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Leading directions and effective distance of larch offspring dispersal at the upper treeline in the Northern and Polar Urals, Russia

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ABSTRACT

Climate has changed sufficiently over the last 150 years and forced out upper treeline advance at the most studied sites around the world. The rate of advance has been extremely variable – from tens to hundreds meters in altitude. This is because the degree at which tree frontal populations respond to climate change depends on the complex interaction of biological and physical factors. The resulting stand pattern is the consequence of the interaction between dispersal and survival functions. A few publications have addressed the question of how this pattern is generated. In order to understand how the spatial structure of tree stands was formed at the upper limit of their distribution in the Ural Mountains, we assessed the distance and direction of dispersal of offspring from maternal individuals. We found that in frontal *Larix sibirica* Ledeb. populations, 'effective' dispersal of offspring ranges from 3 to 758 m (with a median of 20–33 m in open forest and 219 m in single-tree tundra in the Polar Urals and 107 m in open forest in the Northern Urals). We revealed that most of the offspring effectively dispersed not only in the direction of the prevailing winds, but also in the opposite direction up the slope, and the distance can reach 500–760 m. The data obtained can be used to develop an individual-based model which is capable of simulating in detail the dynamics of tree stands at the upper limit of their growth and reliably predicting the future position and pattern of treeline ecotone as growth conditions continue to improve in the face of observed climate change.

1. Introduction

Climate has been changing rapidly since the end of the XIX century, especially in the polar regions and the highlands, and as it was predicted, these changes are likely to continue during this century (IPCC, 2021). This has already led to global species migration and range shifts (Freeman et al., 2018; Mamantov et al., 2021; Miller et al., 2020; Parmesan, 2006; Pauli et al., 2012; Walther et al., 2002; Zu et al., 2021). Model-based projections suggest that expected environmental changes would allow many species to expand their current range (Jump et al., 2009). Therefore, understanding and quantifying species responses to climate change is critical for land-use management and conservation (Greenwood and Jump, 2014). For example, mountain tundra is threatened by range contraction and biodiversity loss as the treeline advances upslope (Barredo et al., 2020; Greenwood et al., 2016). At the same time this will lead to the fragmentation of alpine habitats (Pauli et al., 2007), changes in carbon storage (Moiseev et al., 2022), nutrient cycling (Mayor et al., 2017) and hydrological characteristics of mountain ecosystems (Rasouli et al., 2019).

Investigations in the last decades have shown that the position of the upper treeline has already shifted upslope in 2/3 of the studied sites worldwide during the last hundred years, but the rate of advance was extremely variable - from tens to hundreds of meters in altitude (Hansson et al., 2021; Harsch et al., 2009). One of the main reasons for this for anemochorous trees is the different distance and source (local or lower elevation) of seeds dispersing beyond treeline (Körner, 2012). It is well known that most tree seeds disperse only a few tens of meters (Bullock and Clarke, 2000; Howe and Smallwood, 1982), because they tend to fall due to gravity and wind close to their source (Greene and Johnson, 1996; Robledo-Arnuncio and García, 2007). However, the rapid migration rates (10^2–10^3 $m \cdot yr^{-1}$) recorded for tree species at the end of the Pleistocene (MacDonald, 1993) are far too high to have been caused by such

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short-distance dispersal and required long-distance dispersal (LDD) events (Clark, 1998). This makes LDD very important in the demography and dynamics of tree populations (Hampe, 2011; Nathan, 2006), especially in the context of current climate change, as limited dispersal could threaten some plant populations (Pitelka, 1997; Trakhtenbrotl et al., 2005). However, it is quite difficult and time-consuming to precisely quantify the LDD event using of traditional methods, because it requires physically capturing, tagging and monitoring the dispersal of seeds with a trap (Greene et al., 2004). Traditional dispersal estimates are derived from natural or artificial wind-dispersed seed release experiments using traps placed at varying distances from isolated plants (Damschen et al., 2014; Howe and Smallwood, 1982; Nathan and Katul, 2005). They may only be suitable for use in a limited number of circumstances and to a specific type of landscape, because wind dispersal of seeds can be accurately measured only for one individual at a time with use of sticky trap or under artificial conditions in seed release experiments. It is common to chronically underestimate dispersal distance because they do not detect LDD events (Ashley, 2010; Nathan, 2006) and has problems identifying an individual that is the product of such event (Piotti et al., 2009). In addition, dispersal kernels assessed from direct observations can be misleading, failing to reflect the effects of population density and other factors that determine migration success (Steinitz et al., 2011; Sullivan et al., 2017). However, assessing effective offspring dispersal (successful dispersal of seeds with their germination and establishment of young trees) is biologically more important (Auffret et al., 2017; Nathan and Muller-Landau, 2000), because by showing where seeds come from and how far they are distributed to establish in tundra or alpine meadows, it will be possible evaluate the capacity of frontal tree populations to occupy new territories in a rapidly changing climate (Kruse et al., 2016).

The parentage analysis appears to be a promising method for helping to evaluate the distance and direction of effective offspring dispersal (Bacles et al., 2006; Wang and Smith, 2002). Repetitive sequences in the nuclear or mitochondrial genome (short sequence repeats (SSRs) or minisatellites and microsatellites - tandem repeats of 10–100, or less than 10 base nucleated pairs, respectively) are sufficiently variable genetic markers (Grosser et al., 2023; Schlotterer, 2000). Using these genetic markers and parentage analysis it is possible to determine the physical distance that each established individual has travelled from its maternal source by comparing the individual's genotype with that of its likely parents within a given area and identifying a parental match (Ashley, 2010). Such an analysis can be used to track seed dispersal across a mountainous landscape and determine effective seed dispersal distances. However, it is complicated by the need to perform a comprehensive survey of all individuals contributing genotypes in the area of interest (Johnson et al., 2017). This makes parentage analysis time-consuming for high-density or widely dispersed populations over large areas. However, modern methods of identifying the geographic location of objects using terrestrial laser scanning provide a unique opportunity to cover comparatively large areas (Chen et al., 2006; Liang et al., 2018). This technology is based on the acquisition of a large number of laser reflection points with high spatial resolution (1–3 cm) using special equipment (LiDAR), which makes it possible to determine the geographic position of objects quite accurately and to estimate the morphometric parameters of individual trees, even in high-density tree stands. On the other hand, classical dendrochronological methods allow to estimate the age of trees with a resolution of several years (Hagedorn et al., 2014) and to identify with certainty who is the mother or the offspring in a group of relatives.

Several studies (Johnson et al., 2017; Piotti et al., 2009; Pluess, 2011; Truong et al., 2007) have been conducted to assess the effective dispersal of offspring within or beyond the tree ecotone. This information can shed light on migration movements and reproductive success of trees in a colonization area characterized by extreme ecological conditions in the mountains and contribute to the development of more realistic individual-based models (Kruse et al., 2019; Wieczorek et al., 2017) that simulate tree stand dynamics at the individual level, from a seed to an established seedling to a mature tree that itself produces seeds and thus starts a new generation. In this study, we conducted a parentage analysis of *Larix sibirica* Ledeb. at the upper limit of its distribution in the Northern and Polar Ural Mountains, using an assay of five mitochondrial microsatellites, age and precise geographic position to obtain a reliable assessment of the effective distance and prevailing directions of progeny dispersal. In addition, we are trying to answer the question: “Do the seeds contributing to recruitment come from local tree populations, or from more distant seed sources?”

2. Materials and methods

2.1. Study sites

Part of the study was carried out on the eastern slope of the southern spur of Mt. Serebryanskii Kamen' (59.6285° N, 59.2751° E, Tylaisko–Konzhakovsko–Serebryanskii Massif, the Northern Urals) (Fig. 1). Shallow soils formed on clinopyroxenites and plagiogranites. Coarse-humus lithozems in complex with poorly developed cryoturbated soils are widespread on the tundra. Under open forests and the upper part of closed forests coarse-humus burozems in complex with coarse-humus lithozems are developed. The climate in this part of the Urals is cold and excessively humid. In the valleys, the average temperatures in July and January are 17.0 °C and −16.8 °C, respectively; annual precipitation is 500–700 mm in the mountain taiga and 1,200 mm beyond treeline. The period of air temperatures exceeding 5 °C lasts 145 days in valleys and 107 days on the treeline. Snow forms a permanent cover by the end of September and disappears in the beginning of May in valleys and on one month later in highlands. In summer months, western and south-western winds are usual. Average wind speeds range from 2.4 to 4.5 $m\cdot s^{-1}$, rising to 8–9 $m\cdot s^{-1}$ in the mountain tundra belt. The mountain forest belt reaches 850–900 m a.s.l. and consists mainly of Siberian spruce (*Picea obovate* Ledeb.), Siberian fir (*Abies sibirica* Ledeb.), Siberian stone pine (*Pinus sibirica* (Rupr.) Mayr.), Siberian larch (*Larix sibirica* Ledeb) and white birch (*Betula pubescens* Ehrh.). Open larch and mountain birch (*B. pubescens* Ehrh. ssp. *tortuosa* (Ledeb.) Nyman) forests and sparse stands are widespread within the treeline ecotone, which extends from 900 to 1,000 m a.s.l. The upper part of the mountains above 1,000 m a.s.l. is occupied by the mountain tundra and rocky barrens. The mountain tundra is dominated by vascular plants and the open areas between groups of larches are covered by various shrubs (*Betula nana* L., *Salix* sp.), dwarf shrubs (*Vaccinium* sp., *Empetrum nigrum* L., *Arctous alpine* L., *Dryas* sp.) and herbs (*Carex bigelowii* Torr. ex Schwein., *Festuca ovina* L., *Anemone narcissifolia* L. subsp. *biarmiensis* (Juz.) Jalas, *Polygonum bistorta* L., *Thalictrum alpinum* L.).

