985; Fægri and Iversen, 1989). In this study, the qualitative interpretation of the Lake Kamenistoe pollen record, based on a generally good relationship between modern vegetation of the Kola Peninsula and surface pollen composition (Fig. 2; Gervais and MacDonald, 2001), was complemented by the quantitative approach introduced by Prentice et al. (1996) for assigning pollen spectra to appropriate major vegetation types (biomes) based on modern ecology, bioclimatic tolerance and geographic distribution of pollen-producing plants. This objective method was used successfully to reconstruct past vegetation changes worldwide, including the global vegetation mapping project BIOME6000 (e.g. Prentice and Webb III, 1998) and the Paleoclimate Modelling Inter-comparison Project (e.g. Kageyama et al., 2001). The accuracy of the biome reconstruction approach was verified using representative surface pollen data from Fennoscandia, including the Kola Peninsula and Karelia regions (e.g. Prentice et al., 1996; Tarasov et al., 1998). Successful tests of the method enabled its application to reconstruct post-glacial vegetation and climate dynamics in the northeastern part of Europe (Prentice and Jolly, 2000; Tarasov et al., 1998, 2000, 2022; Wohlfarth et al., 2006, 2007). Following the biome-taxon matrix presented in these studies, all terrestrial pollen taxa identified in the Lake Kamenistoe record were assigned to the corresponding regional biomes. Calculations of the affinity scores for the natural potential regional biomes were performed using an equation first published in Prentice et al. (1996). As suggested in their study, only taxa which exceed the universal threshold of 0.5% influenced the biome reconstruction. For consistency, a square root transformation was applied to the pollen percentage values to increase the influence of minor pollen taxa. The biome with the highest affinity score or the one defined by a smaller number of plant functional types (when scores of several biomes are equal) was assigned to each pollen spectrum (Prentice et al., 1996). The calculation of the difference between the maximum forest biome score (e.g. cold deciduous forest, taiga or cool coniferous forest) and the maximum open biome score (e.g. tundra or cold steppe) was used to qualitatively assess landscape openness, in addition to the more traditional approach using arboreal and non-arboreal pollen percentages (Tarasov et al., 2013).

4. Results

4.1. Lithostratigraphy

The core analysed in this study is represented by two main sedimentary units (Fig. 3a). The uppermost 110 cm unit consists of partly laminated organic gyttja interrupted by a thin peaty layer (88–85 cm) and a layer of sand (106–105 cm) with an increasing silt content between 110 and 106 cm. The lower part of the core (135–110 cm) is composed of low-organic sediments, including silts (112–110 cm), weakly laminated fine sands (112–121 cm), silts with thin layers of fine sand (129–121 cm) and sandy clay (135–129 cm). The results of the LOI analysis (Fig. 3b) confirm this visual description and show low values (ca. 25–35%) in the bottom part of the core below 112 cm and stably high values from 97 cm to the core top. The core interval between 112 and 97 cm shows increasing LOI percentages with an oscillation to lower values (ca. 65%) around 106 cm depth.

