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Betula pendula Roth. survival and growth in treeline is affected by genotype and environment

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Alpine and Arctic treelines are assumed to be shifting toward higher latitudes and altitudes as a consequence of climate warming. Here, we compared the survival and growth of 1264 silver birch (*Betula pendula* Roth.) trees representing nine half-sib families. The trees were planted in two arboreta situated in distinct altitudinal environments in northern Finland in 1976 and 1977. The arboreta were located 9 km from each other and approximately 60 km north from the species' most northern natural growth site at that time. They were fenced to prevent vertebrate grazing, which is known to be among the most important factors limiting the expansion and regeneration of forests in European treeline ecotones. Overall, 90% and 81% of the trees were alive five and 40 years after planting in the two arboreta, respectively. Survival of trees varied among the half-sib families, especially in *Arboretum 1*, situated in a lower altitudinal environment characterized by soils with lower levels of nutrients, a longer growing season, and harsher winter temperatures. Trees were distinctively bigger in *Arboretum 2*: 50% taller (6.2 m vs. 4.4 m) and 68% thicker (9.5 cm vs. 5.6 cm) compared to trees in *Arboretum* 1. Furthermore, the performance of half-sib families varied depending on the garden they were grown in. These results demonstrate that the acclimation capacity of *B. pendula* allows its distribution to expand north from the present range; however, local abiotic environmental conditions (soil fertility and winter temperatures) and other selection pressures (herbivory) are likely to affect the genetic structure and growth of *B. pendula* populations.

Keywords Range expansions across latitudes, Climate change, Birch, Growth, Survival, Soil nutrients, Temperature, Reindeer grazing

Anthropogenic climate warming is considerably faster in the Arctic than the global average[1–6]. Consequently, the treeline ecotone of the subarctic forest-tundra boundary is expected to shift rapidly northwards across latitudes and upwards to higher elevations[7–9]. Adaptive radiation of treeline species during the Holocene distribution history and recent findings of the adaptive capacity of tree species support this scenario[2,10–13]. The northern ecosystems are young in terms of biological time and ecosystem adaptations. The tundra formed following the receding ice was replaced by forests from non-glaciated areas and glacial refugia in Eurasia after the last glacial period, 10,000 years ago[14].

The majority of the present Arctic circumpolar treeline ecotone is predominated by conifers[15], but the treeline species composition varies depending on the postglacial range expansion history of the species due to dissimilarities in geographic coverage of ice sheet and climatic conditions in Eurasia and North America[16]. Biogeographically, northern Europe deviates strikingly from other parts of the circumpolar subarctic zone[17,18]. Compared to other parts of the Arctic, corresponding climatic zones are present at higher latitudes in Western Europe owing to Gulf Stream effects. In northern Fennoscandia, the oceanicity–continentality gradient is narrow and thermal conditions are nearly northern boreal at latitudes characterized by Arctic light conditions, with strong seasonal changes in day length ranging from polar night in the winter to polar day during the summer[19]. Consequently, birch (*Betula* spp.) forms the treeline, and Scots pine (*Pinus sylvestris* L.) grows further north than spruce in Fennoscandia and north-western Russia[18,20]. Larch species (*Larix* spp.), which widely predominate treelines in northern Siberia and Canada, do not reach Fennoscandia due to their distribution history[21]. However, the present distribution of forestline trees does not necessarily indicate their potential distribution or limiting ecological factors. Many tree species are able to withstand the short growing seasons, low minimum

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temperatures, seasonal changes in day length, and relatively low availability of nutrients in soils characterizing the northernmost ecosystems[13,15,19,22,23].

In Finland, mountain birch [*Betula pubescens* Ehrh. subsp. *czerepanovii* (Orlova) Hämet-Ahti], a subspecies of downy birch (*Betula pubescens* Ehrh.), dwarf birch (*B. nana* L.), and their hybrids form the subarctic treeline. In addition to downy and dwarf birch, silver birch (*B. pendula* Roth) occurs naturally in Finland and is known to hybridize with other birch species. Hybridization is particularly common in northernmost Finland, where the short growing season and extreme light conditions are thought to promote it[24]. Both downy and silver birch have economic importance, but silver birch is considered a higher-quality saw timber, veneer, and plywood[25–27]. For this study, we selected silver birch as a model species because it is only rarely found as natural stands above latitudes 65°–67°[28,29], but is likely to expand its distribution range northwards due to climate warming. If natural hybridization occurs more commonly in higher latitudes, we assume that the frequency of hybrids increases in maternal lineages during the northward range expansion of the species. The questions are, however, (1) how abiotic and biotic selection forces filter the species invasions, shaping genetic and species diversity; and (2) how the adaptive evolution of species determines ecosystem functions and services of a subarctic forest–tundra transition region.

To study the adaptive potential of *B. pendula* in the subarctic forest-tundra transition zone, we examined genetic variation of *B. pendula* climate tolerance in two arboreta 500 km north of the Arctic Circle, established in northern Finland (latitude 69°) in the mid-1970s[18]. The arboreta are situated in two divergent habitats along an altitudinal gradient from a forested river valley to the forest-tundra boundary 60 km north from the species present natural occurrence. Similarly to other tree species in the circumpolar Arctic treeline[15], the poleward expansion of silver birch distribution is commonly assumed to largely be limited by temperature and soil fertility[30] as well as by the availability of pollen for self-incompatible trees[31]. Low temperatures, along with a short growing season, primarily limit seedling establishment and then photosynthesis and, therefore, tree growth[32,33]. Furthermore, biotic factors such as plant pathogens and herbivores play crucial roles in modulating tree growth, reforestation, and forest succession[34]. Larger vertebrate herbivores, in particular, have been shown to shape treeline vegetation in northern natural ecosystems[35–39]. In northern Fennoscandia, the semi-domesticated reindeer grazing freely in the area favor birch in their diet, thus preventing the regeneration of birch forest, while coniferous trees are left intact[40,41]. Thus, we assume that the prevalence of pine and spruce will increase in Fennoscandia due to climate change in the future.