The study area in this region (width 160 m, length 280 m, area approx. 4.5 ha, elevation range 985–1,045 m a.s.l., Fig. 2) extends across the upper part of the tree ecotone from the open forest line to the upper larch individuals found, which represent the upper limit of the tree distribution. The comparably dense population begins below the lower boundary of the study area. The surveyed slope is even with no pronounced decreases or increases in mesorelief. Stone fields cover 40% of the study area. Soils are moderately moist. As shown our previous observation on that territory (Grigorieva and Moiseev, 2018), air temperature is 12.1 ± 1.2 °C in June–August and −11.2 ± 1.1 °C in November–April and insignificantly differ (on 0.2–0.4 °C) between upper and low range of study area. Maximal snowpack depth varies between 5 and 25 cm in upper part and 50–70 cm in low part elevation gradient. Soil temperature varies between −10 °C and −4 °C in winter and between 7 °C and 11 °C during growing period (Hagedorn et al., 2014, 2020).

The studies were also carried out on the eastern macroslope of the Polar Urals and are located 4 km east of Mt. Chernaya (1,036 m a.s.l.) on the south-eastern slope of the hill with the land mark 312 m a.s.l. (66.8206° N, 65.5563° E) (Fig. 1). Shallow soils (Haplic Umbrisol (Skeletic), Haplic Leptosol (Skeletic) and Entic Podzols (Skeletic)) are underlain by ultramafic rocks (Zhangurov et al., 2023). This is the area of sporadic permafrost. The mean air temperature in July is 14.2 °C and in January −22.1 °C

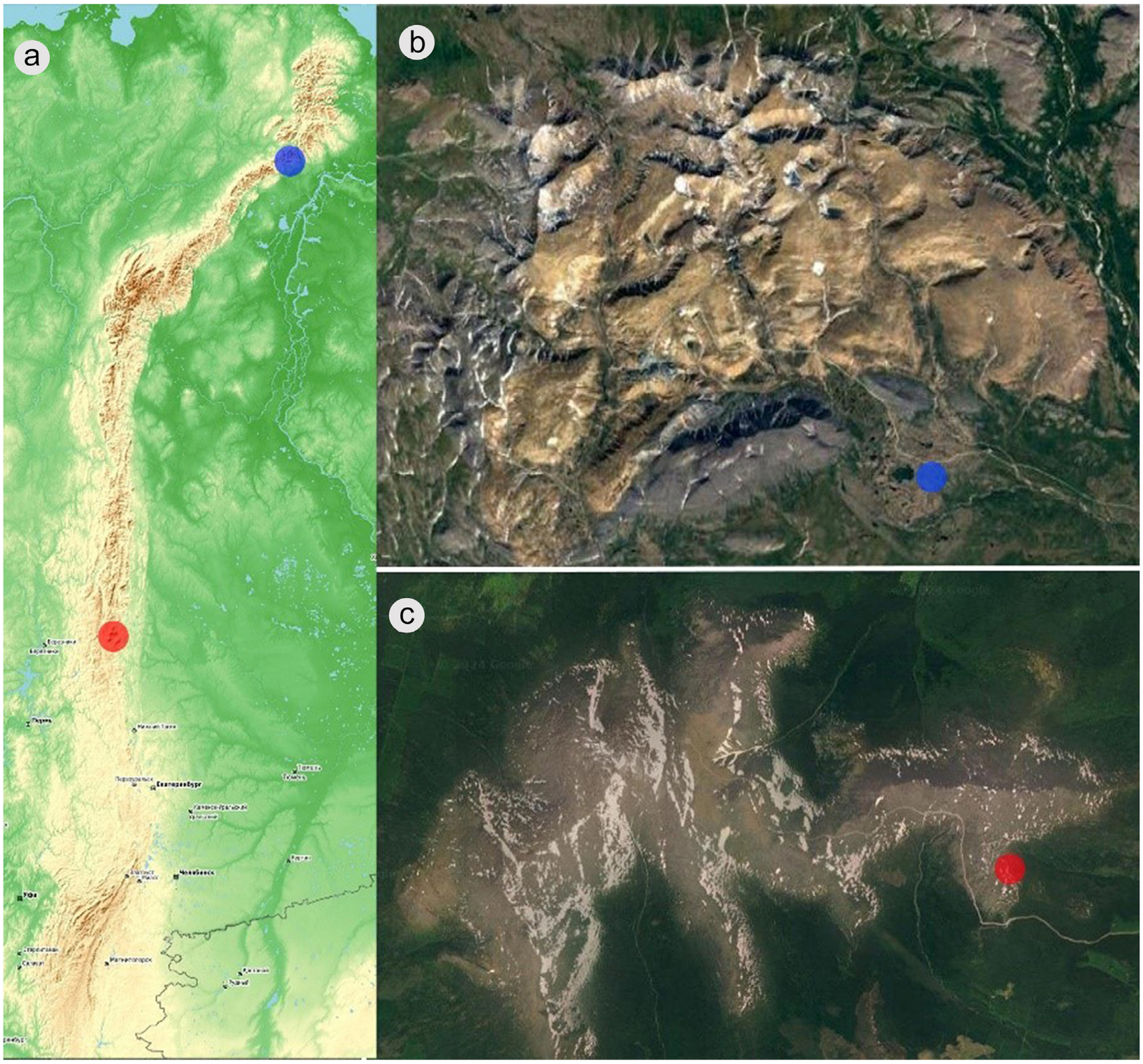

Fig. 1. Location of the study sites (eastern slope of the southern spur of Mt. Serebryanskii Kamen' - red dot; south-eastern slope of the hill with the elevation mark 312.8 m a.s.l. - blue dot) on (a) the Ural Mountains; (b) the area near Mt. Chernaya in the Polar Urals; (c) the Tylaisko-Konzhakovsko-Serebryanskii Massif in the Northern Urals. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

on the valleys floor and plains (Salekhard weather station, 15 m a.s.l., 56 km eastward from study site). However, on top of surrounding summits (weather station Rai-Is, 895 m. a.s.l., 10 km northward from study site) the temperature is 8.5 °C in July and −17.9 °C in January. The average annual precipitation on the valley floor is 460 mm, of which one third falls in summer. On the surrounding peaks, precipitation increases to 880 mm. The growing period (with air temperatures >5 °C) lasts 101–103 days. The snow cover lasts for about 240 days. In the warm season, westerly and south-westerly winds prevail, but in winter westerly and north-westerly winds are normal. Vascular plant dominants of mountain tundra and open areas between groups of larches (*Larix sibirica* Ledeb.) in the treeline ecotone (180–350 m a.s.l.) are the same as in the Northern Urals.

The Polar Urals study area (width 80–450 m, length 110 m, area approx. 30 ha, elevation range 245–312 m a.s.l., Fig. 2) is located in the Northern Urals across the upper part of the treeline ecotone. We surveyed part of slope with no pronounced decreases or increases in mesorelief, where moderately moist soils prevail. The boulder fields cover 5%–10% of studied territory. As shown our previous investigation (Grigorieva and Moiseev, 2018), air temperature is 11.8 ± 1.4 °C in June–August and −15.7 ± 1.6 °C in November–April and insignificantly differ (on 0.3–0.7 °C) between upper and low range of study area. Maximal snowpack depth varies between 10 and 30 cm in upper part and 50–80 cm in low part elevation gradient. Soil temperatures for the growing season range between 6.6 °C and 10.9 °C and are 7.6 ± 1.7 °C in average. Soil temperature varies between −12 °C and −6 °C in winter (Hagedorn et al., 2014, 2020).

At and beyond the treeline, thermal conditions deteriorate and wind loads increase rapidly with upward movement, greatly reducing the habitat in which tree seedlings can successively establish (Körner, 2012). As our previous results have shown, areas with optimal snow cover (not too shallow or too deep) are colonized by trees earlier and stand densities are now highest (Hagedorn et al., 2014). Other reasons that limit tree establishment are soils that are too wet or too dry, and very shallow soil cover or even its absence on boulder fields and rocks (Holtmeier, 2009). Our studies were carried out on slopes where the stoniness does not exceed 40% and the soil moisture content is close to average. In addition, there are no sites that are not covered with snow at all in winter or where snow accumulates in large drifts. In our assessment of effective dispersal of offspring, we specifically selected comparably homogeneous habitats and excluded sites that are extremely unsuitable for tree establishment. On the other hand, we intended to show processes on sites where non-climatic environmental factors were not pronounced.