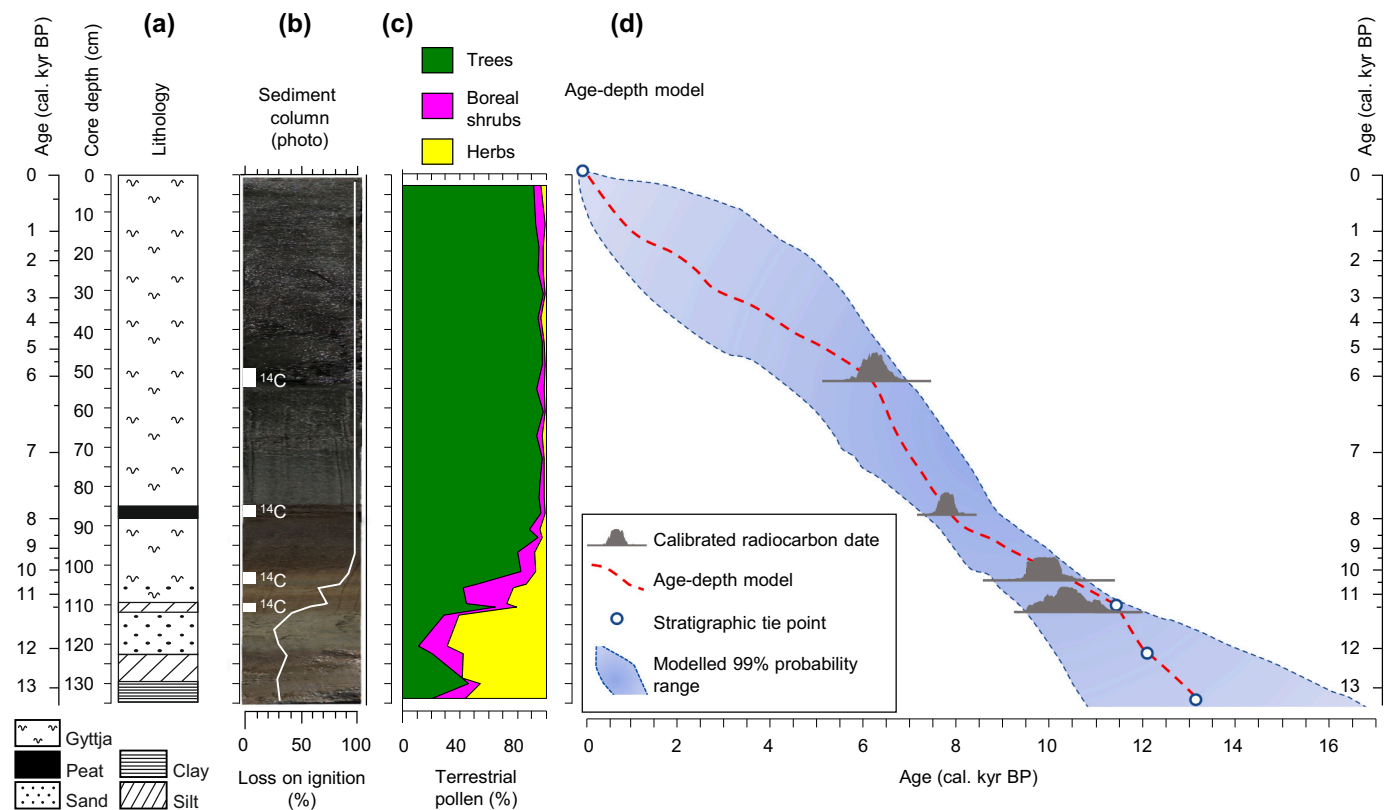


Fig. 3. (a) Lithology, (b) loss on ignition (LOI), (c) terrestrial pollen stratigraphy (cumulative diagram) and (d) age-depth model of the sediment core from Lake Kamenistoe discussed in this study.

4.2. Pollen stratigraphy

The results of the pollen analysis show clear changes in the terrestrial pollen composition along the core (Fig. 3c). Pollen of herbaceous plants predominates in the bottom part of the core (ca. 50 to 70%), with the lowest percentages of tree pollen recorded between 121 and 112 cm. The overlying silty horizon shows an increase in AP to 80% followed by a decrease in shrub and particularly tree pollen fractions between 110 and 105 cm. The part of the core between 105 and 88 cm depth demonstrates a pronounced increase in AP percentages (mainly trees), with the highest values (> 95%) occurring between 88 and 40 cm. In the upper part of the core, pollen of shrubs and herbaceous plants occurs in higher proportions, reaching up to 18% in the top sample.

4.3. Core chronology

The results of radiocarbon dating (Table 1) and age modelling (Fig. 3d) suggest that sedimentation in the analysed core occurred during the last ca. 13 cal. kyr BP. The bottom part of the core below 112 cm is dated to the Lateglacial interval, including the Younger Dryas (YD) stadial and the later phase of the Bølling-Allerød (B-A) interstadial. The upper part of the core represents the entire Holocene interglacial.

In contrast to the lower sections with a denser distribution of calibrated radiocarbon dates and stratigraphic tie points (Fig. 3d), the uppermost 55 cm of the core contain only one date for chronological control. Thus, the age-depth model for the last ca. 6000 years is relatively weak, although age calibration for this interval is not critical for the main thrust of our study. In addition, there is little lithological variation (Fig. 3a) and no visible sedimentary hiatuses in the upper part of the core (Fig. 3b), indicating a relatively stable depositional environment that matches fairly well the extrapolated chronology. Minor fluctuations in the age-depth relationship observed between ca. 15 and

30 cm (Fig. 3d) are possibly related to the fact that the model detected a change in the width of calibrated distributions in this section and should be viewed with caution.

4.4. Pollen assemblages and reconstructed biomes

The results of the palynological analysis are briefly summarised in Fig. 4a. For convenience, the entire record has been divided into five local pollen zones called PZ-1 to 5.

PZ-1 (135–126 cm, ca. 13.2–12.6 cal. kyr BP) is characterised by low pollen concentrations (ca. 2000 grains/g) and moderately high percentages of *Betula* sect. *Albae* (17–38%) and *Pinus* (3–17%) among tree taxa, *Salix* (up to 8%) among shrubs and Cyperaceae (7–23%), Poaceae (11–23%) and *Artemisia* (5–15%) among herbaceous taxa.

Pollen concentrations remain low (ca. 4000 grains/g) in PZ-2 (126–112 cm, ca. 12.6–11.6 cal. kyr BP). The record demonstrates a marked decrease in the percentage values of birch (down to 9%) and pine (down to 2%) trees, an increase in the share of grasses (32–39%) and other NAP taxa (2%) and a relatively high pollen contribution of *Betula* sect. *Nanae/Fruticosae* and *Salix* shrubs.

PZ-3 (112–94 cm, ca. 11.6–8.9 cal. kyr BP) reveals a marked increase in pollen concentrations (from ca. 30,000 to ca. 243,000 grains/g) and in percentages of *Betula* sect. *Albae* (up to 80%), which dominates the pollen assemblages. *Betula* sect. *Nanae/Fruticosae*, Ericales and *Salix* represent shrubby vegetation, while the contribution of grasses, sedges and other herbaceous taxa vary between 7 and 27%. Terrestrial cryptogam spores are more abundant in this zone, with Polypodiaceae ferns showing a maximum (up to 4%).

PZ-4 (94–51 cm, ca. 8.9–5.9 cal. kyr BP) shows a marked change in the AP composition and a dominance of *Pinus* (up to 68%), while *Betula* sect. *Albae* becomes less abundant (24–41%) and *Picea* pollen appears, although in low numbers and discontinuously. The AP taxa absolutely