The successful establishment of silver birch in the studied arboreta, which were fenced to exclude large grazing vertebrates, demonstrates that the species can rapidly expand its range into new geographical areas northward from its current range in the absence of vertebrate grazing. However, we hypothesized that the survival and growth of trees vary among tree genotypes and in general would be higher in *Arboretum 1*, situated in the forested river valley with a longer and warmer growing season compared to *Arboretum 2*, situated higher in altitude on the forest-tundra boundary.

Materials and methods

Study area

This study was conducted near Kevo Subarctic Research Station (69° 45′ N, 27° 01′ E) in the municipality of Utsjoki in Finnish Lapland. Biogeographically, the ecoregion represents the subarctic forest-tundra transition zone with Fennoscandian mountains and fells rolling between 80 and 400 m above sea level and rivers running to the Arctic Ocean through the landscape in valleys. Mountain birch (*Betula pubescens* subsp. *czerepanovii*) forms the treeline in the area[16,42]. As a result of the favorable microclimate, conifers (*Pinus sylvestris*) grow mainly in the river valleys at the species' northernmost limit.

The geographical location of the study area provides a unique opportunity to examine how climate change affects the Arctic treeline. Subarctic Fennoscandia is characterized by relatively simple ecosystems, long winters, short growing seasons, and particularly seasonal changes in day length. The long-term data collected by the Finnish Meteorological Institute (www.ilmatieteenlaitos.fi) reveals that the mean annual temperature has increased by 1.2 °C during the last 60 years (mean annual temperature 1962–1981 – 2.1 °C; 1982–2001 – 1.4 °C; 2002–2021 – 0.9 °C), supporting the global climate scenarios of warming during the last decades. Consequently, the average thermal growing season (days with a mean temperature > + 5 °C) has become two weeks longer during the last 20 years (1961–1981 114 days; 1982–2001 114 days; 2002–2021 130 days). The mean annual precipitation was 395 mm, 442 mm, and 414 mm in Utsjoki, Kevo for the years 1962–1981, 1982–2001, and 2002–2021, respectively. However, as the study area is situated 500 km north of the Arctic Circle, two months of the polar night in winter, limiting primary production, is a stable, abiotic environmental factor that does not change with local or global climate.

Arboreta

To study the adaptability of arctic treeline species to subarctic conditions, the Kevo Subarctic Research Station of the University of Turku, National Board of Forestry and Forest Research Institute (Natural Resources Institute Finland, Luke, since 2015) established three treeline arboreta in Finnish Lapland in the 1970s with seed material obtained circumpolarly[18]. In this study, we used two of them (*Arboretum 1* and *Arboretum 2*; Table 1) situated 9 km apart in different vegetation types, temperature zones, and altitudes. *Arboretum 1* (69° 46′ N, 27° 01′ E) is situated in a mixed pine/birch forested river valley 90 m above sea level (a.s.l.). In contrast, *Arboretum 2* (69° 49′ N, 27° 08′ E) is located higher in altitude, at 270 m a.s.l., where mountain birch is still sparsely growing but the landscape is gradually turning into treeless tundra.

Both arboreta are ca. 4 hectares in size and fenced with a 2.5 m high wire gauze to exclude reindeer and other large grazing vertebrates. Before the trees (mainly birch, larch, pine, and spruce) were planted in the arboreta,

	Arboretum 1	**Arboretum 2**
Coordinates	69° 46′ N, 27° 01′ E	69° 49′ N, 27° 08′ E
Height above sea level	90 m	270 m
Natural trees around garden	Mountain birch, Scots pine, river valley	Mountain birch, tree line
Average growing season*	124 days	105 days
Total temperature sum dd5*,**	573	443
Mean temperature*	−1.5 °C	−1.8 °C
Mean temperature in June-August*	10.1 °C	8.7 °C
Lowest average monthly temperature* (January 1993)	−25 °C	−19 °C
Lowest measured temperature*	−40 °C	−32 °C
Soil type	Sandy till, low humus	Sandy till, low humus
Soil electrical conductivity	0.66 mS/cm	0.42 mS/cm
pH	5.3	5.3
Ca	81 mg/l	165 mg/l
P	< 1.5 mg/l	1.5 mg/l
Storage phosphate	220 mg/l	178 mg/l
Ammonium nitrogen (NH_4^+)	< 0.02 mg/l	0.13 mg/l
Nitrate (NO_3^-)	0.03 mg/l	0.14 mg/l
K	21 mg/l	31 mg/l
Mg	< 20 mg/l	33 mg/l
S	31 mg/l	15 mg/l
B	< 0.15 mg/l	< 0.15 mg/l
Cu	0.5 mg/l	0.9 mg/l
Mn	7 mg/l	15 mg/l
Zn	< 1 mg/l	1.5 mg/l

Table 1. Environmental information from *Arboretum 1* and *Arboretum 2*. Soil analyses results are means from five (*Arboretum 1*) and six (*Arboretum 2*) samples. *Average of years 1993–1996 **dd5 = accumulated temperature sum of the days when mean temperature is > + 5 °C

Mother tree code	**Site**	**Coordinates**	**a.s.l.[a] (m)**	**Arboretum 1[b]**	**Arboretum 2[b]**
R2	Inari, Partakko, FI	69° 14′ N, 27° 55′ E	140	6 (95)	3 (32)
R12	Inari, Kaamanen, FI	69° 04′ N, 27° 12′ E	160	6 (94)	3 (48)
R4	Inari, Kaamanen, FI	69° 01′ N, 27° 01′ E	175	6 (96)	3 (48)
R6	Inari, Myössäjärvi, FI	68° 50′ N, 27° 18′ E	160	6 (95)	3 (48)
R11	Inari, Menesjärvi, FI	68° 47′ N, 26° 35′ E	200	6 (96)	3 (48)
R5	Inari, Ivalo, FI	68° 40′ N, 27° 35′ E	120	6 (96)	2 (32)
R10	Kittilä Sileävaara, FI	68° 01′ N, 25° 12′ E	260	6 (96)	3 (48)
R9	Kittilä, Sileävaara, FI	68° 01′ N, 25° 12′ E	260	6 (95)	3 (48)
S	Kittilä, Sätkenä, FI	67° 43′ N, 24° 51′ E	200	6 (95)	3 (48)

