

The Circumboreal Tundra-Taiga Interface: Late Pleistocene and Holocene Changes

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Creating a global perspective on past treeline changes is problematic due to the varying methods and definitions used. A general lack of a detailed description of the modern treeline position and vegetation complicates any comparative analysis of the magnitude of the most important changes. However, one seemingly common factor in most regions was an extremely rapid dispersal of trees when climate warmed drastically from full glacial conditions. Most Arctic treelines reached their northernmost positions in the early Holocene and receded to present positions starting at about 5.8 ka. The early occupation of the northernmost sites in ice-free and early deglaciated areas was possible because of the close proximity of invading trees in nearby glacial refugia, particularly in Fennoscandia and northern Russia. In Canada, the Northwest Territories and Quebec-Labrador were out of phase with this general trend due to their late deglaciation. However, even here colonization was rapid, indicating that the tree species were present adjacent to the glaciers. Following this trend and based on the present evidence, we propose a scenario of a continuous but modest occupation of eastern Beringia by spruce during the late-Pleistocene instead of an exceptionally rapid spread of conifers from the glacial refugium south of the Laurentide ice sheet (2000 to 3000 km in about 200 years), which typically has been assumed. Macrofossil evidence of scattered occurrences of "exotic species" (for instance Siberian larch in central Sweden) far from their natural range limits in the early Holocene highlight the disparity between pollen and macrofossil analyses. It questions the validity of assigned pollen percentages to indicate the presence of a species within a region as these species were not observed in the pollen record. Thus, it is likely that trees were present at any given site well before the rise in pollen abundance. There is still a large potential to improve our knowledge about the environmental history of the circumboreal treeline areas. In particular, future research should concentrate not only on patterns of species displacement, but on finding the factors, apart from climate, which cause treeline shifts.

INTRODUCTION

The tundra-taiga interface, or forest-tundra (*lesotundra* in Russian, and *tundra forestière* in French), corresponds to the subarctic zone where the closed boreal forest gradually becomes less dense and progressively breaks down into tree islands towards the treeless, Arctic tundra (1). The interface does not form a sharp limit of tree growth in the landscape but is instead a north-south transition zone, which often can extend several hundred kilometers from the continuous forest limit, particularly in Canada and Russia (2–6). The northernmost part of the tundra-taiga interface coincides with the Arctic treeline, which is controlled by cold temperatures, precipitation deficits, strong winter winds, lack of snow protection, as well as past and present influence of human activity particularly in Fennoscandia and Russia. Indeed, the total number of climatic and other forcing factors restricting tree growth and regeneration in the forest-tundra is large and regionally variable (5, 6).

The terminology referring to the tundra-taiga ecotone is relatively well established (7, 8) with forest limit and Arctic treeline as the most important boundaries. The treeline, with trees having a minimum height of 2.5 m, forms the northernmost limit of tree growth. The forest limit corresponds to the northernmost forest, i.e., a stand of several tens of trees with most stems developing vertically (1, 5, 6, 8). The tree species limit extends north of the Arctic treeline in tree species able to grow as shrubs in the circumpolar tundra.

The overall latitudinal temperature gradient change is rather minor when one moves north in flat areas, whereas the change is stronger with elevation. As a result, the vegetation belts in mountainous areas are often sharper and narrower than in lowlands. Treeline changes of the northern edge of the forest-tundra are referred to as Arctic treeline shifts while those within the forest-tundra are called subarctic treeline shifts (1). In contrast to alpine treelines, subarctic treelines are not necessarily controlled by elevation, but instead describe the boundary between tree and treeless communities on well-drained flat and rolling terrain. Therefore, the changing position of subarctic treelines denotes a change in abundance of forest-tundra trees, whereas a changing position of the Arctic treeline corresponds to the latitudinal displacement of the forest-tundra boundary. A southward shift of the boundary indicates death of trees in the northernmost tree outposts. A retreat of the subarctic treeline is due to trees being unable to regenerate at a site and indicates a decreasing abundance of forest-tundra trees.

The tundra-taiga across the circumboreal zone is inhabited by several tree species that experienced major geographical shifts caused by interrelated forcing factors since the last glacial maximum at 20 ka (thousands of years ago, i.e., cal. years BP) (9). The reconstruction of past and recent positions of the Arctic treeline has been a much debated topic during the last three decades. The topic is important for its relevance in the study of the projected magnitude of environmental changes associated with greenhouse warming. In this paper, we review the evidence of treeline dynamics across the circumboreal zone, from the last glacial maximum (i.e. Wisconsinan in North America and Weichselian in Eurasia) to present, and comment on the likely causal factors.

METHODOLOGIES USED IN DETERMINING PAST TREELINES

Establishment dates, rates of migration of forest trees and treeline shifts since the glacial maximum have generally been inferred from indirect pollen evidence, although the use of macrofossil remains is now increasing (10–17). Pollen analysis has been instrumental in describing the broad picture of vegetational changes from the Pleistocene to the Holocene across the Northern Hemisphere, especially the composition of the forest (see among others 18–21). However, pollen data alone are generally insufficient to evaluate when a tree species established at a site and to calculate the magnitude of treeline displacements as the initial small population size and the various ecological constraints experienced by struggling trees may limit the pollen content of lacustrine and terrestrial sediments below the limit of detection.

The analysis of securely identified and radiocarbon-dated tree

macrofossils is by far the best option for the reconstruction of past tree locations in the forest-tundra and Arctic tundra. As these macrofossils are seldom abundant enough for a complete accounting of the biotic changes, we have used both macrofossil and pollen data in this paper to review the evidence of boreal tree spread and treeline shifts since the Late Pleistocene.

The initial establishment, direction, and rates of migration of the dominant boreal tree species from their glacial refugia to modern locations were evaluated in light of the most recent reports based on fossil remains. For North America, we have used securely dated macrofossil evidence available from a compilation of publications including those cited by Ritchie (20, 21), Payette (22), and Jackson et al. (23).

For a given species, the oldest radiocarbon-dated macro-remain found south of the maximum extent of the Laurentian ice sheet was used as the starting point for postglacial recovery and the oldest radiocarbon-dated macro-remain in the northernmost site was used as the realized destination during the Holocene. The rate of spread of the species was calculated from different starting points in order to evaluate the likely routes of migration based on the ecological traits of each species. Deglaciation maps of Dyke and Prest (24) were used as boundary conditions during particular time slices from the glacial maximum to present.

No such rates were calculated for the Eurasian trees as recent macrofossil results indicate that the dominant species were already present at their northern locations in Late Pleistocene and early Holocene times (17, 25).

TREELINE CHANGES IN EURASIA

Late Weichselian Glacial Maximum

The geographical extent of the Eurasian ice has been a matter of debate until recently, with one hypothesis of Maximum Glacial Ice, i.e. a panarctic ice sheet covering the whole Arctic shelf in Eurasia and including central Siberia (26, 27) and a second hypothesis of Minimum Glacial Ice, i.e. a Eurasian ice sheet welding together the ice sheets of Scandinavia, the Kara Sea, and the Barents Sea (28–30). The Minimum Glacial Ice hypothesis, based on mounting evidence of radiocarbon-dated organic sediments and tree macro-remains dating back to the full-glacial period, indicates that much of the Russian Arctic remained ice-free and partly forested (Fig. 1), particularly east of the Kola Peninsula towards Siberia (including the Yamal and Taymyr peninsulas). When the Eurasian ice sheet started to melt, intricate vegetation assemblages, including tundra, steppe, and forest communities, were located near the ice border, particularly south of the ice and eastward into Siberia (31). As a result, several tree

species (Fig. 2) were ready to invade newly deglaciated and ice-free sites as soon as 15–13 ka in Siberia (32), and 13.1 ka in central Sweden (33).