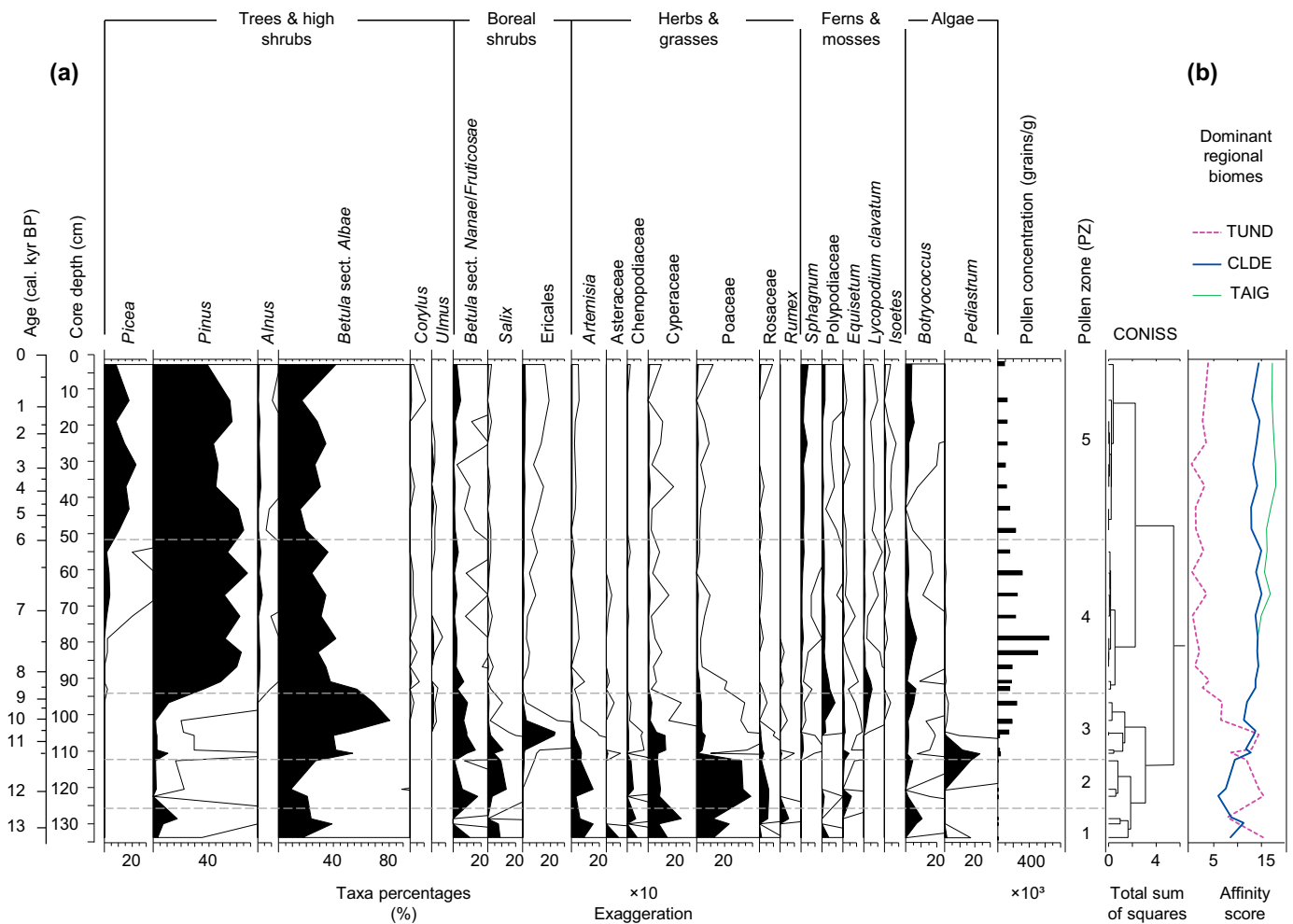


Fig. 4. (a) Percentage diagram of the most abundant arboreal and non-arboreal pollen taxa and representative non-pollen palynomorphs (NPPs) from Lake Kamenistoe along with (b) the pollen-derived affinity scores of the dominant regional biomes (TUND = tundra, CLDE = cold deciduous forest and TAIG = taiga) plotted against the core depth and age axes (this study). Dashed horizontal lines in (a) indicate pollen zone boundaries.

dominate in this zone. Pollen concentrations reach their maximum (ca. 291,000 grains/g on average) in this zone.

PZ-5 (51–0 cm, ca. 5.9 cal. kyr BP to present) demonstrates a marked increase in *Picea* (8–22%), a corresponding decrease in *Pinus* (39–56%) and no major changes in *Betula sect. Albae* (15–41%). *Betula sect. Nanae/Fruticosae* (1–5%), *Ericales* (1–2%) and *Sphagnum* (1–5%) show higher percentages in this zone. The pollen concentration decreases in this zone and averages around 129,000 grains/g.

The pollen-based biome reconstruction (Fig. 4b) suggests a predominantly open landscape during the Lateglacial part of the record (i.e. PZ-1 and PZ-2). A short transitional phase at the beginning of the Holocene interglacial shows very comparable scores of tundra (TUND) and cold deciduous forest (CLDE) biomes. The CLDE biome dominates the entire upper part of PZ-3 and in the lower PZ-4 between 105 and 75 cm (ca. 10.6–7.2 cal. kyr BP) and gives way to taiga (TAIG) after that time.

5. Discussion

5.1. Deglaciation history

Hughes et al. (2016) presented a new time-slice reconstruction of the Eurasian ice sheets (i.e. British-Irish, Svalbard-Barents-Kara Seas and Scandinavian) documenting the spatial evolution of these interconnected large ice masses every 1000 years from 25 to 10 cal. kyr BP. Their time-slice maps of ice-sheet extent are based on a new

Geographical Information System database, which summarises published numerical dates constraining the timing of ice-sheet advance and retreat and, additionally, geomorphological and geological evidence contained within the existing literature. In an attempt to display limitations in knowledge and integrate all uncertainty estimates, the authors provided three ice-margin lines for each time-slice: the most-credible line, derived from the assessment of all available evidence, and the maximum and minimum limits allowed by existing data (Fig. 5a–c). In the Kola Peninsula, this approach, driven by the demands of environmental and climate modelling (Hughes et al., 2016), has an uncertainty of up to 100–150 km (Fig. 5a–c), which cannot be resolved without additional studies.

About 13 cal. kyr BP (Fig. 5a), all three scenarios suggest that the area of Lake Kamenistoe was covered by the Scandinavian Ice Sheet (SIS), the margin of which was located at a distance of 50 to 160 km east of the lake. The data presented in the current study contradict this SIS scenario and suggest lacustrine sedimentation and the presence of sparse tundra vegetation near the lake, while pine and birch pollen could have been introduced from a more southern area. Our interpretation receives strong support from the sedimentary record Co1410 (Fig. 5a) from Lake Imandra (Lenz et al., 2021), ca. 65 km west of Lake Kamenistoe (Fig. 1b), which offers the first continuous and robustly dated record of the Lateglacial and Holocene for this area. According to the chronostratigraphical and pollen data from Co1410, the last ice-sheet coverage of the Imandra basin has to pre-date 13.2 cal. kyr BP (Lenz et al., 2021).