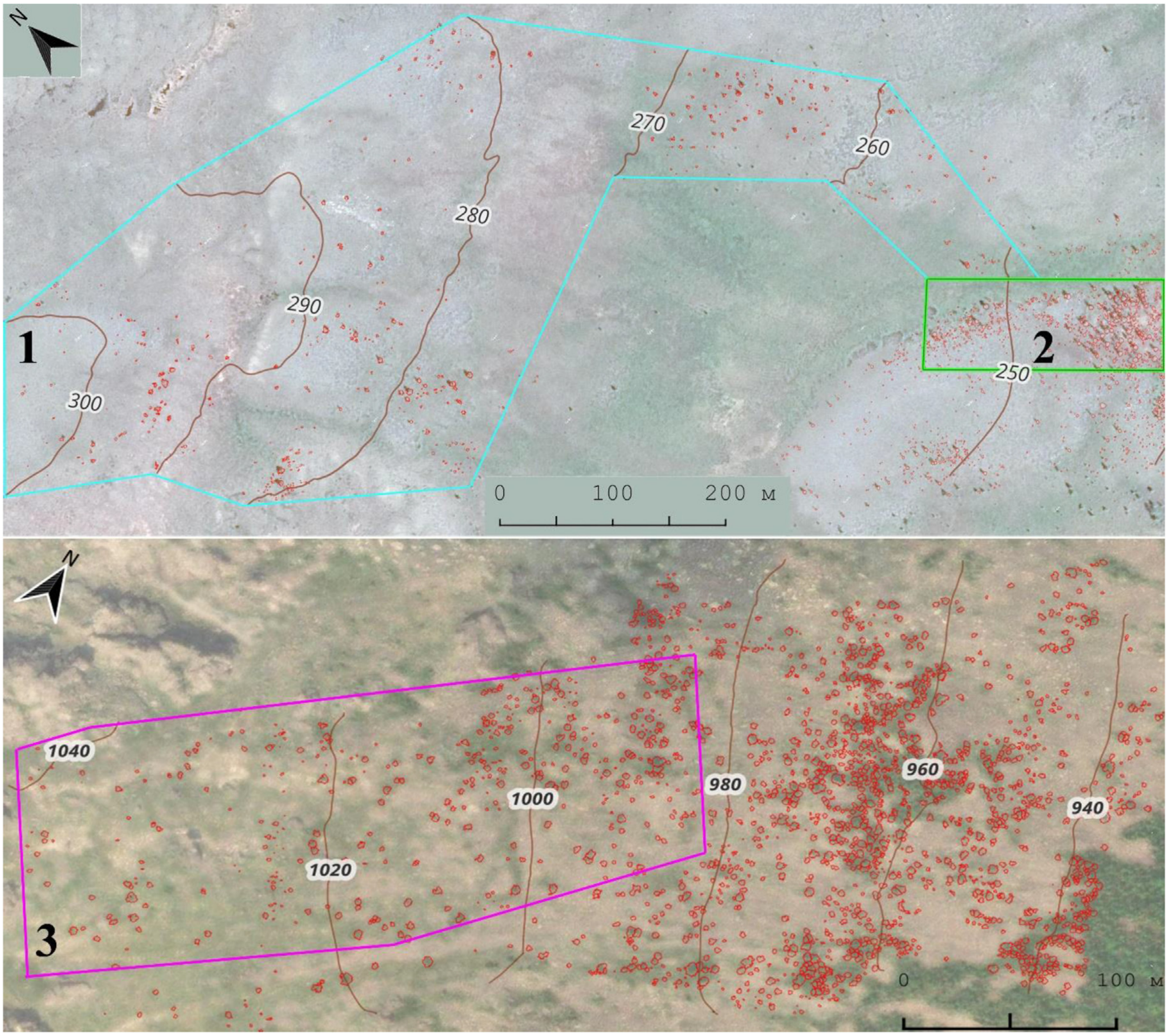

Fig. 2. Map of tree stands in the study areas of the Polar Urals (1: upper part, 2: low part) and the Northern Urals (3). Red counters demonstrate crown of studied trees. Brown lines show elevation lines. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Markers of mitochondrial genome of Siberian larch used for the study.

Locus	GeneBank no.	Position on contig (bp)	PCR primers	Repeat size	**Repeat number**[a]	**Fragment length**[a]
Lm2_1	MT797188.1	1216492	FAM – GTTATCAGGGCTCAGCCAAA, CCACCAAAGGATCAACCAGT	31	15	869
Lm2_2	MT797188.1	2846705	FAM –AACCCCGATCTTCCATATCC, AATCCAAGCTTCCCTCCAAT	32	7	783
Lm3_1	MT797189.1	240291	R6G -GATAGCAGGGGTGGCCTTAT, AGAGACTGGCATCGAAGCAT	32	9	943
Lm3_2	MT797189.1	2272538	ROX - TTCGACCGTCCTTCGTATTC, CGAACACAGAGGTGCTTTGA	31	6	961
Lm4_1	MT797190.1	783971	TAMRA – ATGTTAAGCGGGATCTGGTG, GGATCGCGTTATGATTTGCT	31	12	979

[a] The number of repeats and the PCR fragment size expected based on the nucleotide sequence in GeneBank.

2.2. Study species

Larix sibirica is a predominantly outcrossing tree, with both pollen and seeds dispersed by wind (Kapper, 1954). It is very light-demanded and does not regenerate under the maternal canopy satisfactorily. The Siberian larch is resistant to adverse climatic conditions and undemanding to soil fertility. It is most commonly found in dry condition, although it grows well on waterlogged soils. Free-standing larches begin to produce cones for the first time at 15 years of age, and in closed stands at 30–50 years of age. They produce the largest number of cones at the age of 70–100 years. The generative buds begin to blur simultaneously with the vegetative ones. This takes 10–12 days. Seeds of trees 40–120 years old have the highest germination capacity. In the Siberian forests the seeds ripen in September and then fall from the cones after that within 15–35 days. However, in the northern regions and in the highlands, seed release is observed only from February to April and sometimes until June–July, but this occurs intensively only after the cones have completely dried. The scales of the cones of a subspecies of larch

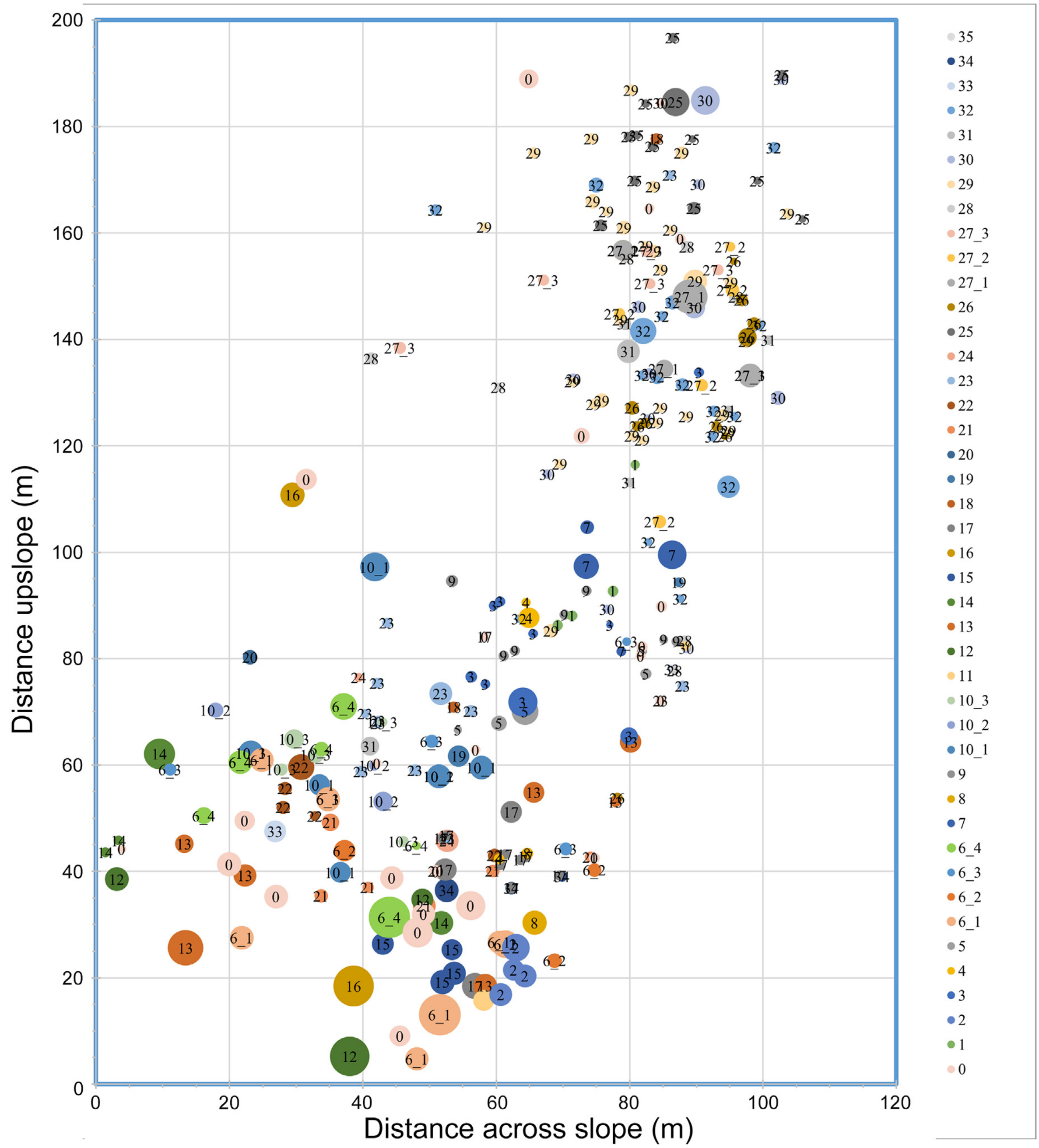

Fig. 3. Spatial distribution of groups of trees with similar haplotype (circles of the same color) in the lower part of the study area on the south-eastern slope of the hill with the elevation mark 312 m a.s.l. near Mt. Chernaya in the Polar Urals (numbers inside the circles indicate a related group and size of circle correlates with age of tree). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

common in the Urals are wide and close together, so the cones open slowly and the seeds fall out with difficulty. The Siberian larch seeds are 4–6 mm long, and together with the wing 11–14 and 2–4 mm wide. The average weight of 1,000 seeds varied between 6.9 and 10.6 g. On average, thirty-one per cent of the seeds are completely filled. In the mast years, thousands of seeds (up to 320–530) can be released per ha in zonal forests. On the Northern Urals it was revealed a remarkable decrease in the parameters of cones (length from 24.0 to 19.3 mm, mass from 1.79 to 0.95 g), the number of seeds in the cones (from 44 to 23), their laboratory germination ability (from 36.4% to 4.9%) with elevation increase within the treeline ecotone (Grigorieva and Moiseev, 2018). On the Polar Urals similar tendency was observed in the parameters of cones (length from 28.2 to 27.0 mm), number of seeds in the cones (from 20–43 to 12–36), their laboratory germination ability (from 8.2% to 7.8%–10.0%). On the Northern Urals the formation of Siberian larch generations occurs only after the mast years repeated every 5–7 years, but on the Polar Urals it is observed every 2–3 years.