The Early Holocene Afforestation of Fennoscandia

According to the traditional view based on pollen analyses, forest expansion in northern Europe began in the early Holocene when abrupt warming ended the Weichselian Ice Age. The abrupt warming ca. 11.5 ka resulted in rapid melting of the Scandinavian ice sheet and several forest trees rapidly colonized newly deglaciated areas. The earliest forest vegetation in northern Fennoscandia at 10 ka consisted of birch (*Betula pubescens* Ehrh.) woodlands. Scots pine (*Pinus sylvestris* L.) forests were growing in northern Finnish Lapland by 9.5–9 ka. Norway spruce (*Picea abies* (L.) Karst) only arrived at its present limit in Lapland at 3–2.5 ka according to pollen evidence (19, 34–37). The time-transgressive change in the vegetation cover and the arrival of the forest trees to the north do not indicate the formation of stable vegetation zones in the early Holocene. For example, pine spread to the Abisko area in northernmost Sweden only a little before 6.5 ka with the marginal stands perishing by 3.5 ka (38, 39). The maximum spread of pine in Finnish Lapland occurred between 7 ka and 4.5 ka (34–37, 40, 41).

Macrofossil data on the slopes of the Swedish Scandes Mountains (25, 42–45) challenge the traditional view of early Holocene vegetation based on pollen analyses (19). Macro-remains of Siberian larch (*Larix sibirica* Lebed.), which are often underrepresented in the pollen record, were found at two sites in the Scandes, and dated ca. 9.5–8.5 ka. This taiga tree spread early in the Holocene, but for some reason could not survive and disappeared from Fennoscandia entirely before the maximum spread of Scots pine. Spruce was already present in the Scandes in the late Pleistocene and throughout the Holocene (33). Further findings in the northern Scandes indicate that pines were growing at sites 500 m above the present pine-tree limit even as early as 10 ka (45).

Many thermophilous tree species also grew at altitudes in the early Holocene that presently are occupied by alpine communities and subalpine birch woodlands. Macrofossil data include lime (*Tilia cordata* Mill.), oak (*Quercus robur* L.) and hazel (*Corylus avellana* L.) amongst common boreal forest species like pine, birch, and grey alder (*Alnus incana* L.) (25). The coexistence of trees, which today do not grow in the same habitats and areas, indicates that the current forest line and treeline areas are not good analogues to those of the early Holocene.

Treeline Changes in Fennoscandia

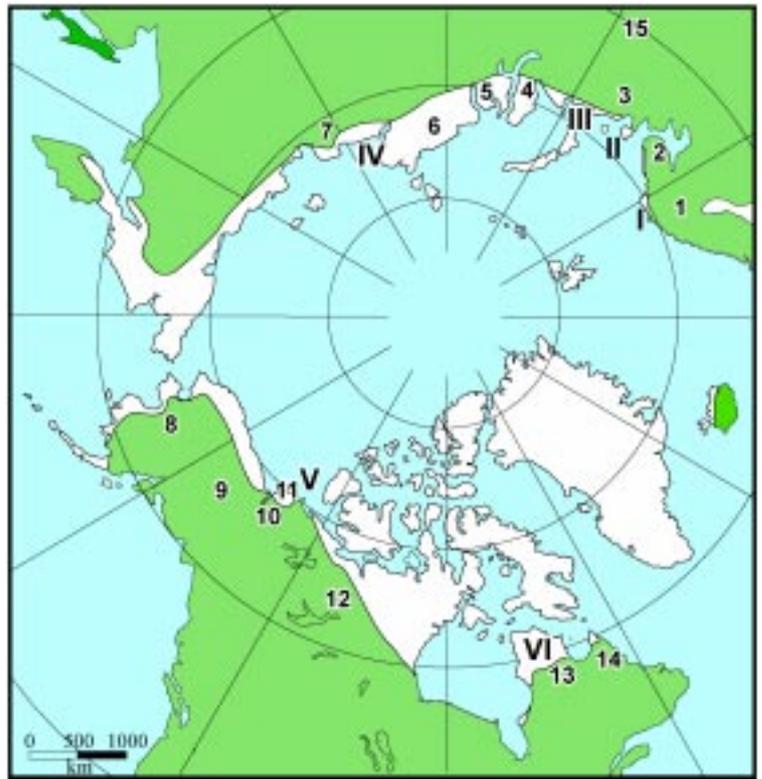
The reconstruction of postglacial tree-limit changes have focussed primarily on Scots pine, which forms the coniferous

Figure 1.
The Eurasian ice sheet during the Glacial Maximum (Minimal Glacial Ice Hypothesis).
1. Taymyr Peninsula,
2. Gydan Peninsula,
3. Yamal Peninsula.



Figure 2.
Dominant tree species across the circum-Arctic treeline:
 I. *Betula pubescens*, *Pinus sylvestris*, *Picea abies*.
 II. *Picea obovata*.
 III. *Larix sibirica*.
 IV. *Larix dahurica*.
 V. *Picea glauca*, *Picea mariana*.
 VI. *Picea mariana*, *Larix laricina*.

- Place Names:**
 1. Fennoscandia.
 2. Kola Peninsula.
 3. Pechora Lowlands.
 4. Yamal Peninsula.
 5. Gydan Peninsula.
 6. Taymir Peninsula.
 7. Lena River.
 8. Alaska.
 9. Yukon.
 10. Mackenzie Delta.
 11. Tuktoyaktuk Peninsula.
 12. Northwest Territories.
 13. Quebec.
 14. Labrador.
 15. Ural Mountains.



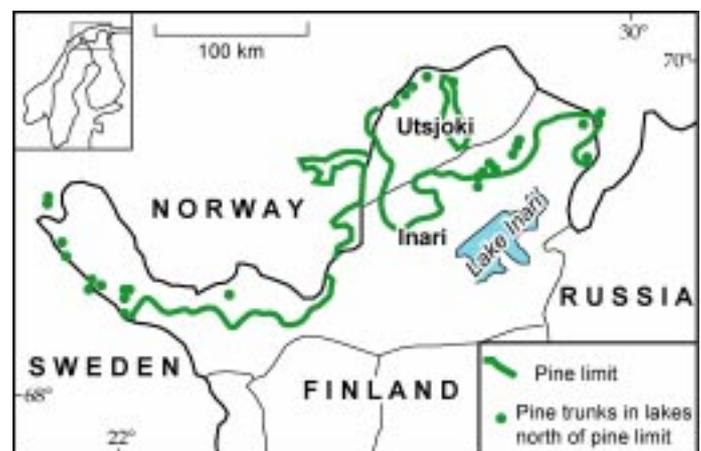
treeline in large areas in the Scandinavian mountains and northern Finnish Lapland. Dendrochronological studies on subfossil pines found in lakes in northern Finland and Sweden have provided substantial information about its former spread (40). Subfossil wood of birch and grey alder, while less common than pine, have also been found preserved above their present treelines in peat, mud, and lake sediments of the Scandes Mountains (16, 44). Birch colonized the mountain slopes rapidly after the regional deglaciation (ca. 9.7 ka), but it was less abundant in the following two millennia. No discrete subalpine birch belt existed in the Swedish Scandes in the early Holocene, but instead gradually developed later with increasing abundance and persistence of snow. The elevation of this belt varies with an upper limit reaching more than 900 m a.s.l. with an average vertical width of 100–150 m on mountain slopes. The early birch belts were formed by a species of the *Betula pubescens* complex other than mountain birch (*Betula pubescens* ssp. *czerepanovii* [Orlova] Hämet-Ahti; *Betula tortuosa* Ledeb.) as this tree was absent in the early Holocene. In addition to birch, grey alder was also present with a marked expansion at ca. 8.5 ka (46, 47).

About 10 ka ago, pine trees were growing at much higher altitudes than today due to the dry continental climate and stronger summer solar insolation that was favorable to pine growth, with the highest occurrences being found about 500 m above the present upper pine limit (45). Since then the lowering of the pine-tree limit in the Scandes Mountains has proceeded almost constantly (although some views are contradictory to this) (48, 49). Towards the present time, the strong seasonality with warm summers and cold winters decreased and a more oceanic climatic regime became prevalent. This change contributed to the development of the subalpine birch belt above the pine limit. While there have been several climatic fluctuations, the long-term trend during the past 6000 years has been cooling, which has caused lowering of the pine-tree limit and birch belt together with various changes in treeline habitats. The Little Ice Age ca. 1550–1850 A.D. was probably the coldest period since the most favorable Holocene climatic period around 6 ka, and caused severe dieback in timberline forests (50). The recent warming, which started in the late 19th century, seems to lead to a pro-

nounced rise in the subarctic treelines on the mountain slopes (51) and probably also to an expansion of the Arctic treelines in areas of smooth topography.

