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Response of woody vegetation and soils to modern climate change in the Altai Mountains

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ABSTRACT

The upper forest boundary in the mountains is a reliable bioindicator of modern climate change, though its dynamics are influenced by multiple factors. Conjugate studies on the structure of tree stands and the soil properties across the elevation gradient were performed at the treeline on slopes of different exposures in the Altai Mountains. The oldest trees on the northern slope were established in the mid-15th century, but intensive expansion began in the 20th century, whereas tree establishment on the eastern slope began later and occurred over a shorter period. A significant positive correlation was revealed between summer and winter temperatures, winter precipitation, and the rate of *Pinus sibirica* establishment. The open forest boundary reaches its highest elevation on the eastern slope, where conditions are intermediate between the northern and southern slopes in terms of snow cover duration and land surface temperature.

The differences in soil types reflect the contrasting conditions influenced by slope exposure. The earlier colonisation of northern slopes has led to the formation of typical forest soils (Skeletic Podzols) at higher elevations under open forest stands. These soils are more acidic, with slower litter decomposition and pronounced accumulation of carbon and nutrients in their organic surface horizons, while their mineral horizons are nutrient-poor. In contrast, soil at the eastern slope (Folic Leptosols) has a higher element content throughout the soil profile and displays minimal disparities and variation in the morphology and chemistry across the treeline ecotone. The mismatch transition between vegetation and soil belts suggests that soil properties respond to climatic changes more slowly than vegetation dynamics.

1. Introduction

The modern climate change and its impact on flora and fauna are currently being intensively debated in the global scientific community (Freeman et al., 2018; Mamantov et al., 2021; Parmesan, 2006; Walther et al., 2002). According to the IPCC report (2021), each of the last four decades since 1850 has been warmer than previous decades. Monitoring the distribution of tree stands at the southern and northern forest edges in lowland areas, as well as at the upper and lower forest boundaries in mountainous regions, is one of the simplest and most effective ways to obtain evidence on the effects of climate change on vegetation (Holtmeier, 2009; Körner, 2012). However, it is much easier to make such observations in the mountains because the width of the transition zone between closed forests and treeless areas is hundreds of meters, compared to tens of kilometers on the plains (Gorchakovskiy and Shiyatov, 1985). Mountains are unique natural complexes, a kind of "arena" for the adaptation to extreme conditions of tree and shrub species that are highly sensitive to environmental changes (Holtmeier, 2009). There is now considerable evidence that the treeline has shifted in many mountainous regions of the world in recent decades (Hansson et al., 2021; Harsch et al., 2009). This has mainly contributed to an increase in the area and the carbon sequestration function of high-elevation forests (Hagedorn et al., 2020; Moiseev et al., 2022; Speed et al., 2015) and a decrease in regional biodiversity (Barredo et al., 2020; Greenwood et al., 2016).

Treeline spatial patterns and dynamics are influenced by a multiplicity of interrelated factors (Gorchakovskiy and Shiyatov, 1985). Soil is undoubtedly one of the most complex factors, but less obvious than

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others, such as heat deficiency, wind, and snowpack (Holtmeier and Broll, 2018; Körner, 2012; Sundqvist et al., 2013). Although air temperature is assumed to be the most important treeline controlling factor (Körner and Paulsen, 2012; Muller et al., 2015), soil factors are also important. For example, an analysis of numerous studies across different mountain regions found that tree growth is also dependent on soil temperature, moisture, water availability, and nutrient status (Muller et al., 2015). Furthermore, such edaphic factors as soil depth and rock fragment content can also affect vegetation patterns (Cairns and Malanson, 1998; Malanson et al., 2002). Soils in the treeline ecotone are influenced by a number of factors, including the elevation gradients of temperature and precipitation, local topography and vegetation, as well as hazards and human impacts (Holtmeier and Broll, 2018). The upward expansion of woody vegetation modifies many soil parameters, with trees beginning to regulate soil temperatures and moisture, root growth, nutrient uptake, mineralisation, and decomposition (Cairns, 2001; Holtmeier and Broll, 2007; Seastedt and Adams, 2001; Shiels and Sanford, 2001; Wang and Godbold, 2017). Subsequently, soils affect tree growth.

The close relationship between soil and tree growth is manifested in positive feedback loops. Trees and shrubs, for example, affect greater snow accumulation than in open areas (Sturm et al., 2005). This results in less soil freezing and higher microbial activity, which in turn improves nitrogen (N) availability and promotes further tree growth (Hagedorn et al., 2014; Schimel et al., 2004). Snow accumulation also increases soil moisture and reduces desiccation (Cairns, 2001). Positive feedbacks between soils and plants could improve the local environment for trees by increasing organic matter (OM) and soil nutrients (Cairns, 1999; Shiels and Sanford, 2001; Wang and Godbold, 2017). It is commonly believed that most high-elevation ecosystems are N-limited with tree growth being restricted by soil N deficiency (Macek et al., 2012; Müller et al., 2017). Consequently, changes in the N supply may promote plant growth and biomass production (Schimel et al., 1996, 2004). Therefore, much research has focused on the content and availability of soil organic carbon and soil nutrients, as well as C and N cycling at the upper treeline (Baptist et al., 2010; Kammer et al., 2009; Loomis et al., 2006; Shiels and Sanford, 2001; Thebault et al., 2014). Some studies revealed qualitative differences in soil organic matter (SOM) across the treeline. In particular, OM in forest soils was more decomposable compared to tundra soils (Kammer et al., 2009; Parker et al., 2015; Sjögersten and Wookey, 2002, 2009; Sjögersten et al., 2003). This should lead to greater nutrient availability, potentially resulting in increased plant N uptake and growth. However, increased leaching and loss of OM, immobilisation by microorganisms, and transfer to the biomass of long-lived woody plants can reduce or even eliminate the availability of elements. Thus, the vegetation–soil interactions in treeline ecotones exhibit complex, often nonlinear dynamics. It is probable that distinct soil properties may either promote or impede the growth of trees at high altitudes within mountainous regions. Therefore, the analysis of vegetation in relation to soils enhances our understanding of the mechanisms governing alpine treeline dynamics and forest boundary shifts.