2.3. Tree stands mapping

The geographic location of each tree was determined using a LiDAR scanner system (L-SCAN-2, Geomatics, Russia). This equipment included: a laser scanner (Velodyne VLP-16) and Applanix Plateau (a GNSS (Global Navigation Satellite System) sensor and an IMU (Inertial Measurement Unit) sensor). The Velodyne VLP-16 laser scanner has the following characteristics: scanning beam wavelength 905 nm, measurement speed 0.3 million points per second, scanning range up to 100 m. The configuration of the L-SCAN-2 complex made it possible to collect

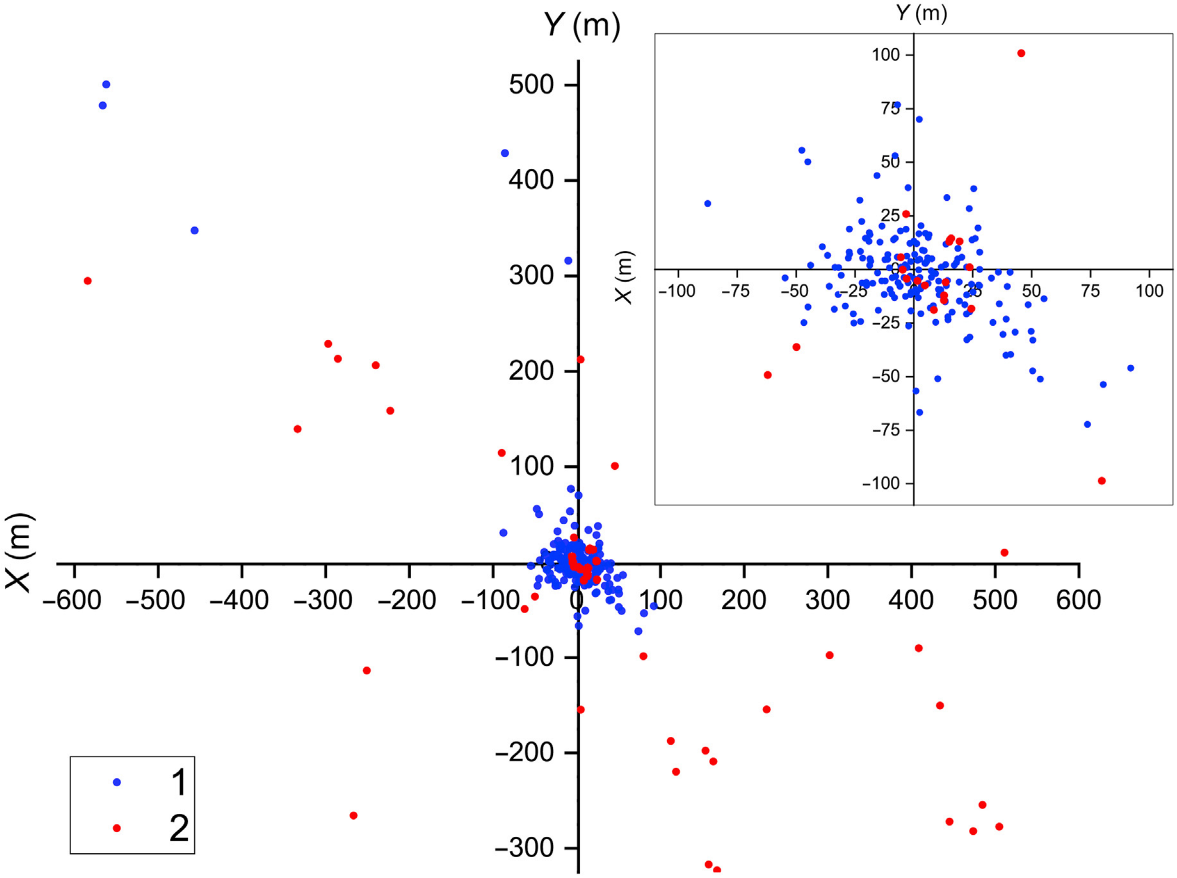

Fig. 4. Location of “daughter trees” relative to “mother trees” (positioned at the point of the axis cross) in the lower (1) and upper (2) part of the study area in the Polar Urals (axis X runs from west to east, Y – from north to south).

georeferenced 1-min files in LAS format in the PosPack MMS 8.4 program, where each data point had a definite latitude, longitude and altitude above sea level. All 1-min files were merged into a single file in the Lidar360 v.4.1 program (Green Valley International Ltd), and further processing covered the entire area. This package was then used to remove ‘outliers’ (points that were clearly outside the main scanning area) and to classify the set of laser reflectance points into two types: points on the ground surface and other higher located points (Chen et al., 2006). A digital elevation model (DEM) was constructed based on the first type of points. Both the first and second types of points were used to construct a digital surface model (DSM). By excluding DEM data from the DSM, a digital canopy height model (CHM) was developed, which is an image of tree crowns in TIFF raster format. A raster cell size of 0.05 m was used to produce all three models. Later, in the Lidar360 v.4.1 software environment, a segmentation procedure was performed on the georeferenced CHM raster, resulting in the extraction of canopy contours from the general surface of the scan points (Chen et al., 2006) and a canopy map was created (Fig. 2). Since crown closure and stand density differed in the lower and upper parts of the study area in the Polar Urals (0.8%–4.6% vs. 0.2%–1.5%), we divided it into two parts.

2.4. *Tree age estimation*

In the field, all mapped trees, whose characteristics (exact geographic position, tree height and crown contour) were obtained by processing the laser scanning data, were found in the ground and wood samples (cores) were taken from them. As the core is taken using an age drill above the root collar, in order to determine the number of years required for the sapling to reach the boring height, cross-sectional discs were taken from 53 young trees growing in the vicinity of the study area and having a height of more than 0.1 m. In the laboratory, each core sample was mounted in a wooden holder and cleaned with a utility knife and razor. To increase the contrast of the annual ring boundaries, tooth powder was rubbed into the top surface of the cleaned samples. Annual increments were measured using the LINTAB-V measuring complex (Rinntech, Germany). Later, all annual rings of the collected wood samples were cross-dated against existing larch chronologies from the Polar Urals and south Yamal Peninsula (Hantemirov and Shiyatov, 2002). Cross-dating enabled the assignment of a calendar year to each annual ring. Finally, the year of formation of the annual ring closest to the trunk center was determined using TSAP-Win™ (Rinn, 1998) and COFECHA software (Holmes, 1995).

If the cores taken did not reach the center of the trunk, the radius of the arc formed by the earliest (closest to the center) annual ring was first determined (Braeker, 1981). This was used to define the time of formation of the central ring. For that it was compared with the lines of circles of different radius (1, 2, …; units: mm) drawn on a transparent film. The number of annual rings in the earliest part of the core corresponding to the calculated radius was then counted and added to the number of identified and dated rings on the sample (Moiseev et al., 2010). As we determined the age of undergrowth above 0.1 m and with a diameter of less than 2 cm from the cross section taken at the level of the root collar (0 cm), this was the most reliable. Using the age of such young trees and the height of their trunks, we calculated a regression equation for the relationship between these parameters, which was used to calculate the time for each tree drilled to reach the sampling height (Hagedorn et al., 2014). By adding this calculated value, we determined the age at the level of the root collar for each tree with a diameter >3 cm. The age of

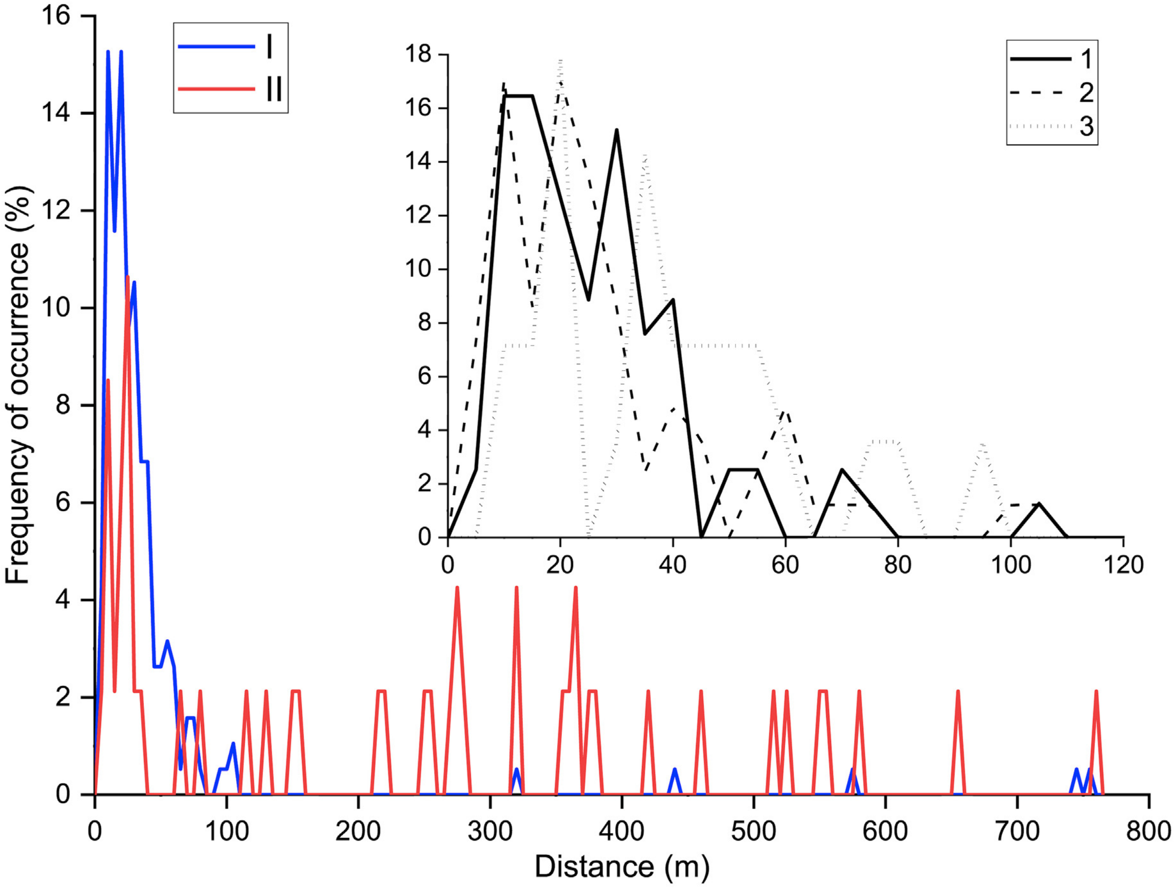

Fig. 5. Frequency of occurrence of distances from "mother" to "daughter" trees in all related groups identified during parentage analysis in the lower (I) and upper (II) part of the study area in the Polar Urals, as well as in groups with different ages of mother trees in the lower part (upper right inset): 1: 90–140 years; 2: 141–250 years; 3: 251–360 years.