Because the topography is gentle in Finnish Lapland, it is difficult to depict past changes in the subarctic treeline. In contrast, the history of the pine-tree limit is well understood due to a 7500-yr long dendrochronological master curve made up of over 2000 subfossil pine samples (52). Many of the subfossil trunks were obtained beyond the present pine-tree limit (Fig. 3). The dates show that the maximum occurrence of pine was around 7–4.5 ka. The combination of ecological factors which favored pine growth in northern Finnish Lapland during the middle Holocene is not yet known. One hypothesis is that pine immigrated to northern Finland later than in the Swedish Scandes. While the pine tree-ring curve extends to 7520 cal. years, pollen data show that pine was present in Finnish Lapland 10.1–9.5 ka ago, indicating that earlier pine trunks were not preserved (36) or have not yet been found.

Figure 3. Past and present distribution of the pine limit in northernmost Finland.



The highest occurrence of subfossil pines are found in north-west Finland in Enontekiö. They are located at 500–560 m a.s.l. and reached their maximum elevation at 5.6 ka. The nearest pine forest is situated 60–70 km southwest at ca. 400 m. This suggests an over 1°C cooling in summer temperatures (11, 40). Kullman (53) estimated tentatively that in the northern Swedish Scandes the summer temperature decrease has been ca. 2.4°C since 9.6–9 ka.

Treeline Changes in Russia

Within the extremely long Arctic treeline zone of northern Russia there are several different treeline tree species with a variety of ecological demands. East of Fennoscandia, spruce (*Picea obovata* Lebed.) replaces mountain birch as the dominant treeline species. At the polar Ural Mountains, Siberian larch is the uppermost tree species. At a relatively short distance east of the Ural Mountains, *Larix gmelini* Rupr (syn. *Larix dahurica* Trautv.) replaces Siberian larch and extends over Siberia until the Russian Far East.

Recent studies are shedding new light on the Holocene development of treelines in the northern part of European Russia, particularly those of Kremenetski and colleagues (17, 54, 55), which are based on radiocarbon-dated tree macrofossils. During the early Holocene, a sustained northward movement of the *Picea* and *Betula* treeline has been recorded (17). During the glacial maximum, spruce persisted in refugia in the southern part of the Ural Mountains. Radiocarbon dated macrofossils showed that *Picea* grew in the Ural Mountains east of the Pechora River soon after 11.5 ka and reached the shores of the Barents Sea in the Bolshezemskaya tundra area by 9.5 ka. Summers were 4°C warmer than present (17).

Scattered sites of *Larix* and birch were apparently numerous during the glacial maximum and persisted across their modern ranges. This explains their quick spread at the end of the glacial maximum. Larch forests grew over much of Siberia, for instance on the shores of Taymyr Lake (74°32'N) at 6.9 ka and 74°20'N at 13.1–11.5 ka, corresponding to summer temperatures 4°C warmer than present. According to dated macro-remains, the northern limit of *Larix* was located more than 500 km north of the modern treeline prior to 4–3.5 ka in the southern parts of the Yamal and Taymyr peninsulas (inferred from Figs 5 and 7 in (17)). Larch retreated to its present position stepwise, but the exact magnitude and causes of the displacements are not known. The *Larix* macrofossils analyzed in these studies were not identified to the species level due to complications arising from their overlapping ranges. In the Yamal Peninsula, birch was present up to 70°N at 9.5–8.9 ka, and reached its present treeline position by 4.5 ka in most parts of northern Russia (17). At the Pleistocene-Holocene transition birch trees were growing north of 70°N near the coast of the Laptev Sea, which corresponded to the northernmost shift of the species across the Russian Arctic, that is, 400–500 km north of the modern treeline position (inferred from Fig. 9 in (17)).

Several other studies are complementing the rich findings of Kremenetski et al. (17). MacDonald et al. (56) added 57 radiocarbon-dated tree macrofossils to the impressive 249 radiocarbon-dated macrofossils provided by Kremenetski et al. (17). These new dates fall within the global scheme already developed by the Russian team. Siberian larch wood dated 17.9 ka indicates that trees were growing in the Gydan Peninsula (between Yamal and Taymyr peninsulas) during the Late Glacial, suggesting warm conditions for tree growth at that time (57). Further west on the Kola Peninsula, Scots pine was growing about 20 km north of the “mapped” present limit of the species between 7.6 and 4.3 ka, and also about 40 m above present treeline from 6.7 to 3.8 ka (58). In the same area, in the Khibiny Mountains region, 49 radiocarbon-dated wood remains of Scots pine found 100–140 m above the modern treeline indicate bet-

ter growth conditions at 1–1.3 ka (55). A climate at least 0.8°C warmer than present was inferred from an assumed lapse rate of 0.6°C per 100 m.

Most peatland initiation in northern Russia occurred at the Pleistocene-Holocene transition, probably due to wetter and warmer conditions (14). Pollen and stomate analyses of a radiocarbon-dated peat section in Ortino, in the Pechora lowlands of northernmost European Russia, allowed the reconstruction of the vegetation over the last 10 ka (59). The presence of stomates, which are the lignified remains of the gas-exchange cells of a leaf, usually indicate the local presence of a species whereas pollen can come from a greater distance. The combined pollen and stomate evidence suggest that *Picea obovata*, accompanied by *Betula* spp., spread to Ortino soon after 11 ka, with forest vegetation reaching its maximum density 6.3 to 3.2 ka. The treeline began to recede rapidly before 3.2 ka, likely as a result of significant cooling. During the last few millennia, the treeline moved about 70 km to the south, from Ortino to Nar'yan-Mar, where the northernmost forest-tundra tree stands are located today. There are some new macrofossil data from the Pechora delta area that suggest that the cooling trend began around 5 ka (A. Kaakinen, pers. comm.). This trend was probably overshadowed by an effect of local (hydrological) conditions in the pollen flora at Ortino.

A similar history was observed in the pollen and macrofossils of 2 other sites in the Pechora lowlands (Warner, Jasinski, and Andreev; unpubl. data). These researchers suggest that increased paludification, possibly caused by changes in the hydrological regime due to spreading permafrost, was not conducive to the regeneration of *Picea obovata* and resulted in a treeline retreat starting at around 5.1 ka. The lack of charcoal at all 4 sites in the region suggests that fire was not a factor in the retreat. However, fire likely played a role in tree abundance in other regions of Russia as suggested by charcoal found in a peatland located in the Lena River valley (60).

One important aspect of treeline dynamics is related to subarctic treeline changes, that is, changes in treeline position within the forest-tundra. In the Yamal Peninsula and further east towards the Lena River, forest trees are located mostly in the lower reaches of rivers. The upper and middle reaches of these rivers are presently treeless indicating a lowering of the subarctic treeline. Since the mid-Holocene, trees were generally excluded from the upper reaches of rivers in the Yamal Peninsula (61). A similar pattern was described for the lower Lena River where larch (*Larix dahurica*) macrofossils indicate the former presence of stands on the now treeless uplands (62). Several upland tree stumps were successfully cross-dated with extant larch trees in the valley. The uplands were forested prior to 1450 A.D., with tree death occurring between 1790 and 1900 A.D., presumably caused by a long-term decrease in temperature. Because the age of all dead trees varied largely, tree death was not associated with senescence, but to complex ecosystem factors acting in a domino-effect fashion caused by the gradual opening of the stands.