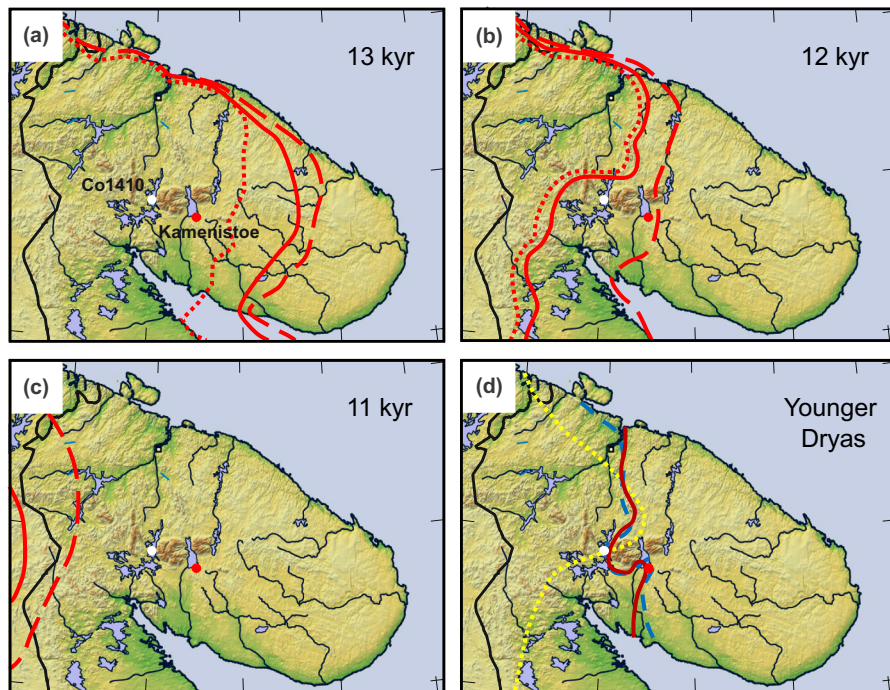


Fig. 5. (a–c) A DATED-1 time-slice reconstruction of the extent of the Scandinavian ice sheet in the study region at (a) 13, (b) 12 and (c) 11 cal. kyr BP (after Hughes et al., 2015). Three lines indicate maximum (red dashed), minimum (red dotted) and most-credible (solid red line) ice extent to represent uncertainty in the data. (d) Reconstructed ice sheet margins during the Younger Dryas interval compiled from Hattestrand et al. (2007) (yellow dotted line), Evzerov (2015) (dashed blue line) and Velichko et al. (2017) (solid brown line). In all maps, the red dot shows the location of Lake Kamenistoe (this study) and the white dot shows the location of the Lateglacial-Holocene Co1410 record from Lake Imandra (Lenz et al., 2021). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

For the 12 cal. kyr BP time-slice (Fig. 5b), which represents the middle of the YD stadial, the Co1410 and Kamenistoe sites appear in the ice-free area suggested by the most-credible scenario. However, both sites remain within the maximum SIS limits shown in Fig. 5b. Expert estimates of the SIS boundaries in the Kola region during the YD (e.g. Fig. 5d) also differ from each other and from the modelled limits shown in Fig. 5b. However, they are consistent in displaying the Lake Kamenistoe and Co1410 records on the ice margin. All previous studies consistently show that most of the Kola Peninsula was ice-free at the beginning of the Holocene interglacial (Fig. 5c).

Thus, the Kamenistoe and Co1410 records indicate the absence of the SIS in the study area since the end of the B-A interstadial. This confirms earlier geomorphological and glaciological evidence from the Khibiny Mountains (e.g. Yevzerov and Nikolaeva, 2008) and allows regional improvement of ice cover reconstructions based on large-scale interpolations (e.g. Fig. 5; Evzerov, 2015; Hattestrand et al., 2007; Velichko et al., 2017).

5.2. Vegetation development

The evolution of vegetation in the European Arctic is one of the most discussed topics in palaeoecological research. However, the absolute majority of lake and peat pollen records from the Kola region published to date (e.g. Korsakova et al., 2021; Kremenetski and Patyk-Kara, 1997; Kremenetski et al., 1999, 2004a, 2004b; MacDonald et al., 2004; Matishov et al., 2005; Snyder et al., 2000; Solovieva et al., 2005) do not cover the entire Holocene (Fig. 6j), while the Lateglacial interval remains poorly explored (Lenz et al., 2021; Seppä et al., 2008; Velichko et al., 2017).

The results of pollen analysis and pollen-based biome reconstruction from Lake Kamenistoe (Fig. 4) provide information on the vegetation development in the study area since the end of the B-A interstadial to the present. The bottommost part of the record is characterised by a high proportion of herbaceous and shrubby taxa in the pollen assemblages. However, tree pollen shows an increase to 46% about 12.8 cal. kyr BP (Fig. 6a), which determines the high scores of the tundra and cold deciduous forest biomes (Fig. 4b) and leads to the reconstruction of a forest-tundra landscape (Fig. 6b). The pollen-based biome