Table 2. *Betula pendula* mother trees with original site information and their half-sibs in treeline *Arboretum 1* and *Arboretum 2*. [a]a.s.l. = above sea level. [b]Number of blocks with 15–16 half-sib trees of a family (total number of study trees).

the native trees were removed and soils were ploughed with a chain rototiller to mix the humus layer with sand and gravel, but the soils were not fertilized[18].

To analyze soil quality in the arboreta, we collected samples from five spots in *Arboretum 1* and six spots in *Arboretum 2* in July 2019. The available humus layer was dug with a small shovel into a bucket, and the rocks and plant material were sieved from the sample. Trace elements, some microelements, pH, and other soil characteristics (Table 1) were analyzed in a certified commercial Eurofins (eurofins.fi) laboratory.

To obtain a detailed microclimate data set to compare the possible temperature differences between the arboreta, the air temperature was measured continuously at three-hour intervals from 1993 to 1996 with data loggers at 2 m height from the ground in both arboreta.

Here, we focus on progenies from nine *Betula pendula* open-pollinated mother trees, hereafter called families, planted in *Arboretum 1* and *Arboretum 2* (Table 2). As the mother trees were naturally wind-pollinated and self-incompatible, we assume the families to mainly consist of half-sibs although full-sibs cannot be ruled out. The seeds were collected from naturally growing *B. pendula* individuals from the northernmost distribution range of the species, from latitudes 67° to 69° and altitudes 120–260 m. Because the mother trees were sporadically growing in the collection sites, and the species commonly hybridize with mountain birch, *B. pubescences* spp. *czepanovii*, dominating the treeline, families may include natural hybrids[43].

The mother trees were at least 6 m tall and their diameter, at 1.3 m, was more than 20 cm at the time when the seeds were collected. Some of the trees were the northernmost single silver birch individuals, but others originated from more contiguous forests (families R9, R10, S) 80–200 km south from the arboreta used in this study. The seeds were germinated and saplings grown in a nursery in Kittilä (67° 66′ N, 24° 93′ E), northern Finland for three years before planting in the arboreta in 1977.

In the arboreta, the tree saplings were planted in rows in blocks of 16 trees (block = usually 16 individuals of a family; 6 out of 81 blocks in total had 15 individuals). In *Arboretum 1* we used six blocks and in *Arboretum 2* we used three blocks from each *B. pendula* family (except the R5 and R2 which had two blocks in *Arboretum 2*).

Survival and growth measurements

Because the survival probability of trees commonly varies across life stages, we examined the survival of the trees distinguishing two critical junctures. First, we analyzed sapling establishment, examining survival after the first five years, and then we re-recorded the survival in the summers of 2017 and 2018 when the trees were about forty years old. To estimate the size variables of these mature trees, we measured the tree height, stem diameter at 1.3 m (diameter at breast height = dbh), and the number of stems (classes 1, 2, or 3 or more stems under dbh).

Statistical analyses

The number of trees (per family and total number) vary between analyses, as more advanced analyses omit trees with missing variables. Survival was analyzed using all 1258 trees (704 of them in *Arboretum 1*). Trees shorter than 2 m were omitted from size analyses due to problems in the residual analysis of the models. These more than 40-year-old trees may have been injured or had otherwise poor growth. Short trees were more common in *Arboretum 1* (70 trees) compared to *Arboretum 2* (3 trees). Complete data for height analysis on trees taller than 2 m was available for 497 trees in *Arboretum 1* and 315 trees in *Arboretum 2*, and diameter (dbh) for 641 trees in *Arboretum 1* and 312 trees in *Arboretum 2*.

All analyses were conducted in R (version 4.4.) using linear mixed models of the package *lme4*. Procedure *lmer* was used for tree height and stem diameter and procedure *glmer* for survival and the number of stems. For trees alive after 40 years, we analyzed the effect of arboretum, family, and the number of stems (classes 1, 2, or more) on tree size measured as height and diameter. Block (in *Arboretum 1* blocks 11, 12, 13, 14, 15, 16; in *Arboretum 2* blocks 21, 22, 23) was used as a random factor. Survival (tree dead or alive after 40 years) was analyzed using a logit model and the binomial link function. The number of stems was analyzed as a dichotomous response variable, i.e., monocormic vs. having several stems. Fixed predictors were arboretum, family and their interaction, and block was used as a random factor. Diagnostics of the models were conducted. The R package *lmerTest* and the Akaike information criterion (AIC) were used to compare the models, and post-hoc analyses were conducted using pairwise contrasts in the *emmeans* package. The procedure *Anova* from the *car* package was used to get the Chi-square values for the traditional anova-tables. We are aware that they are based on Wald tests, and may thus be unreliable. In comparing the hierarchical loglikelihood-models, we focused on the term that differed between the models. In most cases this was the interaction (arboretum*family). In two cases (survival and the number of stems) this comparison gave higher Chi-square (and lower p)-values compared to Wald-tests. In these cases we report the more reliable Chi-value for the interaction and Wald-tests for other predictors.