TREELINE CHANGES IN NORTH AMERICA

Late Wisconsin Glacial Maximum

The maximum extent of the Laurentide ice sheet covered most of Canada, a small part of the northern United States, and southern Alaska (24) (Fig. 4). During the late Wisconsinan full-glacial, a large refugium extended south and east of the Laurentide ice sheet, including the geographical connection of ice-free Siberia with eastern Beringia. The latter consisted of a large part of central Alaska, the Yukon, and possibly a small area of the Tuktoyaktuk Peninsula (63). The pattern of postglacial recovery in North America differed somewhat from that of Eurasia

because most forest trees spread towards northern areas from a large southern refugium. A much debated question still unsettled today is the role played by eastern Beringia, the northern refugium that was totally isolated by inland ice during the glacial maximum, on the postglacial spread of forest trees (20, 64). Another unique aspect of North America is the late deglaciation of some parts of the Laurentide ice sheet, particularly in the Québec-Labrador Peninsula, which was only free of inland ice in the mid-Holocene (65).

The Early Afforestation of Northwestern North America

Several forest tree species form the North American Arctic treeline (Fig. 2), with a co-dominance of white spruce (*Picea glauca* [Moench] Voss) and black spruce (*Picea mariana* [Mill.] BSP.) in Alaska, the Yukon, and western Canada, and dominance of black spruce in central and eastern Canada (2, 8, 20, 21). The tundra-taiga interface is well delineated across the continent with an increasing width eastward from the Northwest Territories to Hudson Bay and Labrador (2, 8).

The northwestern Arctic coast was rapidly occupied by trees during the Pleistocene-Holocene transition, but the migration of trees into the Northwest Territories and eastern Canada was delayed by the late melting of glacial ice in this region. However, a common denominator concerning most deglaciated areas in Eurasia and North America, with the salient exception of the Labrador coast along the Atlantic seaboard, seems to be the relatively rapid colonization of deglaciated land by boreal trees. After the glacial maximum, boreal trees began to move rapidly and, in many instances, they were located at a relatively short distance from the glacier front. This situation likely prevailed, even when the ice sheets were still large at 12-10 ka (Fig. 4).

In the Mackenzie-Yukon region, trees (mostly spruce) reached their northernmost position between 11.5 and 9.5 ka, on the Tuktoyaktuk Peninsula along the Beaufort Sea. The forest re-

treated significantly after 5.8 ka, with a 50-km southward shift of the Arctic treeline (10, 66, 67). In contrast to Eurasia, tree macrofossils above the modern Arctic treeline in the area were seldom found. Two spruce tree stumps in live position at the soil surface on the treeless Tuktoyaktuk Peninsula were dated at 5.7 ka (10) and 7.5 ka (13). Black spruce woodlands were growing near the Arctic Ocean coast between 9.4 and 3.8 ka, some 75 km north of the modern limit of continuous boreal forest (66). In the central Yukon, maximum spruce forest expansion occurred between 11.5 and 6.8 ka, as inferred from pollen and needles preserved in lake sediments; forest changed to tundra after 5.8 ka in the area (68).

Deglaciation of western Canada was rapid between 18 ka and 10 ka, with the separation of the Cordillerian ice sheet from the Laurentide ice sheet occurring around 13 ka (24). Assuming that boreal trees were close to the receding ice front, spruce were moving fast to newly deglaciated sites (69). Based on the first rise in spruce pollen percentages in pollen diagrams from sites located in the southern refugium in the central United States, Manitoba, Saskatchewan, Alberta, the Northwest Territories, and the northernmost Mackenzie Delta region, it was concluded (69) that both ends of the transect were colonized during only a few centuries, at about 10.9 ka, thus suggesting the absence of any time-transgressive spread of white spruce (inferred identification from measurements of spruce pollen); the spread of white spruce was estimated at 2 km yr⁻¹ (69). Although spruce might have been present at a site well before the rise in spruce pollen, it was assumed that the species were coming from a distant source area located far south of eastern Beringia, as first advocated by Hopkins et al. (64). Most researchers dealing with spruce in eastern Beringia assumed that the species were absent from eastern Beringia during the late Pleistocene (20, 64, 69).

In a long and well-dated pollen sequence at Hanging Lake (northern Yukon) spruce pollen grains were relatively abundant

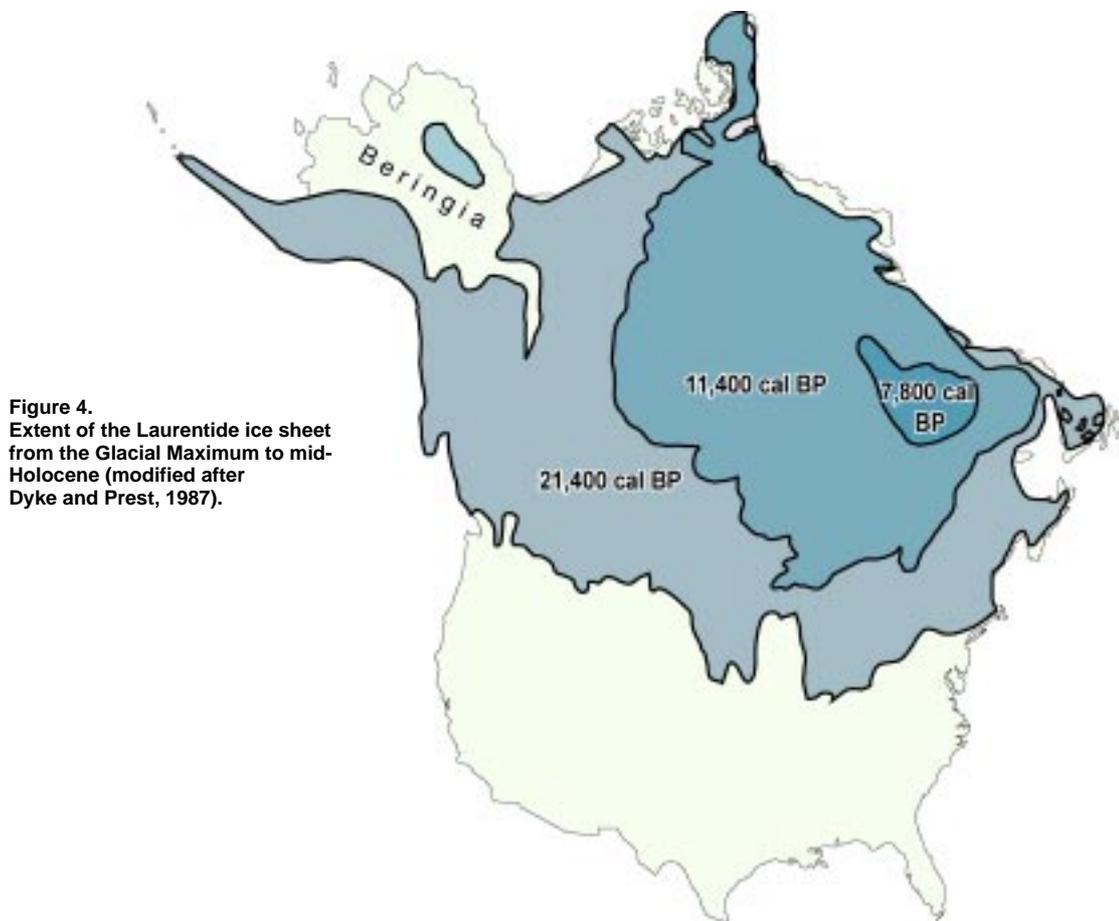


Figure 4.
Extent of the Laurentide ice sheet from the Glacial Maximum to mid-Holocene (modified after Dyke and Prest, 1987).

(>10%) at 22 ka, but with no pollen being recorded between 16.8 ka and 15.6 ka (70). The absence of spruce pollen was interpreted as the exclusion of the species from eastern Beringia at that time. However, spruce pollen is present throughout the sequence from the glacial maximum to present, although generally < 10%. The uniformity in the pollen representation throughout the late Pleistocene and the Holocene raises the problem of the source area. Spruce pollen might come from a regional source area during the Holocene, likely from the nearby forests of southern Yukon, Alaska and the Mackenzie River region. However, the problem remains as to the identification of the source area before the major forest expansion at the end of the Pleistocene. Spruce pollen at Hanging Lake during the Pleistocene must have been produced by refugial spruce as suggested by Cwynar (70) for the 21 600–18 500 BP (21 600 BP exceeds CALIB's data set) interval, but the exclusion of spruce between 16.8 ka and 15.6 ka was possibly a local event that cannot rule out the presence of the species in eastern Beringia during and after the glacial maximum.