reconstruction from Lake Kamenistoe supports an earlier scenario published by Velichko et al. (2017), who suggested open woodland with birch and pine trees in association with herbaceous and dwarf shrub-moss tundra, grass and halophytic vegetation associations across the ice-free eastern and central parts of the Kola Peninsula. However, the reliability of such vegetation reconstructions can be questioned due to the relatively low pollen concentration, which could indicate pollen transport from outside the study region. Even this cannot be totally excluded, the low pollen concentration may also be associated with some other, intra-regional factors. For example, the modern topography around Kamenistoe (Fig. 1c) suggests a larger area occupied by lakes (and therefore less space for terrestrial vegetation) during the Lateglacial, when this area became free of the ice sheet. On the other hand, minerogenic sediment from high latitude sites with well-developed tundra or forest-tundra vegetation commonly demonstrate much lower pollen concentrations compared to sites with organic gyttja sedimentation located in the taiga zone (Müller et al., 2010). Their analysis shows high pollen percentages for shrubs and dwarf shrubs of birch, willow and heath as well as for sedges and grasses, but very low percentages of arboreal taxa. This is in line with the treeless character of the surrounding vegetation and the present-day vegetation communities of the arctic tundra zone where the surface samples were collected. The pollen concentrations vary from 100 to 1800 grains/g, thus are lower than in the Lateglacial records from the Kamenistoe and Imandra lakes discussed here. Relatively low pollen concentrations (ca. 1900–7200 grains/g) and the predominance of herbaceous taxa (mainly Cyperaceae, Poaceae and *Artemisia*) were recorded in the silty clay deposits from Lake Billyakh in the present-day cold deciduous forest zone of arctic eastern Siberia, which accumulated between ca. 30 and 13 cal. kyr BP when productive herbaceous tundra and cold steppe vegetation covered the area (Tarasov et al., 2021). For comparison, the gyttja unit from the same lake accumulated in the past 500 years is characterised by moderate pollen concentrations (ca. 15,300–50,000 grains/g) and high pollen percentages of boreal shrub and tree taxa (Müller et al., 2010).

The pollen-based reconstruction of tundra, as the dominant biome around Lake Kamenistoe during the YD interval (Fig. 4b) reflects a noticeable decrease in the pollen percentages of birch and pine trees (Fig. 4a). The distribution of herbaceous and dwarf shrub tundra