Table 2
Statistics of distances from "mother trees" of different age to "daughter trees" in all related groups on the study area in the Polar and Northern Urals.

Statistics	Polar Urals								Northern Urals
	Upper half of low part	Lower half of low part	Both half of low part	Lower part with outstanding offspring in upper part				Upper	
				90–140 years	141–250 years	251–360 years	all ages	80–140 years	85–177 years
Mean	24.6	28.2	26.6	31.3	42.5	62.9	40.7	229.5	102.3
Standard error	1.9	2.1	1.4	7.2	10.8	26.9	6.7	30.3	7.4
Median	20.6	20.9	20.9	21.1	19.9	33.7	21.1	218.7	106.6
Excess	4.4	2.0	2.8	67.6	35.8	25.6	42.1	−0.5	−0.63
Asymmetry	1.7	1.4	1.6	8.0	5.7	5.0	6.3	0.6	0.11
Interval	101.2	100.1	101.2	570.9	739.5	744.8	750.7	753.2	217.6
Minimum	2.1	2.9	2.1	2.9	2.1	8.0	2.1	4.7	2.3
Maximum	103.3	103.0	103.3	573.8	741.6	752.8	752.8	757.9	219.9
Number	84	101	185	79	82	27	190	47	60

understorey trees >0.1 m in height, from which it was not possible to take core samples due to their small stem size, was calculated using the above regression equations.

2.5. Parentage analyses

Needle samples from mapped and aged larch individuals were collected from mapped tree stands in the summer of 2022 and 2023 at the Northern (231) and Polar Urals (446) study sites. We collected needles from every adult (>2 m) and every other second young tree, and placed them in a plastic zip-lock bag with silica gel for preservation. We stored the bags at approximately 10 °C in the field until they were shipped back to the laboratory. Upon return from the field, the samples were stored in a −20 °C freezer to await DNA extraction and sequencing. DNA was extracted from silica gel dried needles using the DNeasy 96 Plant Kit (QIAGEN) or the CTAB method (Devey et al., 1996).

To establish parent-offspring pairs, in contrast to the commonly used as genetic markers, nuclear DNA microsatellites, which have a length of up to 10 base pairs of nucleotides, we were employed mitochondrial DNA minisattelites, which is inherited along the maternal line in conifers. The markers used were regions of the mitochondrial genome containing tandem repeats with a motif length of 10–60 nucleotides, which are known to be prone to rapid length mutations and which contain a sufficient level of polymorphism. The search for such polymorphic loci was

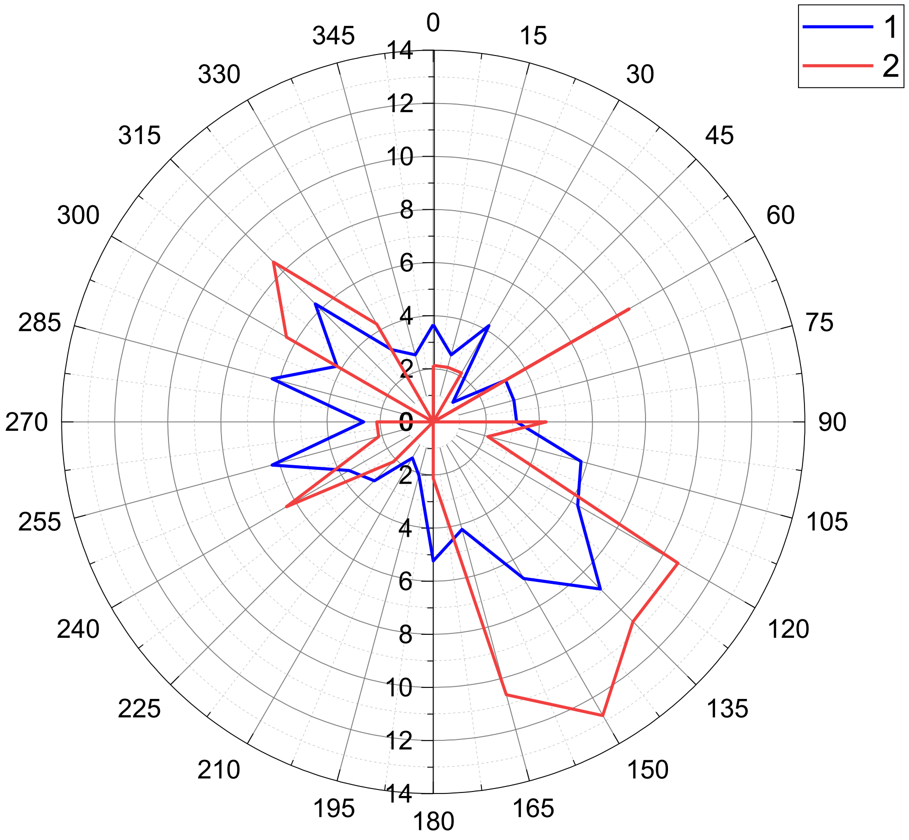

Fig. 6. Distribution of the direction of location (% of the cases) of "daughter" trees from "mother" trees in all related groups identified during parentage analysis in the lower (1) and upper (2) part of the study area in the Polar Urals.

carried out in the complete mitochondrial genome sequence of the Siberian larch (Putintseva et al., 2020). The online service Tandem Repeat Finder (https://tandem.bu.edu/trf/home) was used for the search (Benson, 1999). Among the found loci, ten were selected, having a motif of 31 or 32 nucleotides and repeating 10–15 times. For their amplification by polymerase chain reaction (PCR), primers were developed using Primer3 online service (Untergasser et al., 2012) and the success of amplification and polymorphism were preliminarily tested by electrophoresis on a 1.5% agarose gel. The five loci that had the most stable amplification and were highly variable - at least 5 alleles per 24 randomly selected plants - were chosen. They are designated as loci Lm2_1, Lm2_2, Lm3_1, Lm3_2, Lm4_1. Two approaches were used for the typing of all samples collected: 1) electrophoresis in 1.5% agarose gel, staining in ethidium bromide solution and determination of the relative size of fragments, using the 1 kb marker (Sibenzym, Novosibirsk); 2) determination of sizes using a NANOFOR 05 sequencer (Syntol, Moscow). For this purpose, fluorescence-labelled forward PCR primers (FAM, R6G, ROX, TAMRA) and an internal size standard SD-1200 (Synthol) were used. The second approach gives more accurate size estimates. However, it does not allow the analysis of fragments longer than 1,200 nucleotides and fluorescent primers cause more amplification failures. Therefore, both methods were used for mitochondial DNA analysis.

Based on the sequences used to develop the markers, we determined the expected PCR fragment sizes depending on the number of repeats (Table 1), and converted the fragment sizes obtained by capillary electrophoresis and agarose electrophoresis in the studied trees to the number of repeats. In this case, the closest expected size was taken.

As a result, each sampled tree has a combination of repeat numbers from five loci, regarded as a 'haplotype'. The identity of the haplotypes of two trees allows us to say with a high degree of confidence that they belong to single maternal lineage and likely they are either half-sibs or a maternal tree and its descendant. Since there is some error in size estimation, haplotypes that differ by 1–2 repeats at 1–2 loci can be considered identical. After editing the results using the sequencer data, these errors have been corrected. It is also important to bear in mind that the mutation rate of tandem repeats in the plant mitochondrial genome has not been sufficiently studied and can be so high that the haplotype of the offspring may differ from the haplotype of the maternal tree at some locus. Knowing the haplotype of the trees, we combined them into related groups with identical haplotypes. Based on the age comparison, we identified the maternal tree in these groups - the oldest and different from the younger ones at least at 40 years – the average age of the beginning of seed production by larch. Then, using a special tool in QGIS 3.28, the distance and direction (azimuth) from each parent tree to its offspring were determined. The basic statistics of these parameters were then calculated using the program Statistica 10.

3. Results

In the study areas, 697 individuals were genotyped in two populations with five selected mitochondrial minisatellite loci (see Tables S1–S3), which were highly polymorphic, varying from 15 to 28 alleles and had 200 combination in each population.

3.1. Polar Urals

In the Polar Urals, 450 trees (287 in the lower and 163 in the upper part) were genotyped and their age and exact geographical location were