A similar, continuous record of spruce pollen was registered at Antifreeze Pond, southern Yukon, with a sharp rise dated 9.8 ka, roughly coinciding with a marked change in sediments from clayey silts to organic lake sediments (gyttja) (71). Sustained low percentages of spruce pollen suggest that spruce may have been present near the site throughout the late Pleistocene. Detrital organic sediments obtained from the upper Porcupine River basin in the northern Yukon and containing spruce needles were dated 16.3 and 19 ka. The radiocarbon dates were rejected because of possible redeposition due to wind action on older Pleistocene sediments (64). However, the redeposition of needles was more inferential than verified from field surveys, thus raising the possibility of spruce presence at that time. Another line of evidence for the early presence of boreal trees in the area comes from 14.1 ka to 13.1 ka year-old driftwood (unidentified wood logs) buried at the top of pingo sediments in the Mackenzie Delta area (72). Although redeposition is highly probable from a nearby source, the macrofossil evidence points to the presence of coastal trees before and very soon after deglaciation. At Twin Lake, near Inuvik, basal peat containing white spruce needles, cones and seeds, and spruce wood dated at 13.5 ka suggest the rapid occupation of the site after deglaciation (73). These data were judged invalid (20) because they were different from those of 3 pollen sites in the same area and also because of the apparent anomaly in green alder pollen and macrofossil representation. Based on the available pollen and the macrofossil data cited above, the spread of spruce would have been as fast as 25 km yr⁻¹ from southern Canada to Inuvik (20, 69): this rapid migration rate is probably not realistic and raises the possibility of colonization of the Mackenzie-Yukon sites by a spruce refuge, a simpler and more probable scenario.

Treeline Changes in Central and Eastern Canada

Macrofossil evidence for treeline shifts in this area of extensive Precambrian plateaux are rather scarce. In the Northwest Territories, postulated treeline shifts are largely derived from pollen data. north of Yellowknife, a 25-km advance of black spruce into the Arctic tundra at 5.8 ka, and retreat to modern positions beginning at 3.8 ka, were inferred from fossil pollen (74). Additional pollen and diatom evidence at 2 other nearby lake sites (75) supported earlier conclusions (74) of modest treeline shifts in the area; a rapid transformation of tundra to forest-tundra in only 150 yrs was also inferred from the sharp rise in the percentage of spruce pollen (75). Although awaiting more information on the modern position of treeline trees and vegetation in the area, it is possible that spruce krummholz surrounding the sampling sites are the remains of mid-Holocene forest stands. The retreat of black spruce woodlands at Sleet Lake (66), in the Mackenzie region around 3.8 ka coincides with that of north of

Yellowknife (75), but the causes of the receding treeline are not known.

In the Dubawnt Lake region, maximum spruce percentages in peat sediments were interpreted as indirect evidence of a > 100 km northward advance of the forest limit relative to its modern position (76). In the same region (Ennadai Lake and Great Slave Lake areas), significant treeline shifts from present position were inferred from spruce pollen percentages in peat deposits, i.e. a 350-km advance at 6.9–5.8 ka, a retreat between 5.8 ka and 4.5 ka, and then a 300-km readvance at 4.5–3.8 ka (77). Because the coring sites are located in the forest-tundra, changing spruce pollen percentages cannot be securely attributed to past positions of the treeline; it is probable that the changes are linked to fluctuating subarctic treelines within the forest-tundra.

East of Hudson Bay, the immigration of boreal trees to their present range distribution occurred late in the Holocene because of delayed deglaciation (22). Maximum influx values of spruce pollen were used to infer a northward displacement of the treeline several tens of kilometers at 4.0 ka, in the southern part of the Ungava Peninsula (78). However, other pollen studies in the same region reported maximum spruce colonization at treeline sites before 2.0 ka without any apparent tree expansion into the Arctic tundra (79). Only a minor advance of 5 km of the Arctic treeline was depicted based on eastern larch (*Larix laricina* [DuRoi] K. Koch) macrofossil evidence in the southern part of the Ungava Peninsula (12). The Arctic treeline 30 km east of Hudson Bay remained stable during the last 3.2 ka, as inferred from black spruce macro-remains buried in peat just south of the present treeline (80). Minor black spruce treeline displacements (about 5 to 12 km) occurred during the last climatic excursion from the Little Ice Age to present, according to the shift from stunted to normal tree forms, in established populations along the eastern coast of Hudson Bay (81, 82). A similar trend was also depicted in the Scandes Mountains in Sweden (83, 84). Lowering of subarctic treelines has been inferred from decreasing tree pollen content in lake sediments with estimated shifts of 150 m in the George River area (85) and > 40-m in Labrador (86). However, the only direct evidence of downward subarctic treelines during the late Holocene come from spruce macro-charcoal on treeless uplands of the forest-tundra in northwestern Québec (1), i.e. an average lowering of 50–60 m and 10–30 m from the center of the forest-tundra to the present Arctic treeline, and from the center of the forest-tundra to the northern limit of continuous forest, respectively, corresponding to a decreasing rate of about 10–15 m per degree of latitude. In a context of general cooling, wildfire is the major factor having influenced the overall downward shift of subarctic treelines. Instead of significant changes in Arctic treeline position, most changes of boreal tree populations in the forest-tundra during the late Holocene were characterized by fluctuating abundance of white spruce, black spruce and eastern larch (80, 87, 88).

Based on radiocarbon-dated tree macrofossils, all boreal tree species spread to northern Quebec and Labrador at a rate of < 0.4 km yr⁻¹. *Picea* spp. migrated at a rate of 0.2 to 0.4 km yr⁻¹, depending on the location of the source area south of the late Wisconsinan ice border (89, 90). Eastern larch also migrated at a modest speed of < 0.30 km yr⁻¹ from the southern refugium east of the Prairie in northeastern USA (91) to northern Quebec. According to pollen and macrofossil data, the species arrived during the late Holocene in northwestern Quebec (92). The oldest macrofossils of jack pine (*Pinus banksiana* Lamb.) at its northernmost position near the southern edge of the forest-tundra (93), dated back to 3.2 ka, indicating that the species migrated at a low rate of < 0.17 km yr⁻¹, slower than estimated from pollen evidence (94). Because of sustained frequency of wildfire, jack pine abundance is presently increasing in the James Bay region (L. Sirois, pers. comm.). Balsam fir (*Abies balsamea* [L.] Mill.) also spread at a rate similar to that of jack pine, to its

northernmost position, in the southern part of the forest-tundra at 4.7 ka (95), and in northwestern boreal Quebec at 4.2 ka (96). According to macrofossil data, the abundance of balsam fir in northern Quebec since the mid-Holocene is steadily decreasing due to wildfire (D. Arseneault, pers. comm.).

DISCUSSION

The circumboreal tundra-taiga ecotone is a dynamic system which has been changing since late Pleistocene times. Regional climate changes have been the main forcing factors causing the vegetation cover to change, but there are many other variables affecting the climate and development of ecosystems on the long-term time scale. Fire disturbance is an important factor of vegetational change during periods critical to forest regeneration. In the forest-tundra, where tree growth and reproduction are constrained by reduced warmth, fire results in extensive deforestation of upland sites (97). Other factors, including paludification and changing albedo, also play roles but are less understood. In addition, most of our knowledge of these processes have come from modern ecological studies and have not been studied in or applied to paleoecological investigations.

The most important factor influencing the late Pleistocene and Holocene climatic evolution was the changes in the geometry of the Earth's orbit, which according to the Milankovitch theory, resulted in changes in the solar insolation in time spans of thousands and tens of thousands of years. The reduced seasonality and lowering temperatures since the early Holocene are in line with the changes forced by the celestial mechanics (98, 99). During the Pleistocene-Holocene transition, the summer solar insolation at high latitude was about 8% stronger than at present and winters were correspondingly colder. Weaker seasonality resulted in cooler summers and wetter conditions in the late Holocene.