Results

Weather

Due to the difference in altitude, the mean temperature in June, July, and August in the years 1993–1996 was 1–2 °C higher in *Arboretum 1* than in *Arboretum 2*. The growing season was on average two weeks longer in *Arboretum 1*. In contrast to summer temperatures being higher in *Arboretum 1*, the highest winter temperatures were measured in *Arboretum 2*. The lowest average monthly temperature (January 1993) was − 25 °C in *Arboretum 1*, while in *Arboretum 2* it was − 19 °C (Table 1). Furthermore, the lowest measured temperature in *Arboretum 1* was − 40 °C, while temperatures lower than − 32 °C were never recorded in *Arboretum 2* during the monitoring period (Table 1, Fig. 1). This phenomenon is due to the persistent inversion during the winter months in the area[44].

Soil

In both arboreta, the soil type is sandy till with low-medium humus content; the soil pH was 5.3, and the phosphate (P) content remained below the analyzing threshold value (< 1.5 mg/l). Soil nitrogen content (both NH_4 and NO_3) was very low in both arboreta but higher in *Arboretum 2* compared to *Arboretum 1* (Table 1). Overall, the available micro- and macronutrients in the soil were more abundant in *Arboretum 2* compared to *Arboretum 1* (Table 1).

Survival rates of the trees

Five years after the establishment of the arboreta, 90% of the experimental trees were still alive. The survival rate was higher ($\chi^2 = 7.4$, df = 1, $p = 0.007$) in *Arboretum 1* (92%) compared to *Arboretum 2* (85%). Early survival rates of the trees among the families did not differ between the arboreta ($\chi^2 = 8.8$, df = 8, $p = 0.36$) or in *Arboretum 2* ($\chi^2 = 2.8$, df = 8, $p = 0.941$, range from 79 to 90%) but tended to differ within *Arboretum 1* ($\chi^2 = 13.8$, df = 8, $p = 0.087$, range from 87 to 98%).

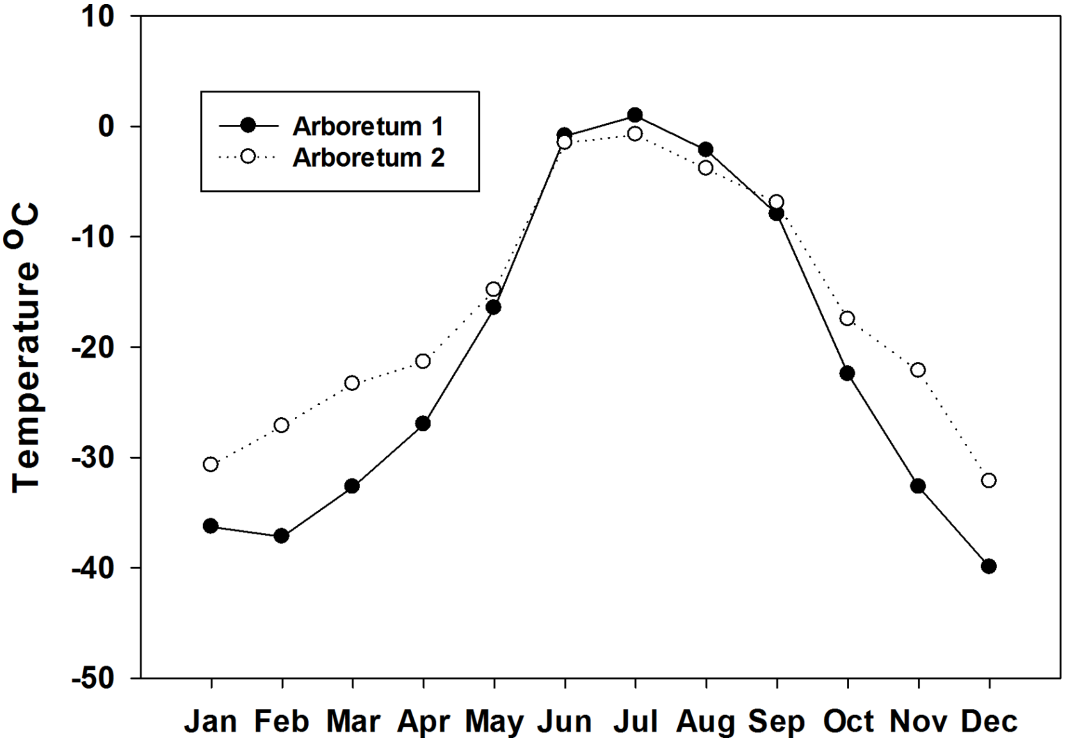

Fig. 1. Lowest monthly temperature in *Arboretum 1* and *Arboretum 2* in 1993–1996 measured with data loggers at 2 m height from the ground.

	df	Chisq	*P*
Arboretum	1	1.178	0.278
Family	8	24.31	0.002**
Arboretum * Family	8	14.49	0.042*

Table 3. Survival of *Betula pendula* trees in the two arboreta after 40 years of planting. Survival of each tree was analyzed in both arboreta (*Arboretum 1* and *Arboretum 2*) and all nine families together with their interactions.

Overall, 81% of the trees survived until the end of the 40-year period. In contrast to survival rates during the first 5 years, the survival rate after 40 years varied among the families but interactively within arboreta (Table 3; Fig. 2). Total survival rate in *Arboretum 1* was 82% (ranging from 69% in R10 to 93% in R9), and in *Arboretum 2* 79% (ranging from 69% in R9 to 88% in R10). Although survival rates varied interactively between families and arboreta ($\chi^2 = 14.5$, df = 8, $p = 0.032$), differences between the arboreta were mainly due to interactions (direct comparison between the arboreta $\chi^2 = 0.8$, df = 1, $p = 0.37$). Post-hoc analysis revealed statistically significant differences between family R4 with the highest survival rate and family R10 with the lowest survival rate in *Arboretum 1* (z = 3.9, df = inf, $p = 0.01$).