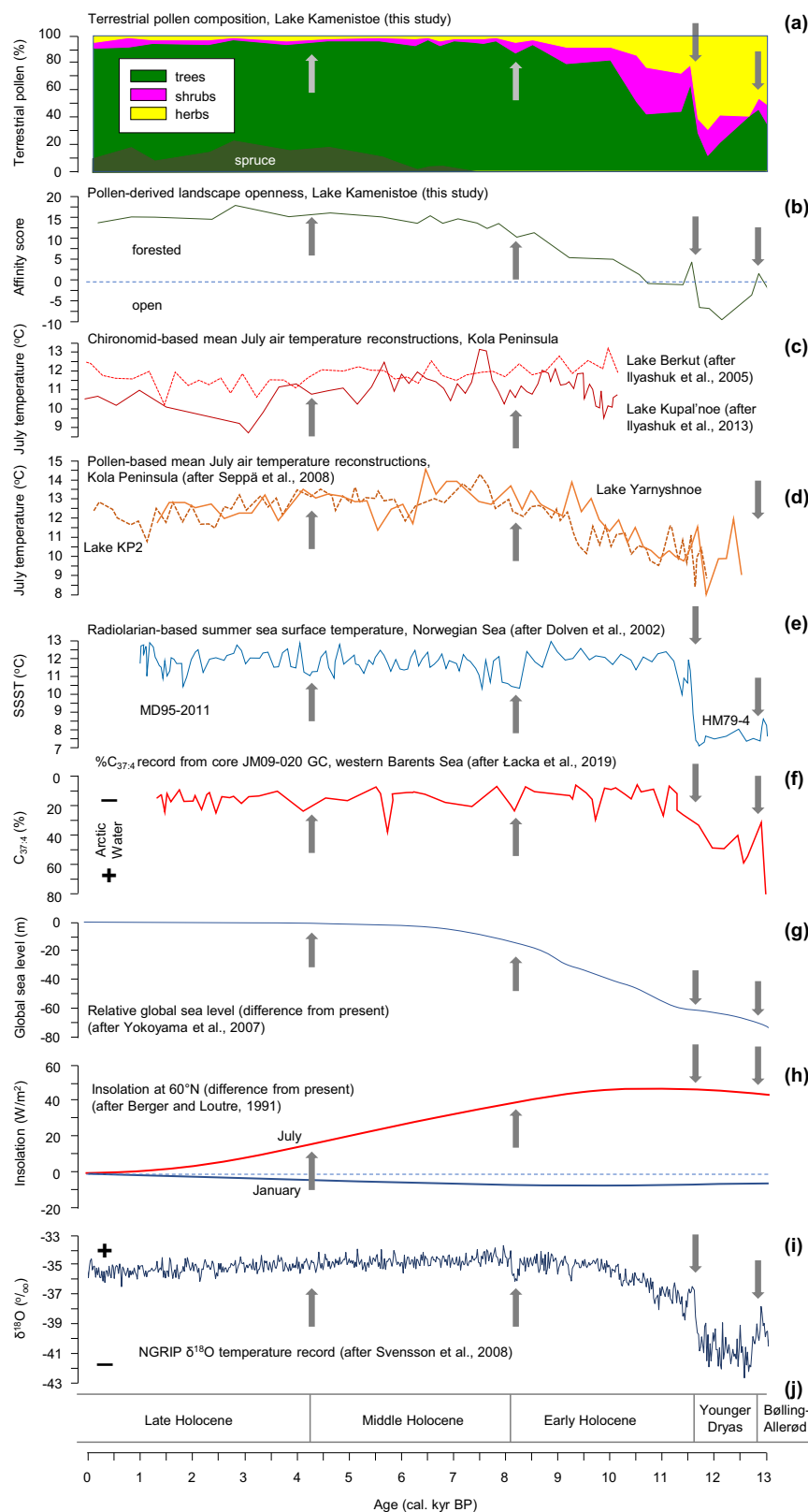


Fig. 6. Summary chart showing selected (a, b) vegetation and (c, d) mean July air temperature records from the Kola Peninsula based on the pollen analysis of Lake Kamenistoe (this study), chironomid analysis of Lake Berkut (Ilyashuk et al., 2005) and Lake Kupal'noe (Ilyashuk et al., 2013), and pollen analysis of Lake Yarnyshnoe and Lake KP2 (Seppä et al., 2008) sediment cores, along with selected records from the North Atlantic region and Northern Hemisphere climate drivers: (e) radiolarian-based summer sea surface temperature (SSST) reconstruction from the Norwegian Sea (after Dolven et al., 2002), (f) %C_{37:4} Arctic Water impact record from the western Barents Sea (after Lacka et al., 2019), (g) relative sea level change (after Yokoyama et al., 2007), (h) computed mean summer (June–August) and winter (December–February) insolation anomalies at 60°N (after Berger and Loutre, 1991) and (i) δ¹⁸O ice core record from Greenland, as indicator of the Northern Hemisphere air temperature (after Svensson et al., 2008). (j) Geochronological units discussed in the text. Light grey arrows indicate the onset of the Late (ca. 4.2 cal. kyr BP), Middle (ca. 8.2 cal. kyr BP) and Early Holocene (ca. 11.7 cal. kyr BP) (Walker et al., 2012), and of the Younger Dryas stadial (ca. 12.8 cal. kyr BP) (e.g. Nakagawa et al., 2021).

communities in ice-free areas of the Kola Peninsula is shown on the palaeovegetation map representing the YD time-slice (Velichko et al., 2017). Based on the sedimentary and pollen records from Lake Imandra, climate cooling and a decrease in precipitation were reconstructed in the YD, which led to the re-advance of mountain glaciation and a decrease in

vegetation cover in the Khibiny region and in different locations along the SIS margin (Lenz et al., 2021 and discussion therein).

With the onset of the Holocene, a noticeable spread of boreal tree (mainly birch) and shrub taxa occurred around Lake Kamenistoe (Fig. 6a), however, the biome scores of tundra and cold deciduous forest

remain very close (Fig. 4b), suggesting a woodland or forest-tundra landscape until ca. 10.5 cal. kyr BP (Fig. 6b). The regional palaeovegetation map presented by Velichko et al. (2017) shows light pine-birch and pine forests in the middle and southern parts of the Kola Peninsula, and woodlands and tundra vegetation common in the north at that time. The number of Holocene pollen records from northeastern Fennoscandia is an order of magnitude higher than that of the Lateglacial, allowing for a better understanding of vegetation dynamics across this large area. The pollen record from Churozero (Fig. 1b; Pavlova et al., 2011) to the east of Lake Kamenistoe indicates the predominance of light forests in combination with shrubby (mainly Ericaceae and *Salix*) and herbaceous associations, while pine trees were clearly underrepresented in the vegetation cover. The Co1410 pollen record (Fig. 1b) also demonstrates the gradual expansion of birch-dominated forests around Lake Imandra in the Early Holocene, although open vegetation still played a significant role, as evidenced by the AP/NAP ratio (Lenz et al., 2021).

The sediment core from Lake Poteryanny Zub (Fig. 1b) situated in birch forest-tundra, south of the Barents Sea coast, provides fossil pollen and stomate evidence for the entire Holocene (Gervais et al., 2002). The Early Holocene record shows a quick replacement of the postglacial herbaceous tundra by birch-dominated woodland with Polypodiaceae ferns and grasses, which is rather similar to the pollen spectra (and vegetation) composition from the more southern sites on the Kola Peninsula (e.g. Korsakova et al., 2021; Lenz et al., 2021; Matishov et al., 2005; Pavlova et al., 2011) including Lake Kamenistoe. Another detailed and well-dated Holocene record from Loitsana Lake at Sokli (Fig. 1b), northern Finland (Salonen et al., 2013), also demonstrates a quick transition from the pollen assemblages dominated by grasses and sedges, suggesting an open vegetation with *Betula nana*, Ericaceae, *Artemisia* and *Rumex*, to the assemblages characterised by pollen of tree birch (over 60%) and spores of ferns and *Equisetum*, indicating the development of birch-dominated northern boreal forest and wetland vegetation in this area after ca. 10.5 cal. kyr BP. The maximal contents of *Betula* sect. *Albae* pollen and fern spores in the Early Holocene pollen spectra of the studied sediment cores suggest a substantially wider distribution of birch trees and fern-dominated local wetlands in northern and northeastern Fennoscandia than today, with the northern boundary of the birch forest zone probably reaching the coasts of the Barents and Norwegian seas (Matishov et al., 2005).

Compared to the distinct similarity of the Early Holocene pollen assemblages (and vegetation composition) in northeastern Fennoscandia, the Middle and Late Holocene records show greater site-to-site variability (e.g. Giesecke and Bennett, 2004; Kremenetski et al., 2004b), which can be explained by local environmental conditions (Salonen et al., 2013), different in soils, micro-climate, topography and the impact of sea currents. This variability is especially pronounced in the spatial-temporal patterns of the Holocene distribution of *P. sylvestris* (Gervais et al., 2002), whose maximum distribution on the Kola Peninsula falls in the Middle Holocene, and *P. abies* (Giesecke and Bennett, 2004), which becomes most abundant in the Late Holocene. In the Lake Kamenistoe record (Fig. 4a), the highest *Pinus* pollen percentage values are recorded between 8.2 and 4.2 cal. kyr BP and *Picea* pollen peak about 3 cal. kyr BP. The presence of fossil pollen, stomata and wood of *P. sylvestris* in the record from Lake Poteryanny Zub (Gervais et al., 2002) indicates that pine appeared near this site as early as 9.3–9 cal. kyr BP. The record from Loitsana Lake in northern Finland (Salonen et al., 2013) shows a rapid increase in *Pinus* pollen from ca. 10% at 9.3 cal. kyr BP to ca. 60% at 8.6 cal. kyr BP. A similar trend can be seen in the pollen diagram from Lake Kamenistoe (Fig. 4a), while the pollen record from Lake Imandra (Lenz et al., 2021) shows that a similar increase in pine percentages started even earlier, i.e. ca. 10.5–10 cal. kyr BP.