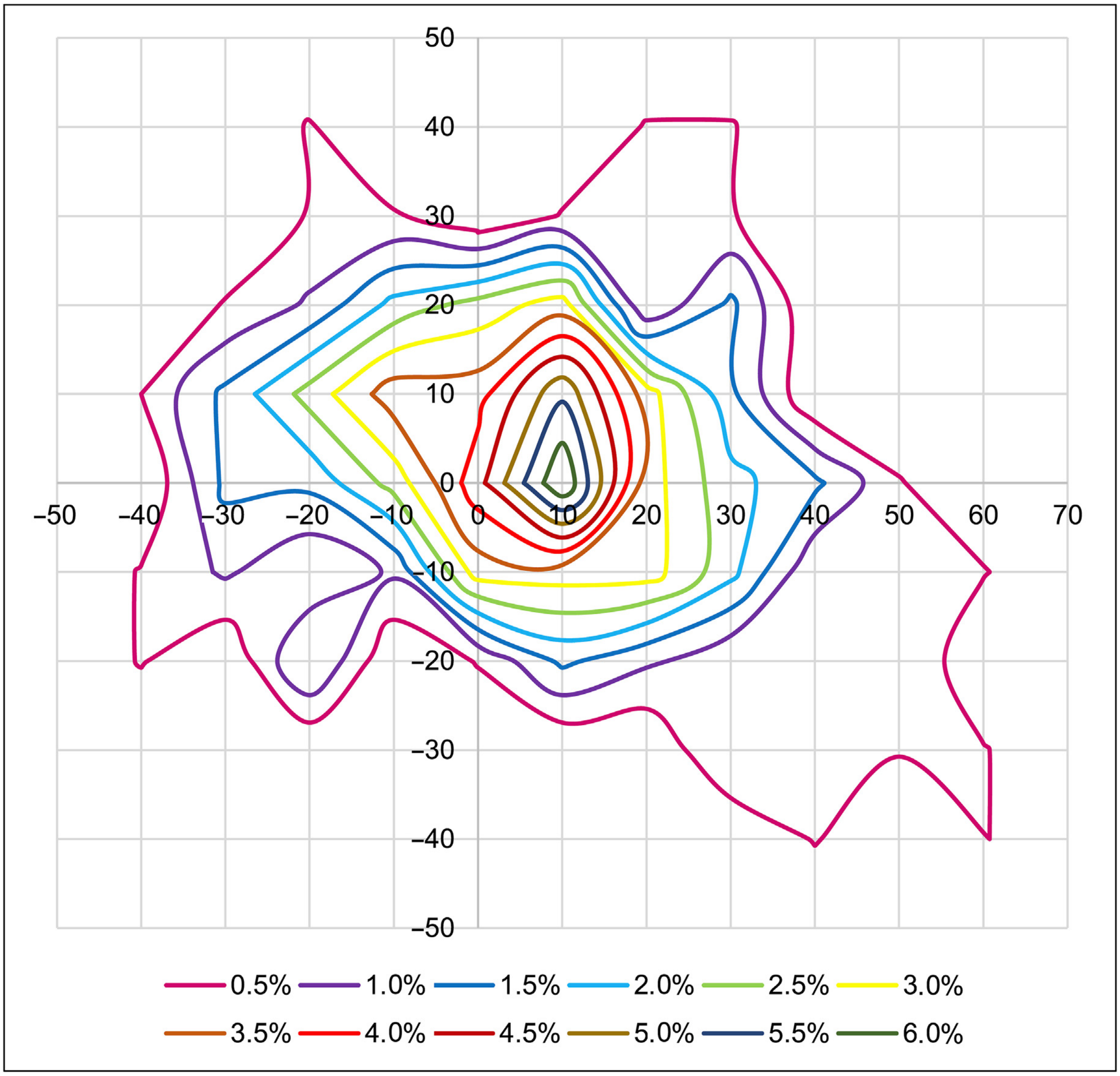

Fig. 7. Probability (%) contours of occurrence of "daughter trees" relative to "mother trees" (positioned at the point of the axis cross) in the lower part of the study area in the Polar Urals (axis *X* runs from west to east, *Y* from north to south).

determined. Analysis of the entire data array showed that in the lower part of the study area (245–260 m a.s.l.), where crown closure decreases from 4.6% to 0.8% upslope, representatives of 35 larch groups with identical haplotypes (related groups) currently grow (Fig. 3). Twenty-three trees (7.7% of the total) did not belong to any of the groups. In total, we found 57 haplotypes among the trees studied. Fourty trees (15% of the total) belong to nine related groups in which trees are very close in age to each other and possible maternal trees are located outside the study area or are dead to date. The size of 28 related groups with detected putative maternal trees ranges from 2 to 31 individuals and includes twelve groups of 2–4 trees, seven of 5–11 trees, seven of 13–31 trees. Thus, 128 trees (47%) were derived from 7 trees (27% of the total number of maternal trees). The median size of related groups with a maternal tree is 8 trees.

We found that the tree groups contain several generations: the first consists of trees 177–350 years old, the second 90–140 years old and the third 18–45 years old (see groups #6, #10 and #27 on Fig. 3).

We revealed that in groups with maternal trees aged from 90 to 250 years, the offspring grow at a distance of 3–30 m in 72% of the cases (Figs. 4 and 5 and Table 2). In 25.5% of the cases, the offspring are located at a distance of 31–105 m, and some 2.5% individuals at a distance of 316–742 m. The median distance is 19.9–21.1 m.

In the groups with maternal trees aged 251–360 years, offspring grow in 37% of the case at a distance of 3–30 m, in 59.3% at a distance of 31–105 m and in 3.7% (single tree) of the cases at a distance of 753 m (see Table 2). The median distance is 33.5 m in the groups with this age of parent trees.

Analysis of the direction of location of the offspring from the maternal tree in all related groups showed that in 27.7% of the cases the offspring were located at azimuths between 91° and 150° (direction of the prevailing winds) and in 25.7% of the cases between 241° and 315° (upslope direction close to the opposite of the prevailing winds). For other azimuths, they occur in 2%–5% of cases (Fig. 6).

Analisys of the probability of offspring appearance showed that "daughter" trees were dispersed in a shape close to an ellipse with center to 10 m to the east and the long axis extending from north-west to south-east (prevailing winds direction) (Fig. 7).

In the upper part of the study area (261–300 m a.s.l.) in the Polar Urals where crown closure decreases from 1.5% to 0.2% across upslope, representatives of additionally 16 larch groups with identical haplotypes

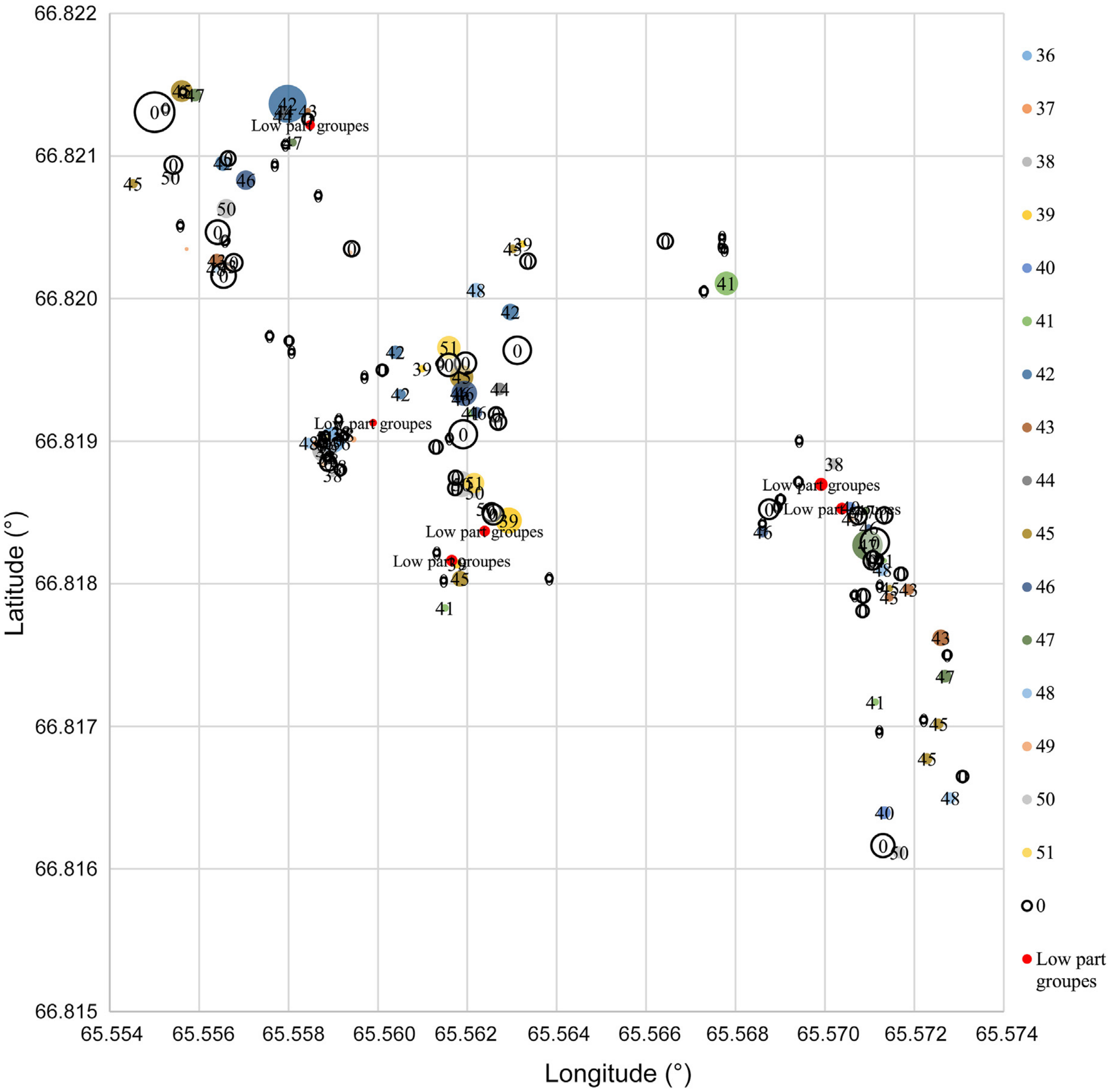

Fig. 8. Spatial distribution of groups of trees with similar haplotype (circles of the same color) in the upper part of the study area on the south-eastern slope of the hill with the elevation mark 312 m a.s.l. near Mt. Chernaya in the Polar Urals (numbers inside the circles indicate a related group and size of circle correlates with age of tree). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

were revealed (see Fig. 8). The seventy-four trees (45% of the total) were not related to any of the groups. In total, we found 70 haplotypes among the trees on that part of the study area. The size of related groups in this area varies from 2 to 11 individuals, with a median of 5 trees. The age of the mother trees ranges from 80 to 140 years. Currently, 30% of offspring are growing at a distance of 6–30 m and 6% at a distance of 31–80 m (Figs. 4 and 5). In about 62% of the cases, the offspring are located between 81 and 760 m, with a median of 219 m (Table 2). Our calculation showed that 69% of the trees migrated from outside this part of the study area. An analysis of the direction of location of “daughter trees” from “mother trees” showed that in 45% of cases the offspring were located at azimuths between 106° and 165° (the direction of the prevailing winds), and in 19% at azimuths between 286° and 330°. For other azimuths, they occur in 0–8% of cases (Fig. 6).