Number of stems

Overall, the number of stems per tree did not differ between the gardens ($\chi^2 = 1.25$, df = 3, $p = 0.53$). Proportion of monocormic (one stem) trees was 73% in *Arboretum 1* and 76% in *Arboreta 2*. The proportion of monocormic trees was highest in family R11 (81%) and lowest in R9 (67%) and R4 (68%), but the differences were not statistically significant ($\chi^2 = 20.1$, df = 16, $p = 0.217$). However, families performed differently in terms of the stem number in the two arboreta (Table 4). This interaction between family and arboreta was explained by three families differing from each other in the proportion of monocormic trees in the two arboreta. The proportion of monocormic trees of two families was higher in *Arboretum 2* (R2: 96%; R5: 96%) compared to *Arboretum 1* (R2: 63%; R5: 73%). In contrast, the proportion of monocormic trees of family R11 was higher in *Arboretum 1* (85%) compared to *Arboretum 2* (72%).

Size of the trees

All the analyses suggest that trees had more vigor in *Arboretum 2*, and the family-mean size varied interactively within arboreta. On average, trees were 2 meters higher in *Arboretum 2* (mean 6.64 m ± SE 0.07 m, median = 6.8 m)

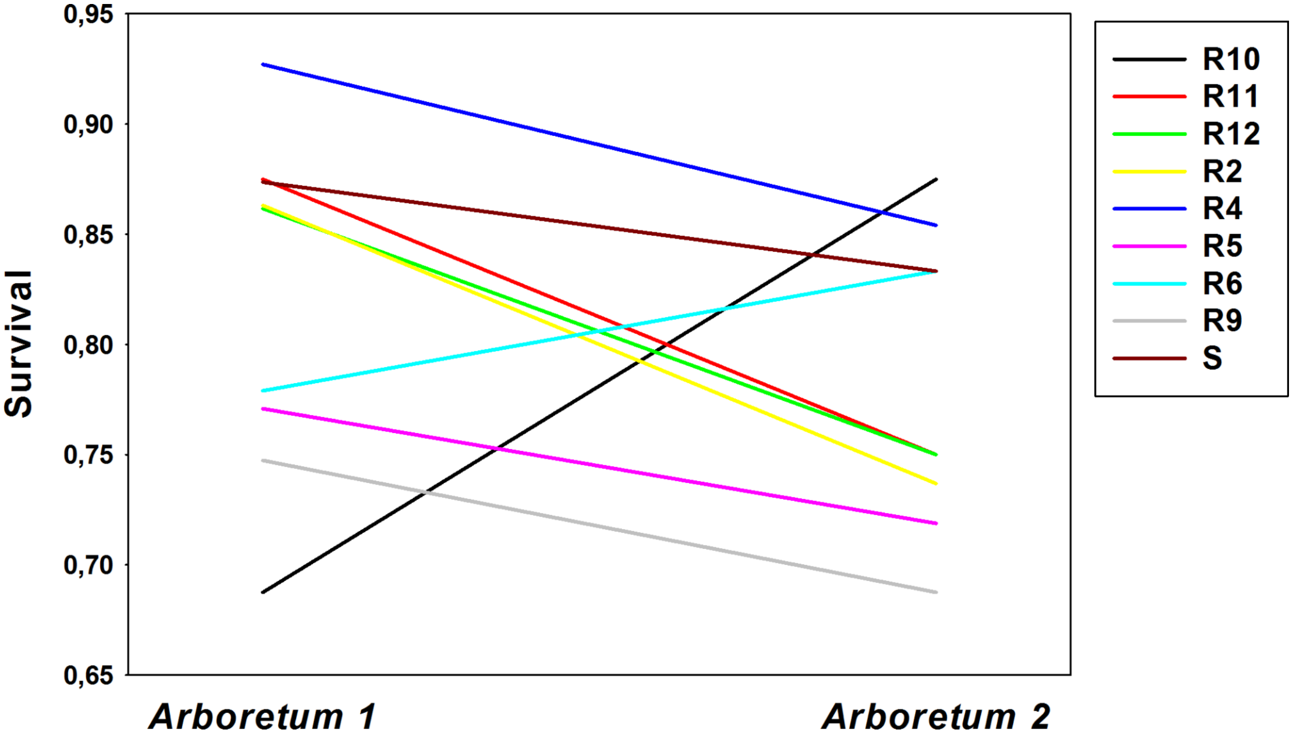

Fig. 2. Survival of nine *Betula pendula* families in *Arboretum 1* and *Arboretum 2* varied interactively between the arboreta after forty years of planting.

	df	Chisq	*P*
Arboretum	1	0.01	0.918
Family	8	13.321	0.101
Arboretum * Family	8	23.76	0.006**

Table 4. Monocormic status (one stem) of *Betula pendula* trees in the two arboreta after 40 years of planting. Status was analyzed in both arboreta (*Arboretum 1* and *Arboretum 2*) and all nine families together with their interactions. Test of the interaction term is based on loglikelihood comparison of the models with (AIC 1172.4) and without (AIC 1183.4) the interaction term.

compared to *Arboretum 1* (mean 4.43 m ± SE 0.09 m, median = 4.5 m). Furthermore, the proportion of trees shorter than 2 m was lower in *Arboretum 2* (3 trees) compared to *Arboretum 1* (70 trees) ($\chi^2 = 35.5$, df = 1, $p < 0.001$). The proportion of short trees varied among families ($\chi^2 = 30.5$, df = 8, $p < 0.001$). In *Arboretum 1*, the highest proportion of short trees was found in families R10 (18%) and R9 (15%), both of which were also the weakest families in terms of their survival rates (Fig. 2). In other families the proportion of short trees ranged between 4 and 12%.