These results confirm an earlier conclusion about the rapid spread of pine forests in northeastern Fennoscandia in the Middle Holocene (Gervais et al., 2002), however, they are not entirely consistent with the assumption that this was the result of a frontal spread from the more

southern regions of Karelia after 10.3 cal. kyr BP (Matishov et al., 2005). The available data rather indicate that the noticeable spread of pine forests in the Kola region began with scattered small populations of pine that already existed there in the Early Holocene. Such scenario has been suggested to explain the quick afforestation of large regions of Siberia and Beringia (i.e. the modern taiga zone) during the Lateglacial (Brubaker et al., 2005; Müller et al., 2010; Petit et al., 2008; Tarasov et al., 2021) and may better explain the almost simultaneous appearance of pine in the northern and southern parts of the study region. Similarly, small outposts of Early Holocene spruce were confirmed by macrofossil finds from the Swedish Scandes (e.g. Kullman, 2001), challenging the traditional interpretation of *Picea* distribution and predating the main ESE to WNW spread of spruce forests in Fennoscandia during the Middle and Late Holocene (Giesecke and Bennett, 2004).

5.3. Sensitivity to regional and extra-regional climate changes

In recent decades, terrestrial sedimentary archives from northern and northeastern Fennoscandia have been widely used to reconstruct postglacial climate dynamics. Pollen (e.g. Hammarlund et al., 2002; Kremenetski et al., 2004a, 2004b; Seppä and Birks, 2001; Seppä, 2002; Seppä et al., 2008; Solovieva et al., 2005) is by far the most frequently used proxy for qualitative and quantitative reconstructions of temperature and precipitation, followed by chironomids (e.g. Heinrichs et al., 2006; Ilyashuk et al., 2005, 2013), diatoms (e.g. Bigler et al., 2006; Davydova and Servant-Vildary, 1996) and diatom-based isotopes (e.g. Jones et al., 2004; Rosqvist et al., 2004; Solovieva and Jones, 2002).

Despite the relatively large number of published palaeoclimatic records, the main problem remains the high variability of reconstructed trends and absolute values (Fig. 6c–d), which challenges comparisons between individual sites and proxies and calls into question climatic sensitivity of different proxies and the reliability of the quantitative reconstructions. This problem is illustrated by the July air temperatures reconstructed for the Kola Peninsula from chironomid (Fig. 6c) and pollen records (Fig. 6d). The observed spatial and temporal variability may reflect the strong influence of local and regional settings, response time and sensitivity of different proxies to a given climate variable, but also chronological issues and problems with the reference modern proxy-climate datasets used for calibration. However, pollen records and pollen-based biome reconstructions seem to be less sensitive to local factors than chironomid and diatom assemblages from the lakes of the region. Thus, the Lateglacial and Holocene trends in the pollen composition (Fig. 6a) and landscape openness (Fig. 6b) at Lake Kamenistoe are comparable with the reconstructed July temperature trends for two lakes in the northern Kola Peninsula (Fig. 6d), but are even more consistent with records representing supra-regional climatic drivers (Fig. 6e–i) such as long-term changes in solar insolation at high latitudes (Berger and Loutre, 1991) and global sea level/ice volume (Yokoyama et al., 2007) transmitted to shorter-term Arctic sea water (Dolven et al., 2002; Lacka et al., 2019) and air (Svensson et al., 2008) temperature variability recorded in ice and ocean sediment.

The temperature reconstructions obtained using a transfer function technique based on a combined Norwegian–Finnish–Swedish pollen-climate calibration set (Fig. 6d; Seppä et al., 2008) agree with the estimation of the approximate 2 °C higher than present regional summer temperatures, which would be necessary to stimulate the regional expansion of boreal forests and move the pine treeline to the coast of the Barents Sea in the Middle Holocene (Gervais et al., 2002). New high-resolution regional climate model simulations using a pollen-based land-cover reconstruction (Strandberg et al., 2022) also suggest that the 6 cal. kyr BP climate in northeastern Europe was warmer than in pre-industrial times, with the largest differences (ca. 4–6 °C) in winter and less pronounced differences in summer (i.e. 1–3 °C). The simulated Middle Holocene winter in Scandinavia was ca. 10–25% wetter than in preindustrial times, which implies enhanced cyclone activity (Strandberg et al., 2022). The simulated onset of wetter climate conditions in

the Kola Peninsula corroborates the increase in *Picea* percentages in the pollen record from Lake Kamenistoe (Fig. 6a) and explains the strengthening of the taiga biome (Prentice et al., 1996) in the region after ca. 6 cal. kyr BP. This process was further accelerated by the Late Holocene climate cooling seen in the pollen-based temperature reconstructions from the Kola Peninsula (Fig. 6d) and in the oxygen isotope temperature record from Greenland ice (Fig. 6i), in line with the gradually decreasing summer insolation at 60°N (Fig. 6h).

5.4. Human habitation and palaeoenvironments

Human colonisation of the Arctic and the interaction between early human migrations and palaeoenvironments (e.g. Kotlyakov et al., 2017; Pitul'ko, 1999 and references therein) are of great scientific and public interest, although the search for clear answers to the fundamental questions of how and why people colonised the circumpolar regions and why only one representative of the genus *Homo* successfully occupied this most hostile zone of the world (Hoffecker, 2019) is still in progress. The timing of the initial settlement of the Kola Peninsula by Mesolithic groups of hunter-gatherers remains understudied, mainly due to the lack of reliably dated archaeological sites and the often poor preservation of sites and materials. Shumkin (2017) provides a map showing locations of 70 archaeological sites typologically attributed to the Mesolithic period (roughly covering the Early and the first half of the Middle Holocene). All sites, with a few exceptions, are located on the coast, which indicates the importance of marine resources to subsistence. A total of 15 Early Mesolithic sites and most of the Middle Mesolithic sites are located in the northwesternmost part of the Kola region, near the state border with Norway. Late Mesolithic sites are more numerous and distributed along the coasts of the Barents and White seas, although some sites are found further inland (e.g. north of Lake Umbozero) in association with lake and river terraces, suggesting broadening of the subsistence strategy during the Middle Holocene (Shumkin, 2017).