An extremely rapid dispersal of trees, and probably other plants, took place when climate warmed drastically from full glacial conditions. Overall, most Arctic treelines reached their northernmost positions in the early Holocene and receded to present positions starting about 5.8 ka. Only the late deglaciated areas of northern Canada (Northwest Territories and Quebec-Labrador) were out of phase with this general trend. It is likely that the early occupation of the northernmost sites in ice-free and early deglaciated areas was possible because of the close proximity of invading trees in nearby glacial refugia, particularly in Fennoscandia and northern Russia. In northwesternmost North America, a similar pattern existed, but most researchers speculated that the early arrival of tree species was due to the exceptionally rapid spread of conifers crossing a stretch of land of 2000

to 3000 km in just a few centuries from the glacial refugium south of the Laurentide ice sheet. Based on present evidence, there are no scientific reasons to discard the scenario of a continuous but modest occupation of eastern Beringia by spruce during the late Pleistocene. One line of scrutiny already advocated by Ritchie (20) is to look at the genetic diversity of tree populations (white spruce, black spruce and eastern larch) distributed across the Mackenzie-Yukon region. The use of molecular techniques to unravel the eastern-Beringian paradox is urgently needed.

Creating a global perspective on past treeline change is problematic due to the large arrays of methods and definitions used. In addition to the problem of comparing pollen- and macro-fossil-based approaches, the delineation of the changing position of the Arctic treeline has been generally based on rather loose criteria. A general lack of detailed descriptions of the modern treeline position and vegetation in several areas complicates any comparative analysis of the magnitude of the most important changes, for instance in northern Russia and in the Northwest Territories.

There is a strong disparity between the results based on pollen and macrofossils. Small occurrences of plant species have been overshadowed by abundant pollen rains. This implies that the use of assigned pollen percentages to indicate the presence of a species within a region may not be valid, particularly where a species is at the edge of its geographical range. It is likely that trees were present at any given site well before the rise in pollen abundance (100). Macrofossil data, although seldom abundant, provides the most direct proof of species establishment.

A problem made apparent by recent tree macrofossil discoveries are the evanescent presence of "exotic" species during early Holocene in sites far from their natural range limits, for instance Siberian larch in central Sweden. These trees survived for some time and then were wiped out by competition and/or by changing environments and climate. Macro-remains indicating the scattered occurrences of other temperate and boreal species, dating to the Pleistocene-Holocene transition, and which are now absent from the present alpine and subalpine communities, have also been found in the Scandinavian Mountains (26, 33, 43, 44). These findings shed valuable new light on the late Pleistocene and Holocene vegetational, climatic and environmental changes and suggest that there still is a large potential to improve our knowledge about environmental history in circumboreal treeline areas since the glacial maximum. In particular, future research should concentrate not only on patterns of species displacement, but on identifying the factors, apart from climate, which cause treeline shifts.

References and Notes

- Payette, S., Fortin, M.-J. and Gamache, I. 2001. The subarctic forest-tundra: the structure of a biome in a changing climate. *BioScience* 51, 709-718.
- Rowe, J.S. 1972. *Forest Regions of Canada*. Department of Environment, Canada Forestry Service, Publication 1300. Ottawa.
- Amo, S.F. 1984. *Timberline. Mountain and Arctic Forest Frontiers*. The Mountaineers, Seattle, Washington.
- Payette, S. and Lavoie, C. 1994. The arctic tree line as a record of past and recent climatic changes. *Environ. Rev.* 2, 78-90.
- Veijola, P. 1998. *The Northern Timberline and Timberline Forests in Fennoscandia*. The Finnish Forest Research Institute. Research Paper 672. Gummerus, Saarijärvi.
- Tuhkanen, S. 1999. The northern timberline in relation to climate. In: *Sustainable Development in Northern Timberline Forests*. Proceedings of the Timberline Workshop, Whitehorse, Canada, Kankaanpää, S., Tasanen, T. and Sutinen, M.-L. (eds). The Finnish Forest Research Institute, Research Paper 734, Gummerus, Saarijärvi.
- Hustich, I. 1979. Ecological concepts and biogeographical zonation in the North: the need for a generally accepted terminology. *Holarctic Ecol.* 2, 208-217.
- Payette, S. 1983. The forest tundra and present tree-lines of the northern Québec-Labrador Peninsula. In: *Tree line Ecology*. Morisset, P. and Payette, S. (ed.). *Nordicana* 47, 3-23.
- All radiocarbon ages are given in calibrated radiocarbon years before present (cal. yr BP) unless stated (yr BP). These ages correspond approximately to the calendar years and are generally older than the non-calibrated radiocarbon years, which are still commonly used. See <http://depts.washington.edu/qil/calib/> and <http://radiocarbon.pa.qub.ac.uk/calib/> and also Stuiver, M. and Reimer P.J. 1993. Extended ¹⁴C data base and revised CALIB 3.0 ¹⁴C age calibration program. *Radiocarbon* 35, 215-230.
- Ritchie, J.C. and Hare, F.K. 1971. Late-Quaternary vegetation and climate near the arctic tree-line of northwestern North America. *Quat. Res.* 1, 331-342.
- Eronen, M. 1979. The retreat of pine forest in Finnish Lapland since the Holocene climatic optimum: a general discussion with radiocarbon evidence from subfossil pines. *Fennia* 157, 93-114.
- Gagnon, R. and Payette, S. 1981. Fluctuations holocènes de la limite des forêts de mélèzes, Rivière aux Feuilles, Nouveau-Québec: une analyse macrofossile en milieu tourbeux. *Géogr. Phys. Quat.* 35, 57-72.
- Spear, R.W. 1983. Paleocological approaches to a study of tree line fluctuation in the Mackenzie Delta Region, Northwest Territories: preliminary results. In: *Tree line Ecology*. Morisset, P. and Payette, S. (ed.). *Nordicana* 47, 61-72.
- Khotinskiy, N.A. 1984. Holocene vegetation history. In: *Late Quaternary Environments of the Soviet Union*. Velichko, A.A. (ed.). University of Minnesota Press, Minnesota. pp. 179-200.
- Peteet, D.M. 1991. Postglacial migration history of lodgepole pine near Yakutat, Alaska. *Can. J. Bot.* 69, 786-796.
- Kullman, L. 1995. Holocene tree-limit and climate history from the Scandes Mountains, Sweden. *Ecology* 76, 2490-2502.
- Kremenetski, C.V., Sulerzhitsky, L.D. and Hantemirov, R. 1998. Holocene history of the northern range limits of some trees and shrubs in Russia. *Arctic Alp. Res.* 30, 317-333.
- Webb, T., III, Cushing, E.J. and Wright, H.E., Jr. 1983. In: *Late-Quaternary Environments of the United States. The Holocene*. Wright, H.E., Jr. (ed.). Holocene changes in the vegetation of the Midwest. Volume 2. University of Minnesota Press, Minneapolis. pp. 142-165.
- Huntley, B. and Birks, H.J.B. 1983. *An Atlas of Past and Present Pollen Maps for Europe: 0-13 000 years ago*. Cambridge University Press, Cambridge.
- Ritchie, J.C. 1984. *Past and Present Vegetation of the Far Northwest of Canada*. University of Toronto Press, Toronto.
- Ritchie, J.C. 1987. *Postglacial Vegetation of Canada*. Cambridge University Press, Cambridge.
- Payette, S. 1993. The range limit of boreal tree species in Québec-Labrador: an ecological and palaeocological interpretation. *Rev. Palaeobot. Palyn.* 79, 7-30.
- Jackson, S.T., Overpeck, J.T., Webb-III, T., Keatch, S.E. and Anderson, K.H. 1997. Mapped plant-macrofossil and pollen records of late Quaternary vegetation change in