We omitted trees below 2 m from more detailed statistical analyses of height due to problems with normality. In the remaining data, the average height of trees in *Arboretum 1* increased (mean = 4.80 m ± SE = 0.08 m, $n = 445$) but remained unchanged in *Arboretum 2* (mean = 6.70 m ± SE 0.06 m, $n = 312$). Similarly, the dbh (diameter at 1.3 m) was about 77% higher in *Arboretum 2* (mean 12.1 cm ± SE 0.18 cm, median = 9.4 cm) compared to *Arboretum 1* (mean 7.3 cm ± SE 0.16 cm, median = 7.0 cm). The difference between the arboreta was statistically significant both for height (t = 17.6, df = 743.0, $p < 0.001$) and dbh (t = 168.0, df = 542.8, $p < 0.001$).

Arboretum, family, and their interaction significantly affected tree height (Fig. 3; Table 5) 40 years after planting. Post-hoc analysis indicated that in *Arboretum 1* the highest family R2 differs from families R10, R9, and R11 (t = 6.3–8.1, df = 750 for all within arboreta contrasts, $p < 0.001$); the shortest families, R10 (t = 4.2–6.2, $p < 0.01$) and R9 (t = 3.6–5.4, $p = 0.0001–0.03$), also differed from the group of next highest families, R6, R5, R4, and R12 (Fig. 3). The families did not differ statistically significantly in *Arboretum 2*. Families R9 and R11 were at the borderline to differ between the arboreta ($p = 0.08$). According to the model, trees with one stem were 18 cm higher compared to trees with two stems, and 63 cm higher compared to trees with three or more stems.

Tree dbh was measured for the 465 and 313 trees with dbh more than 2 cm in *Arboretum 1* and *Arboretum 2*, respectively. Arboretum, family, their interaction, and stem number affected dbh (Table 6). Diameter for monocormic trees was 0.7 cm thicker than two stem trees and 1.5 cm thicker compared to trees with three or more stems. Post-hoc analysis (Fig. 4) indicates that in *Arboretum 1* the thickest family, R2, differed from the

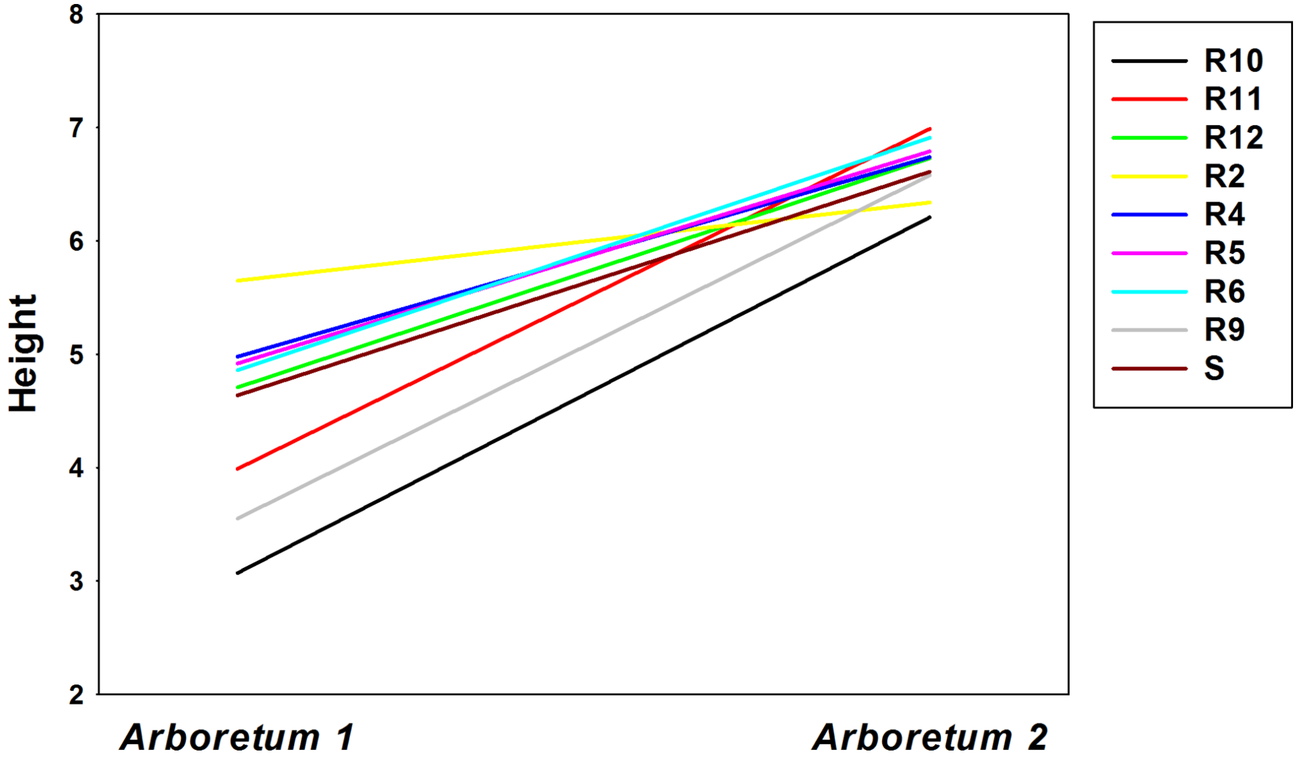

Fig. 3. Linear predictions for tree height of nine *Betula pendula* families in *Arboretum 1* and *Arboretum 2* after forty years of planting. Data from the model shown in Table 5.

	df	Chisq	*P*
Arboretum	1	9.42	0.002**
Family	8	77.40	< 0.001***
Arboretum * Family	8	42.15	< 0.001***
Number of stems	2	9.15	0.010*

Table 5. Height of *Betula pendula* trees in the two arboreta after 40 years of planting. The height of each tree was analyzed in both arboreta (*Arboretum 1* and *Arboretum 2*) and all nine families together with their interactions. Short trees below 2 m were omitted from the analysis.

	df	Chisq	*P*
Arboretum	1	18.3	< 0.001***
Family	8	29.8	< 0.001***
Arboretum * Family	8	24.8	0.002**
Number of stems	2	20.5	< 0.001***

Table 6. Stem diameter at 1.3 m (dbh) of *Betula pendula* trees in the two arboreta after 40 years of planting. Stem dbh of each tree was analyzed in both arboreta (*Arboretum 1* and *Arboretum 2*) and all nine families together with their interactions.

thinnest families, R10, R11 (t-values from 5.1 to 4.0, df = 683, $p < 0.01$), R5, and R9 (t = 3.58–3.53, $p < 0.05$). In *Arboretum 2*, the thickest families, R12, R11, and R9, differed from the thinnest family R10 (t from 5 to 4.2, p from 0.001 to 0.04). Family R9 also differed between the arboreta (t = 4.8, $p = 0.042$).