To date, 28 dwellings from the Neolithic–Bronze Age on the Kola Peninsula were excavated, including a dwelling of the Gressbakken type at Kharlovka 1–6 (Fig. 1b) that was studied most recently and dated to ca. 4550–4250 cal. yr BP (Kolpakov et al., 2021). Excavations of this coastal site demonstrated very good preservation of organic matter and a large number of faunal remains, allowing reconstruction of the subsistence strategy of the local population at the end of the Middle Holocene. The faunal complex of Kharlovka 1–6 is rich and bears a strong resemblance to the modern fauna of the region. It is dominated by bones of marine mammals (harp seals and walrus) and seabirds, which, together with fishing and hunting tools (harpoon and leister heads), clearly indicate marine adaptation. However, the bones of tundra and forest birds and mammals (e.g. wild reindeer, fox, elk, hare, beaver, lemmings) suggest that terrestrial hunting and gathering was also practiced (Kolpakov et al., 2021). We are not aware of any zooarchaeological records of similar quality from the Kola Peninsula dated to the Mesolithic, but evidence from other regions of northern Europe (e.g. Pitul'ko, 1999; Schulting et al., 2022) suggests that elk and reindeer were more important in the subsistence economy of hunter-gatherers at that time, supplemented by fishing, hunting for other mammals and birds, and gathering.

Archaeological research and radiocarbon dating carried out in the northern part of Finnish Lapland, at the Sujala site, suggests that it was occupied about 10.2 cal. kyr BP (Rankama and Kankaanpää, 2011). This inland site at Lake Vetsijärvi, in a tundra region characterised by cold winter temperatures, low atmospheric precipitation and extremely thin snow cover, is the first robustly dated evidence of Mesolithic pioneers in northeastern Fennoscandia. Another site, Fállegoahtesajeguolbba, presumably of the same age, was discovered in the Varangerfjord area on the Barents Sea coast ca. 60 km northeast of Sujala. The characteristic stone assemblages of both sites provide strong evidence of people arriving from the Post-Swiderian cultural sphere about 1000 km to the southeast into northernmost Lapland during the Early Holocene (ca.

10.5–10.2 cal. kyr BP) and indicate the adaptation of inland hunter-gatherers to the maritime environment (Rankama and Kankaanpää, 2011). The climate-sensitive pollen/vegetation records of Lake Kamenistoe and the regional temperature records (Fig. 6) indicate that this migration occurred during a sustained phase of climate warming and a significant spread of forest vegetation. These significant climatic and environmental changes affected the entire continent and led to the extinction of typical glacial species, such as reindeer (one of the main game animals), in the more southern regions of Europe (Drucker et al., 2011). However, this process could have taken longer, as evidenced by a direct date of a reindeer bone from the Mesolithic site of Rottenburg-Siebenlinden (Southwest Germany), which confirms the survival of this species in the Early Holocene, i.e. until 10,500–10,270 cal. yr BP (Drucker et al., 2011). The Early Holocene ages of the reindeer bones (as young as ca. 10,400 cal. yr BP) from northern Europe are reported by Aaris-Sørensen et al. (2007). These authors also related the major changes in the reindeer distribution area with the postglacial climate warming and associated changes in vegetation, arguing that modern reindeer normally stays north of the 12–13 °C July isotherm and experiences heat stress at temperatures above 15 °C. According to the proxy-based climate reconstructions, northern Scandinavia (Fig. 6c–d and Seppä et al., 2008) remained comfortable for reindeer populations during the entire Holocene, while close-to-stress temperatures were reached in southern Scandinavia (Aaris-Sørensen et al., 2007) and in the Baltic-Belarus area (Veski et al., 2015) at ca. 10.5 to 10 cal. kyr BP.

The generally low occupation of the Kola Peninsula during pre-industrial times and the absence of archaeological sites in the vicinity of Lake Kamenistoe suggest that the pollen record presented here was not affected by human activities and can be securely used as an archive for reconstructing natural vegetation and climate dynamics in the study area.

6. Conclusions

Examination of archaeological data and historic documents about human occupation on the Kola Peninsula suggests that the present pollen record has not been impacted by human activities and thus represents an archive of natural vegetation and climate change in the study region over the last ca. 13,000 years. Since well-dated palaeoenvironmental records from the peninsula covering the entire post-glacial interval are still rare, the sedimentary archive from Lake Kamenistoe proves valuable. Together with the core lithology, the pollen record allows a partial revision and refinement of existing deglaciation scenarios.

The biome reconstruction suggests that Kamenistoe was surrounded by forest-tundra at the end of the B-A interstadial. Comparing these results with other published vegetation records from the Eurasian boreal forest zone, we conclude that the reconstructed local growth of trees and shrubs is real and not an artefact of long-distance pollen transport. We argue that the Lateglacial spread of arboreal taxa as well as the spread of pine and spruce in the Holocene did not follow a zonal expansion, but rather originated from small pioneer populations scattered within the study region.

The current pollen record and existing pollen-based temperature reconstructions indicate that the arrival and spread of hunter-gatherers in the study region, which probably occurred in the mid-Early Holocene, is more or less synchronous with the expansion of boreal forests and continuous warming. We hypothesise that this initial human colonisation was facilitated not only by improving climatic conditions, but also by the northward migration of reindeer in response to rising summer temperatures.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

Data availability

Data will be made available on request.

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