3.2. Northern Urals

In the Northern Urals (the eastern slope of Serebryansky Kamen), where canopy closure decreases from 7.1% to 1.5% upslope, 231 trees were genotyped and their age and exact geographic location were determined. The five selected mitochondrial microsatellite loci were also highly polymorphic as in the Polar Urals, varying from 11 to 20 different alleles. In total, we detected 153 hyplotypes among the studied trees. Analysis of the results obtained for this study area detected here 40 larch groups with identical haplotypes. All of them include maternal trees (Fig. 9). The one hundred and twelve trees (49% of the total) were not related to any of the groups. The size of the 40 related groups with maternal trees varies from 2 to 16 individuals, 32 of which consist of 2–3 trees, 7 of 4–6 trees and 1 of 16 trees. Our calculation showed that 66% of the trees migrated from outside the study area.

The age of the “mother trees” ranges from 80 to 165 years. We found that the “daughter trees” are now growing at a distance of 3–35 m in 17% of the cases and at a distance of 36–80 m in 18% of the cases. In about 57% of the cases the “daughter trees” are between 81 and 170 m, with a median of 107 m (Figs. 10 and 11 and Table 2). The maximum revealed distance from the “mother trees” to the offspring is 220 m. An analysis of the direction of location of the offspring from the “mother trees” showed that in 42% of the cases the offspring are located at azimuths between 1°

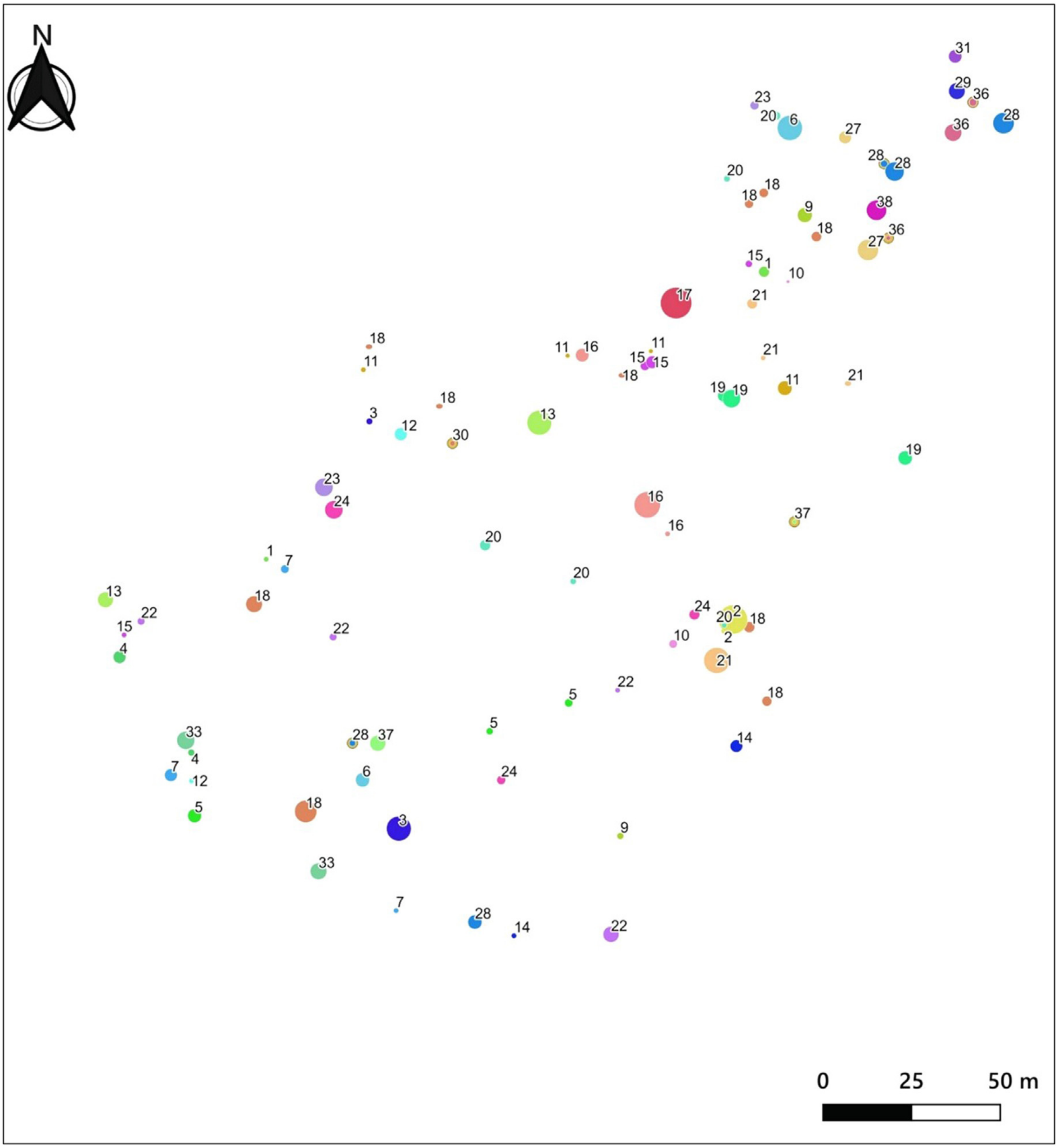

Fig. 9. Spatial distribution of groups of trees with similar haplotype (circles of the same color) on the eastern slope of the southern spur of Mt. Serebryanskii Kamen' in the Northern Urals (numbers inside the circles indicate a related group and size of circle correlates with age of tree). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

and 75°, and in 30%, 181°–255° (the direction of the prevailing winds). For other azimuths, they occur in 0–5% of the cases (Fig. 12).

4. Discussion

A common paradigm is that species range limits primarily reflect the distribution of suitable habitat (i.e. niche limits), beyond which populations have a tendency to decrease along with their disappearance (Davis and Shaw, 2001; Sexton et al., 2009). Some range shifts may lag behind environmental changes as space and time (Svenning et al., 2008), because some frontal population are also limited by dispersal of propagules (Bayly and Angert, 2019). Thus, plants rapidly occupy new territories when adult individuals growing at the areal boundary produce sufficient numbers of viable seeds (Koshkina et al., 2008; Mamet et al., 2019), which are dispersed over long distances (Dullinger et al., 2004; Hampe, 2011), germinate (Milbau et al., 2009) and emerge after new individuals have successfully crossed several ecological barriers (Holtmeier and Broll, 2007; Svenning et al., 2014). The rate and spatial pattern of a frontal tree populations' reaction to climate change are mostly defined by aforementioned process (Shay et al., 2021). Migration rate may increase if plants in the species' range begin to produce sufficient numbers of viable seeds more frequently. If seed dispersal distance increases, the frontal pattern may change from an abrupt line to a wide patchy transition zone (Clark, 1998; Nathan and Muller-Landau, 2000).

Our assessment of five highly polymorphic mitochondrial microsatellites genotyped all 697 individuals, allowing us to infer, based additionally on tree age and location, the pattern of a related trees within the upper part of the treeline ecotone. As a result, at our study sites in the Northern and Polar Urals, the effective dispersal distance of offspring in sparse larch stands was found to be significantly greater (from 20–33 to

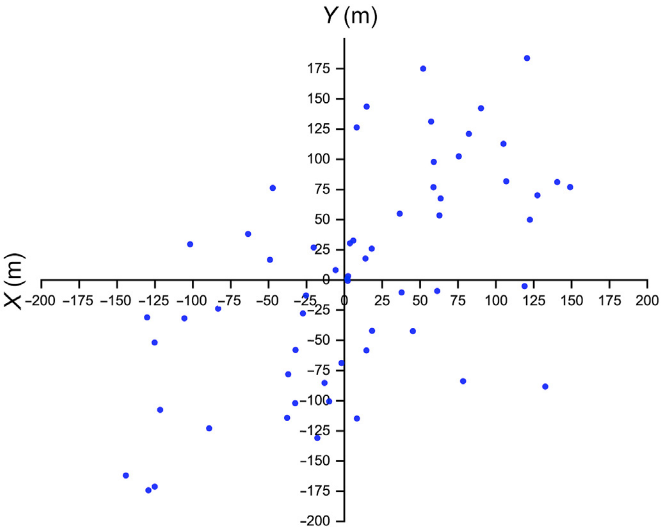

Fig. 10. Frequency of occurrence of distances from “mother” (located at the point of the axis cross) to “daughter” trees in all related groups identified during the parentage analysis on the eastern slope of the southern spur of Mt. Serebryanskii Kamen' in the Northern Urals (axis *X* extends from west to east, *Y* from south to north).

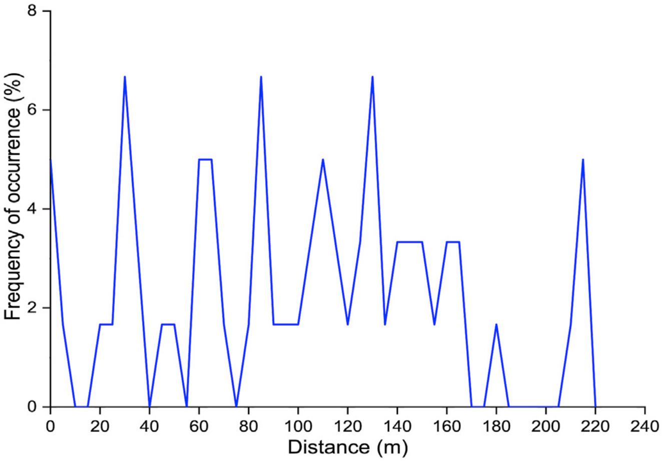

Fig. 11. Frequency of occurrence of distances from “mother” to “daughter” trees in all related groups identified during parentage analysis on the eastern slope of the southern spur of Mt. Serebryanskii Kamen' in the Northern Urals.