Discussion

In accordance with the hypothesis, our results demonstrate that the acclimation capacity of northern silver birch (*Betula pendula*) allows the expansion of its distribution north from its present range. Overall, 81% of the 1258

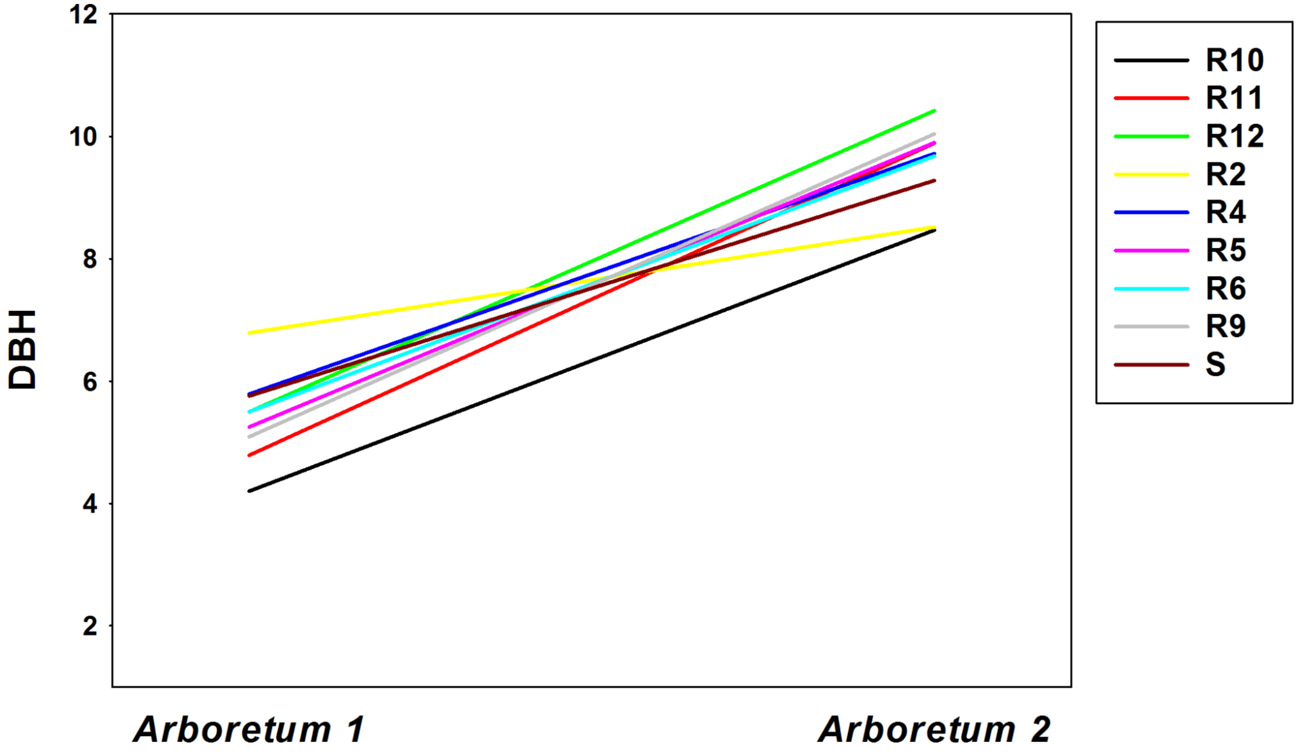

Fig. 4. Linear predictions for tree trunk diameter (dbh measured at 1.3 m) of *Betula pendula* trees in the two arboreta after 40 years of planting. Data from the model shown in Table 6.

trees representing the nine half-sib families selected for this study were alive 40 years after planting about 60 km north of the species' most northern natural growth site.

Survival rates and growth of trees differed between the two arboreta located in distinct altitudinal environments. However, contrary to the hypothesis, the trees were more vigorous in *Arboretum 2*, which is higher in altitude on the forest-tundra boundary. These results emphasize the importance of other environmental factors than climate warming alone to the distribution range of a species in the higher latitudes. The complex interplay between multiple environmental factors can affect the genetic structure of populations and the phenotypic differentiation of species across temporarily dynamic territorial habitat mosaics. The unanswered questions are: (1) What are the environmental factors that have prevented the establishment of silver birch in Fennoscandian treeline ecosystems? and (2) Why were the trees particularly vigorous in the high-elevation forest-tundra transition zone? Unarguably, freely grazing semi-domesticated reindeer prevent the regeneration of birch forests in subarctic Fennoscandian mountain ecosystems[45], but this solely fails to explain why the tree line ecotone is dominated by closely related mountain birch (*Betula pubescens* spp. *czerepanovii*). Other purported abiotic forces limiting the expansion of silver birch include soil fertility and temperature[13,30]. Our finding that trees were more vigorous in *Arboretum 2* with higher soil nitrogen content suggests that soil fertility may regulate silver birch survival and growth. Furthermore, the tree genotypes differed in their resilience to temperature, being highest in the families with the northernmost origin. In addition, our results revealed that the performance of tree genotypes varied when they were subjected to different abiotic environments, commonly referred as genotype-environment (GxE) interactions in literature.