- eastern North America. *Quat. Sci. Rev.* 16, 1–70.
24. Dyke, A.S. and Prest, V.K. 1987. Late Wisconsinan and Holocene history of the Laurentide ice sheet. *Géogr. Phys. Quat.* 41, 237–263.
 25. Kullman, L. 1998. The occurrence of thermophilous trees in the Scandes Mountains during the early Holocene: evidence for a diverse tree flora from macroscopic remains. *J. Ecol.* 86, 421–428.
 26. Grosswald, M.G. 1998. Late-Weichselian ice sheets in Arctic and Pacific Siberia. *Quat. Internat.* 45/46, 3–18.
 27. Grosswald, M.G. 1980. Late Weichselian ice sheets of northern Eurasia. *Quat. Res.* 13, 1–32.
 28. Forman, S.L., Ingólfsson, O., Gataullin, V., Manley, W.F. and Lokrantz, H. 1999. Late Quaternary stratigraphy of western Yamal Peninsula, Russia: new constraints on the configuration of the Eurasian ice sheet. *Geology* 27, 807–810.
 29. Larsen, E., Lysa, A., Demidov, I., Funder, S., Houmark-Nielsen, M., Kjær, K.H. and Murray, A.S. 1999. Age and extent of the Scandinavian ice sheet in northwest Russia. *Boreas* 28, 115–132.
 30. Mangerud, J., Svendsen, J.I. and Astakhov, V.I. 1999. Age and extent of the Barents and Kara ice sheets in northern Russia. *Boreas* 28, 46–80.
 31. Grichuk, V.P. 1984. Late pleistocene vegetation history. In: *Late Quaternary Environments of the Soviet Union*, Velichko, A.A. (ed.) Longman, London, pp. 155–178.
 32. Möller, P., Bolshiyakov, D.Y. and Bergsten, H. 1999. Weichselian geology and paleoenvironmental history of the central Taymir Peninsula, Siberia, indicating no glaciation during the last global glacial maximum. *Boreas* 28, 92–114.
 33. Kullman, L. 2000. The geocological history of *Picea abies* in northern Sweden and adjacent parts of Norway. A contrarian hypothesis of postglacial tree immigration patterns. *Geotika* 21, 141–172.
 34. Hyvärinen, H. 1975. Absolute and relative pollen diagrams from northernmost Fennoscandia. *Fennia* 142, 1–23.
 35. Hyvärinen, H. 1976. Flandrian pollen deposition rates and tree-line history in northern Fennoscandia. *Boreas* 5, 163–175.
 36. Hyvärinen, H. 1993. Holocene pine and birch limits near Kilpisjärvi, western Finnish Lapland: pollen stratigraphical evidence. *Paläoklimaforsch. Palaeoclim. Res.* 9, 19–27.
 37. Donner, J. 1995. *The Quaternary History of Scandinavia*. World and Regional Geology 7. Cambridge University Press, Cambridge.
 38. Berglund, B.E., Barnekow, L., Hammarlund, D., Sandgren, P. and Snowball, I.F. 1996. Holocene forest dynamics and climate changes in the Abisko area, northern Sweden: the Sonesson model of vegetation history reconstructed and confirmed. *Ecol. Bull.* 45, 15–30.
 39. Barnekow, L. 1999. Holocene tree-line dynamics and inferred climatic changes in the Abisko area, northern Sweden, based on macrofossil and pollen records. *The Holocene* 9, 253–265.
 40. Eronen, M. and Huttunen, P. 1993. Pine megafossils as indicators of Holocene climatic changes in Fennoscandia. *Paläoklimaforsch. Palaeoclim. Res.* 9, 29–40.
 41. Hyvärinen, H. and Mäkelä, E. 1996. Parallel trends of Holocene tree-line changes and lake and mire development in northwestern Finnish Lapland. *Paläoklimaforsch. Palaeoclim. Res.* 20, 293–300.
 42. Kullman, L. 1998. Tree-limits and montane forests in the Swedish Scandes: sensitive biomarkers of climate change and variability. *Ambio* 27, 312–321.
 43. Kullman, L. 1998. Palaeoecological, biogeographical and palaeoclimatological implications of early Holocene immigration of *Larix sibirica* Ledeb. into the Scandes Mountains, Sweden. *Global Ecol. Biogeogr. Lett.* 7, 181–188.
 44. Kullman, L. 1998. Non-analogous tree flora in the Scandes Mountains, Sweden, during the early Holocene: macrofossil evidence of rapid geographic spread and response to palaeoclimate. *Boreas* 27, 153–161.
 45. Kullman, L. and Kjällgren, L. 2000. A coherent postglacial tree-limit chronology (*Pinus sylvestris* L.) for the Swedish Scandes: aspects of paleoclimate and recent warming, based on megafossil evidence. *Arctic Antarctic Alp. Res.* 32, 419–428.
 46. Mäkelä, E. 1998. The Holocene history of birch as recorded in Lake Ilompolo, Inari Lapland, NE Finland. *The Holocene* 8, 55–67.
 47. Mäkelä, E. and Hyvärinen, H. 2000. Holocene vegetation history at Vätsäri, Inari Lapland, northeastern Finland, with special reference to *Betula*. *The Holocene* 10, 75–85.
 48. Dahl, S.O. and Nesje, A. 1996. A new approach to calculating Holocene winter precipitation by combining glacier equilibrium-line altitudes and pine-tree limits: a case study from Hardangerjøkulen, central southern Norway. *The Holocene* 6, 381–398.
 49. Karlén, W. and Kuylenstierna, J. 1996. On solar forcing of Holocene climate: evidence from Scandinavia. *The Holocene* 6, 359–365.
 50. Kullman, L. 1987. Little Ice Age decline of a cold marginal *Pinus sylvestris* forest in the Swedish Scandes. *New Phytologist* 106, 567–584.
 51. Kullman, L. 2001. 20th century climate warming and tree-limit rise in the southern Scandes of Sweden. *Ambio* 30, 72–80.
 52. Eronen, M., Zetterberg, P., Briffa, K., Lindholm, M., Meriläinen, J. and Timonen, M. The supra-long Scots pine tree-ring record for northern Finnish Lapland. *The Holocene*. (In press).
 53. Kullman, L. 1999. Early Holocene tree growth at a high elevation site in the northernmost Scandes of Sweden (Lapland): a palaeobiogeographical case study based on megafossil evidence. *Geogr. Ann.* 81A, 63–74.
 54. Kremenetski, C., Vaschalova, T. and Sulerzhitskiy, L. 1999. The Holocene vegetation history of the Khibiny Mountains: implications for the post-glacial expansion of spruce and alder on the Kola Peninsula, northwestern Russia. *J. Quat. Sci.* 14, 29–43.
 55. Hiller, A., Boettger, T. and Kremenetski, C. 2001. Mediaeval climatic warming recorded by radiocarbon dated alpine tree-line shift on the Kola Peninsula, Russia. *The Holocene* 11, 491–497.
 56. MacDonald, G.M., Velichko, A.A., Kremenetski, C.V., Borisova, C.K., Goleva, A.A., Andreev, A.A., Cwynar, L.C., Riding, R.T., Forman, S.L., Edwards, T.W.D., Aravena, R., Hammarlund, D., Szeicz, J. and Gataullin, V.N. 2000. Holocene tree line history and climate change across northern Eurasia. *Quat. Res.* 53, 302–311.
 57. Petet, D., Andreev, A., Bardeen, W. and Mistretta, F. 1998. Long-term arctic peatland dynamics, vegetation and climate history of the Pur-Taz region, western Siberia. *Boreas* 27, 115–126.
 58. MacDonald, G.M., Gervais, B.R., Snyder, J.A., Tarasov, G.A. and Borisova, O.K. 2000. Radiocarbon dated *Pinus sylvestris* L. wood from beyond tree-line on the Kola Peninsula, Russia. *The Holocene* 10, 143–147.
 59. Kaakinen, A. and Eronen, M. 2000. Holocene pollen stratigraphy indicating climatic and tree-line changes derived from a peat section at Ortino, in the Pechora lowland, northern Russia. *The Holocene* 10, 611–620.