219 m on average and up to a maximum of 760 m) than previously reported. For example, Kruse et al. (2019) inferred from genetic parentage analysis using nuclear microsatellite markers that the effective seed dispersal distances of *Larix gmelinii* Rupr. in open forests in the Russian subarctic (southern Taymyr Peninsula) are short – on average about 15.0 m (median of 9.8 m, with a minimum of 0.8 m and a maximum of 56.1 m). Using an analogous method effective seed dispersal distances of 2–48 m were revealed in open and close forests of *Larix decidua* Mill. in the Swiss Alps (Pluess, 2011). In Minnesota (the northern USA) 94% *Larix laricina* (Du Roi) K. Koch seeds were dispersed within 18 m of the producing trees (Duncan, 1954). In a study of wetlands in Alaska (Brown et al., 1988), the number of fallen seeds decreased sharply away from the open forest edge. Factors explaining the short dispersal distance of larch seeds in Alaska (Brown et al., 1988) include small tree stature and low wind speed. In the Italian Alps, within treeline European spruce population, the range of distances between maternal trees and their offspring is 39–833 m (mean 345 ± 191 m s.d., in 91.7% of the case exceeding 100 m, in 74.2%–200 m, in 23.3%–500 m and in 1%–800 m) and only six local adults generated almost 62.4% of juveniles (Piotti et al., 2009). At our study site in the Polar Urals, the effective seed dispersal distances were longer (median is 219 m) in the sparse tree stands (0.2%–1.5% crown closure) in the upper part, but became shorter (median 22–25 m) as soon as the stand density increased to 3.0%–4.6% in the lower part, because the wind speed decreased. Seed dispersal is also determined by the release height (Matlack, 1987), which in our case was rather low due to of the low tree stature (mean: 2.1–3.9 m in 1960) (Shiyatov, 1965). The most cones are produced on larch branches growing at about half of the tree's height, as is common in sparse stands, and which in many cases determine short-distance dispersal of offspring (Duncan, 1954; Kruse et al., 2019; Pluess, 2011).

We suspect that the dispersal distance also depends on the period when the seeds were released. If it happens in a cold period with a stable snow cover, then the seeds are spread by the wind along its surface over long distances (hundreds of meters), and if it happens in a snowless period, then they fall close (tens of meters) to the source only under the influence of gravity. Shiyatov (1965) noted that in the Polar Urals *Larix sibirica* mostly releases seeds in June of the following year and suggested that this was due to the short and cold vegetation period, which delayed seed maturation and cone desiccation (Shiyatov, 1965). The timing of *Larix laricina* seedfall at Bonanza Creek (Alaska) was in late October, when the most viable seeds (98%) were released (Brown et al., 1988), as in Minnesota (Duncan, 1954). In the northern Quebec, however, 15%–67% of *L. laricina* seeds were released by mid-July of the following year (Payette et al., 1982). At that time, a period of three to four successive sunny, windy, and dry days was sufficient to facilitate cone opening and seed dispersal. Brown et al.(1988) also pointed out that low summer temperatures can prevent cone ripening until the following growing season and delay seedfall timing (Brown et al., 1988). At our study site in the Northern Urals crown closure was 1.5%–7.1%, which is higher than in the Polar Urals (max 4.6%), but the effective seed dispersal distances were longer (median is 107 m) than in the low part of the Polar Urals (median is 22–25 m). We assume that this is related to more frequent episodes of seed release in spring and seed dispersal by wind along the snow surface, because the vegetation period is 10 days longer on the Northern Urals than on the Polar Urals (Hagedorn et al., 2020) and cones are sufficiently dried for opening after several successive sunny days in early spring.

We established that the offspring effectively dispersed not only in the direction of the prevailing wind, but also in the opposite direction up the slope, and the distance could reach 500–760 m (Figs. 6 and 11). In Alaska (Kenai Peninsula), of the 18 identified parent-offspring matches of *Tsuga mertensiana*, dispersal events occurred over distances ranging from 1.4 to 326.9 m (mean 73 m), and 16% of them were upslope to higher elevations at distances between 50 and 98 m (Johnson et al., 2017). This fact is important for understanding how tree stands advance upslope not only on windward, but also on leeward (opposite to the prevailing wind) slopes.

On the basis of the obtained data, we assume that in the Polar Urals study area, at the beginning of the twentieth century as it was previously noted (Hagedorn et al., 2014; Shiyatov and Mazepa, 2011) tree colonization followed two paths. First, when “forest islands” began to form along the entire altitudinal gradient around relict multi-stemmed trees that had survived in local refugia beyond the close forest border from the previous period of their wider distribution (Mazepa, 2005). This occurred when creeping stems rapidly changed their growth form to vertical (Devi et al., 2008) and began to produce greater numbers of viable seeds. Such afforestation processes were similar to the post-glacial expansion of tree populations in non-glaciated subarctic regions, when closed forests rapidly formed in these areas as a result of an increase in the size and density of small, persistent, marginal tree populations (Väliranta et al., 2011). Second, this also occurred through the episodic dispersal of tree offspring over long distances (>100 m), as previously

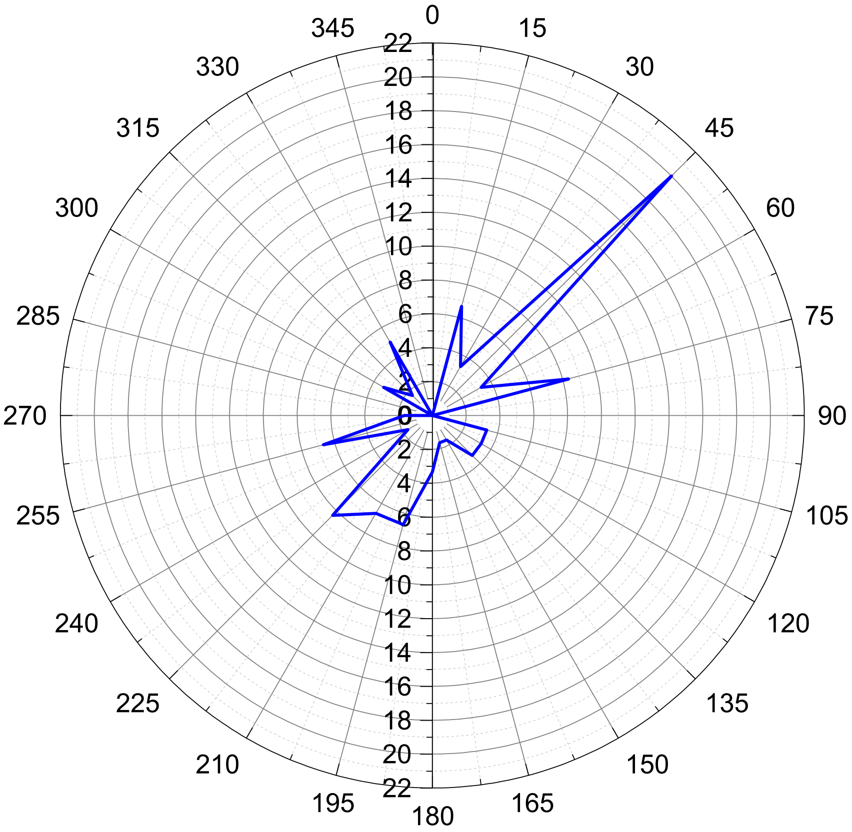

Fig. 12. Distribution of direction of location (% of cases) of "daughter trees" from "mother trees" in all related groups identified during parentage analysis on the eastern slope of the southern spur of Mt. Serebryanskii Kamen' in the Northern Urals.

suggested in the work of Stephan Kruse and colleagues on open forest studies on the Taymyr peninsula (Kruse et al., 2019). We hypothesize that seeds may be dispersed upslope over the snow surface by warm air currents (anabatic winds) during spring period, when the snow cover disappears in the valleys and the dark ground surface there begins to heat up sufficiently by solar radiation.

In conclusion, genotype, age and location analysis provided valuable information on the origin of larches involved in the colonization of areas beyond the open forest boundary in the Northern and Polar Urals. We have shown that the "effective" dispersal of offspring in frontal *Larix sibirica* populations ranges from 2 to 760 m (with a median of 20–33 m in open forest and 219 m in single-tree tundra in the Polar Urals and 102 m in open forest in the Northern Urals). These values are significantly higher than in the open forests of *Larix gmelinii* on Taimyr peninsula (range 0.8–56 m, median 9.8 m) and *Larix decidua* in the Alps (range 2–48 m). We found that the number of migration events from outside the study area was more than 2 times lower in sparse tree stands than in single-tree tundra, indicating high gene flow from the lower part of the slope, even in the opposite direction to the prevailing winds. Our analyses show that some trees had outstanding reproductive success and played a major role in the afforestation process. The large proportion of offspring established far from their mother trees confirms the high dispersal capacity of *Larix sibirica* in harsh subarctic conditions. Further studies based on nuclear microsatellite analysis are needed to improve the data obtained on dispersal processes at the upper limit of the tree's distribution. In addition, the pattern of tree immigration can be elucidated by increasing the sampling effort in surrounding stands to determine the origin of the offspring not belonging to any mother trees, and by comparing the contribution of trees from stands of different densities to the colonization of areas beyond the closed forest line. The effective seed dispersal data generated by our research can be used to create and 'debug' a spatially accurate model capable of simulating the dynamics of tree stands at the upper limit of their growth, allowing the most reliable prediction of the future pattern and position of tree ecotones.

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CRediT authorship contribution statement

P.A. Moiseev: Writing – review & editing, Writing – original draft, Supervision, Investigation, Funding acquisition, Data curation, Conceptualization. **V.L. Semerikov:** Writing – original draft, Investigation, Formal analysis. **T.V. Semerikova:** Investigation. **D.S. Balakin:** Investigation. **I.B. Vorobiev:** Investigation. **S.O. Viuykhin:** Investigation.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Moiseev P.A., Semerikov V.L., Semerikova T.V., Balakin D.S., Voroviev I.B., Viuykhin S.O. report that financial support was provided by Russian Center for Scientific Information. Moiseev P.A., Semerikov V.L., Semerikova T.V., Balakin D.S., Voroviev I.B., Viuykhin S.O. report that

financial support was provided by Russian Scientific Foundation. The funders had no role in the design of the study, in the collection, analyses, or interpretation of data, in the writing of the manuscript, or in the decision to publish the results. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2024.100218.

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