None of the tree families was supreme over the others, and the differences between them were slight, especially in *Arboretum 2*. In *Arboretum 1*, the size of trees belonging to family R2 differed from most other families (R5, R9, R10, and R11), as it produced both the tallest and largest dbh trees. However, in *Arboretum 2*, the progeny of the family R2 turned out to be the next to worst both in tree height and trunk dbh. These results indicate that R2 may be better adapted to the colder winter temperatures in *Arboretum 1*. However, compared to other families, R2 appears to benefit less from the more fertile soil or other favorable conditions present in *Arboretum 2*. Family R2, together with family R12, are from the most northern mother trees, and both families showed average survival rates in both arboreta. However, family R12 was growing better in *Arboretum 2* and produced there the largest dbh.

Other studies have revealed that long-distance cross-latitudinal transfer within the species distribution range can negatively affect the survival and growth of silver birch as well as some other tree species[46–48]. In contrast to these past studies, we examined the birch performance north of its current range. The performance of the family R10 collected from the southern end of the family gradient (~ 250 km south from arboreta) strikingly differed from the other families. It produced the shortest trees with the smallest dbh in both arboreta, and its survival rate was the lowest of all families in *Arboretum 1*. However, its survival rate was the highest in *Arboretum 2*, demonstrating that differences in the responses of tree genotypes to environmental variation may determine the species' distribution potential and the evolution of birch populations[49,50]. Mother trees for families R4 and R9 grew close to R10, but their survival rates were quite opposite: R4 was among the best in both arboreta, and R9 among the worst in both arboreta. R4 produced thick trunks in *Arboretum 1*, and R9 in *Arboretum 2*.

The small size of the tree (height below 2 m) after 40 years of planting indicates severe problems in the growth history of the individual. Most likely frost, heavy snow, or browsing have repeatedly cut off or killed the shoot. Severely damaged mountain birch growing in the area can, however, often recover by sprouts from dormant basal buds if the root stays alive[45]. Notably, the two families R9 and R10 with the highest number of short trees in *Arboretum 1* also had poor survival rates in *Arboretum 1*. The families represent the two southernmost mother trees, and the result may thus reflect their poor adaptation to more northern conditions. However, a third southern family S appears to be capable to cope with these conditions. Overall, the tree families from the northernmost limits of the species range are well adapted locally. However, all of the families grew better in *Arboretum 2* compared to *Arboretum 1* suggesting phenotypic plasticity.

The differences among the tree families' performance may also reflect their ancestral variation derived from hybridization. Recently, hybridization has been recognized to play a significant role in adaptive evolution and radiation particularly in higher latitudes within the Arctic circle where stabilizing selection by a combination of seasonal variation of day length and a short growing season should narrow the variance in reproductive timing and increase the synchrony of reproductive phenology among species[50]. Birch species show high levels of hybridization and introgression, especially in northern conditions[16,51–54]. The study region, the subarctic birch zone of the Fennoscandian forest tundra[55], is dominated by mountain birch (*B. pubescens ssp. czerepanovii*), dwarf birch (*B. nana*), and their hybrids, which are well adapted to harsh conditions. The great success of mountain birch in the northernmost treeline ecotone is partly explained by its vigorous vegetative regeneration ability by basal sprouts after tree damage caused by reindeer, insect outbreaks, fires, severe winter weather, and deforestation by human activities[45,56]. In contrast, as silver birch (*B. pendula*) is monocormic, we should not rule out that the higher resilience of some of the studied families detected in *Arboreta 1* is a result of a vegetative re-establishment ability gained from introgressive hybridization with the mountain and/or dwarf birch. Silver birch and dwarf birch are of the same ploidy, and hybrids between them are known to occur both spontaneously and as a result of artificial crossings[43]. Birch is mainly self-incompatible[31], but the overlapping distribution ranges, anthesis of the species, and the clear minority of silver birch pollen compared to other birch species may contribute to the hybridization. Thus, our results call for taking into account hybridization in future studies.

As the external biotic causes of damage by reindeer grazing were prevented by enclosures in this study, we propose that higher winter temperatures in conjunction with higher soil nutrition explain the more vigorous performance of the trees in *Arboretum 2* situated in the forest-tundra ecotone. Cold-air accumulation at low elevations is well known to be critical for plants and animals[57–59]. In the study area, temperature differences of up to 5 °C are commonly detected between the extremes of altitudinal gradient in most months of the year, and intensities can reach 15 °C during the winter months[59]. Thus, we suggest that the ponding of cold air in *Arboreta 1* at low elevation has controlled the survival and growth of the study trees depending on their genetically determined ability to recover vegetatively with basal shoots.

We conclude that in the absence of vertebrate grazing inhibiting seedling regeneration, the acclimation ability of *B. pendula* allows it to expand its range poleward in northern Europe. However, contrary to our hypothesis that trees would perform better in forested river valleys — where the growing season is longer and warmer—trees were more vigorous in the arboreta situated in higher-altitude area at the forest-tundra boundary. Winter temperatures presumably play a more crucial role than climatic conditions during the growing season. Accordingly we propose that cold-air pooling in valleys due to temperature inversion during winter may canalize the distribution of the most well-adapted tree genotypes, favoring their establishment on hilltops within the forest-tundra transition zone in the future. The detected differences among families suggest that they are distinctively adapted to local conditions. These differences may arise from epigenetic control of gene expression, resulting in varying levels of phenotypic plasticity of the trees, or from hybridization. A key question for future studies is whether introgressive hybridization facilitates the recovery ability of the trees and promotes the expansion of the silver birch distribution range into the northernmost treeline ecotone.

Data availability

The datasets used and/or analysed during the current study available from the corresponding author on reasonable request.

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Author contributions

KS wrote the main manuscript. All authors collected the data and IS analysed it. All authors reviewed the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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