 60. Jasinski, J.P.P., Warner, B.G., Andreev, A.A., Aravena, R., Gilbert, S.E., Zeeb, B.A., Smol, J.P. and Velichko, A.A. 1998. Holocene environmental history of a peatland in the Lena River valley, Siberia. *Can. J. Earth Sci.* 35, 637–648.
 61. Hantemirov, R.M. and Shiyatov, S.G. 1999. Main stages of woody vegetation development in the Yamal Peninsula during the Holocene. *Russian J. Ecol.* 30, 141–147.
 62. MacDonald, G.M., Case, R.A. and Szeicz, J.M. 1998. A 538-year record of climate and tree line dynamics from the lower Lena River region of northern Siberia, Russia. *Arctic Alpine Res.* 30, 334–339.
 63. Hopkins, D.M., Matthews, J.V., Schweger, C.E. and Young, S.B. (eds). 1982. *Paleoecology of Beringia*. Academic Press, New York.
 64. Hopkins, D.M., Smith, P.A. and Matthews, J.V., Jr. 1981. Dated wood from Alaska and the Yukon: implications for forest refugia in Beringia. *Quat. Res.* 15, 217–249.
 65. Lauriol, B. and Gray, J.T. 1987. The decay and disappearance of the Late Wisconsinan ice sheet in the Ungava Peninsula, northern Québec. *Arctic Alpine Res.* 19, 109–126.
 66. Spear, R.W. 1993. The palynological record of Late-Quaternary arctic tree-line in north-west Canada. *Rev. Palaeobot. Palyn.* 79, 99–111.
 67. Hyvärinen, H. and Ritchie, J.C. 1975. Pollen stratigraphy of Mackenzie pingo sediments, N.W.T., Canada. *Arctic Alpine Res.* 3, 261–272.
 68. Cwynar, L.C. and Spear, R.W. 1991. Reversion of forest to tundra in the central Yukon. *Ecology* 72, 202–212.
 69. Ritchie, J.C. and MacDonald, G.M. 1986. The patterns of post-glacial spread of white spruce. *J. Biogeogr.* 13, 527–540.
 70. Cwynar, L.C. 1982. A Late-Quaternary vegetation history from Hanging Lake, northern Yukon. *Ecol. Monogr.* 52, 1–24.
 71. Rampton, V. 1971. Late Quaternary vegetational and climatic history of the Snag-Klutlan area, south-western Yukon Territory, Canada. *Geol. Soc. Amer. Bull.* 82, 959–978.
 72. Mackay, J.R. and Terasmae, J. 1963. Pollen diagrams in the Mackenzie Delta area, N.W.T. *Arctic* 16, 229–238.
 73. Fyles, J.G., Heginbottom, J.A. and Rampton, V.N. 1972. *Quaternary Geology and Geomorphology, Mackenzie Delta to Hudson Bay*. Excursion A-30. XXIV International Geological Congress, Montréal, Québec.
 74. Moser, K.A. and MacDonald, G.M. 1990. Holocene vegetation change at tree line north of Yellowknife, Northwest Territories, Canada. *Quat. Res.* 34, 227–239.
 75. MacDonald, G.M., Edwards, T.W., Moser, K.A., Pienitz, R. and Smol, J.P. 1993. Rapid response of tree line vegetation and lakes to past climate warming. *Nature* 361, 243–246.
 76. Kay, P.A. 1979. Multivariate statistical estimates of Holocene vegetation and climate change, forest-tundra transition zone, N.W.T., Canada. *Quat. Res.* 11, 125–140.
 77. Nichols, H. 1975. *Palynological and Paleoclimatic Study of the Late Quaternary Displacement of the Boreal Forest-Tundra Ecotone in Keewatin and Mackenzie, N.W.T.*, Canada. Institute of Arctic and Alpine Research, University of Colorado, Boulder. Occasional Paper 15.
 78. Richard, P.J.H. 1981. *Paléophytogéographie Postglaciaire en Ungava par l'Analyse Pollinique*. Paléo-Québec Vol. 13. Université du Québec à Montréal, Montréal.
 79. Gajewski, K., Payette, S. and Ritchie, J.C. 1993. Holocene vegetation history at the boreal forest-shrub tundra transition in northern Québec. *J. Ecol.* 81, 433–443.
 80. Lavoie, C. and Payette, S. 1996. The long-term stability of the boreal forest limit in subarctic Québec. *Ecology* 77, 1226–1233.
 81. Lavoie, C. and Payette, S. 1994. Recent fluctuations of the lichen-spruce forest limit in subarctic Québec. *J. Ecol.* 82, 725–734.
 82. Lescoq-Sinclair, K. and Payette, S. 1995. Recent advance of the arctic treeline along the eastern coast of Hudson Bay. *J. Ecol.* 83, 929–936.
 83. Kullman, L. 1986. Recent tree-limit history of *Picea abies* in the southern Swedish Scandes. *Can. J. Forest Res.* 16, 761–771.
 84. Kullman, L. and Engelmark, O. 1991. Historical biogeography of *Picea abies* (L.) Karst. at its subarctic limit in northern Sweden. *J. Biogeogr.* 18, 63–70.
 85. McAndrews, J.H. and Samson, G. 1977. Analyse pollinique et implications archéologiques et géomorphologiques, Lac de la Hutte Sauvage (Mushuau Nipi), Nouveau-Québec. *Géogr. Phys. Quat.* 31, 177–183.
 86. Lamb, H.F. 1985. Palynological evidence for postglacial change in the position of tree limit in Labrador. *Ecol. Monogr.* 55, 241–258.
 87. Payette, S. and Filion, L. 1985. White spruce expansion at the tree line and recent climate change. *Can. J. Forest Res.* 15, 241–251.
 88. Morin, A. and Payette, S. 1984. Expansion récente du mélèze à la limite des forêts (Québec nordique). *Can. J. Bot.* 62, 1404–1408.
 89. Kneller, M. and Petet, D.M. 1994. Late-Quaternary climate in the ridge and valley of Virginia, U.S.A. Changes in vegetation and depositional environment. *Quat. Sci. Rev.* 12, 613–623.
 90. Anderson, T.W. 1982. Pollen and plant macrofossil analyses on late Quaternary sediments at Kitchener, Ontario. *Geol. Surv. Can. Paper* 82, 131–136.
 91. Petet, D.M., Daniels, R.A., Heusser, J.S., Vogel, J.S., Southon, J.R. and Nelson, D.E. 1993. Late-Glacial pollen, macrofossils and fish remains in northeastern U.S.A.: the Younger Dryas Oscillation. *Quat. Sci. Rev.* 12, 597–612.
 92. Penalba, M.C. and Payette, S. 1997. Late-Holocene expansion of eastern larch (*Larix laricina* [DuRoi] K. Koch) in northwestern Québec. *Quat. Res.* 48, 114–121.
 93. Despons, M. and Payette, S. 1993. The Holocene dynamics of jack pine at its northern range limit in Québec. *J. Ecol.* 81, 719–727.
 94. MacDonald, G.M., Cwynar, L.C. and Whitlock, C. 1998. The late Quaternary dynamics of pines in northern North America. In: *Ecology and Biogeography of Pinus*. Richardson, D.M. (ed.). Cambridge University Press, Cambridge, pp. 122–136.
 95. Richard, P.J.H., Larouche, A. and Bouchard, M.A. 1982. Âge de la déglaciation finale et histoire postglaciaire de la végétation dans la partie centrale du Nouveau-Québec. *Géogr. Phys. Quat.* 36, 63–90.
 96. Sirois, L. 1997. Distribution and dynamics of balsam fir (*Abies balsamea* [L.] Mill.) at its northern limit in the James Bay area. *Ecosci.* 4, 340–352.
 97. Payette, S. 1992. Fire as a controlling process in the North-American boreal forest. In: *A Systems Analysis of the Global Boreal Forest*. Shugart, H.H., Leemans, R. and Bonan, G.B. (eds). Cambridge University Press, New York, pp. 144–169.
 98. Berger, A. 1989. Pleistocene climatic variability at astronomical frequencies. *Quat. Internat.* 2, 1–14.
 99. COHMAP Members 1988. Climate changes of the last 18,000 yr: observations and model simulations. *Science* 241, 1043–1052.
 100. Bennett, K.D. 1985. The spread of *Fagus grandifolia* across eastern North America during the last 18,000 years. *J. Biogeogr.* 12, 147–164.

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