It is known that forest vegetation is a more sensitive and readily observable indicator of climate change compared to soil. Soil responses to changing climate are a long-term process lagging far behind forest advance (Holtmeier and Broll, 2018). The coinciding of transitions in soil and vegetation along the elevation gradient is evidence of the profound restructuring of ecosystems due to the close interaction between vegetation and soil (Ryzhova and Shamshin, 2001). However, specific data on the rate of soil horizon formation and the changes in soil properties under different climatic conditions are very scarce. The advantage of high-mountain ecotones (from treeless to forested areas) is that soil formation processes at different stages—spanning several decades—can be observed within a short distance. Comparing treeline and soil dynamics provides an opportunity to assess the response time of soil parameters to changes in climatic factors.

Mountain regions located in the north of Eurasia (Fennoscandia, Polar Urals, Putorana Plateau), where the influence of temperature on the growth of woody plants is the most pronounced, have been and remain very attractive for studying the response of forest stands in the forest-tundra transition zone and other ecosystem components to climate change (Grigoriev et al., 2022; Kullman and Öberg, 2009; Mazepa, 2005; Moiseev et al., 2022; Rees et al., 2020). Recent publications have shown that slope exposure is one of the key landscape features in subarctic mountains that determine the elevation position of the treeline and its rate of upward shift. The greatest shift of the treeline in these regions occurred on warmer slopes that were mainly facing south (Dearborn and Danby, 2017, 2020; Grigoriev et al., 2022; Moiseev et al., 2022).

Slope exposure is considered an important soil-forming factor that affects the redistribution of solar radiation and, consequently, heat and moisture, soil temperature, soil water retention and availability, nutrient dynamics, and soil microbiological activity (Bardelli et al., 2017; Carletti et al., 2009; Egli et al., 2006, 2009; Xue et al., 2018). A comparative analysis of vegetation and soil characteristics across slope aspects provides an opportunity to assess the role of exposure-modified factors in processes occurring at the upper forest boundary at both regional and local levels.

The Altai Mountains are a unique mountainous region of modern glaciation in the central part of Eurasia, where temperature is the main determinant of the elevation of snow and treeline (Klinge et al., 2003; Volkov et al., 2021). The biogeographic isolation of these mountains, particularly their location surrounded by steppes and semi-deserts, results in a high level of endemism and implies a high level of biodiversity and ecosystem sensitivity to the current climate warming. However, the role of slope exposure, particularly in the coupled analysis of treeline shift and associated soil changes, has not been studied in the continental climates of mountainous regions of Eurasia, specifically the Altai Mountains.

Therefore, the objectives of our study in this region were to (1) identify differences in elevation and stand structure of treeline associated with slope exposure, (2) analyze changes in soil formation processes and soil chemical properties depending on elevation gradient and slope exposure, (3) reconstruct stand dynamics and correlate them with regional climate data, and (4) compare soil formation and forest formation processes on slopes of different exposures.

We tested following hypotheses: (1) Species composition of vegetation, the elevation position of treeline, and the rate of tree establishment are strongly dependent on slope exposure; (2) slope exposure has a more pronounced effect on soil types and their chemical properties than altitude within the forest-tundra ecotone; (3) upward shift of the treeline is closely related to climatic parameters; (4) soil properties, in conjunction with climatic factors, can either facilitate or inhibit the advance of woody species on slopes of varying exposure; (5) correspondence of boundaries in vegetation and soil cover depends on the history of tree stand formation and slope exposure.

2. Materials and methods

2.1. Study site

The study area is located in the eastern part of the Kholodny Belok Ridge (10 km × 17 km) in the central part of the Altai Mountains (50.03° N, 85.79° E) (Fig. 1). The climate in the Altai Mountains is strongly continental, with an extreme variety of conditions depending on elevation and geographical position. The climate is influenced by three main factors: the intracontinental location (considerable distance from the oceans), the transport of air masses from the Atlantic Ocean, and the influence of the Asian anticyclone in winter. The mean temperatures in July are 16.2 ± 1.2°C at 980 m a.s.l. (according to the Ust'-Koksa weather station) and 7.1 ± 1.3°C at 2,600 m a.s.l. (according to the Kara-Turek weather station); the mean temperatures in January drop to

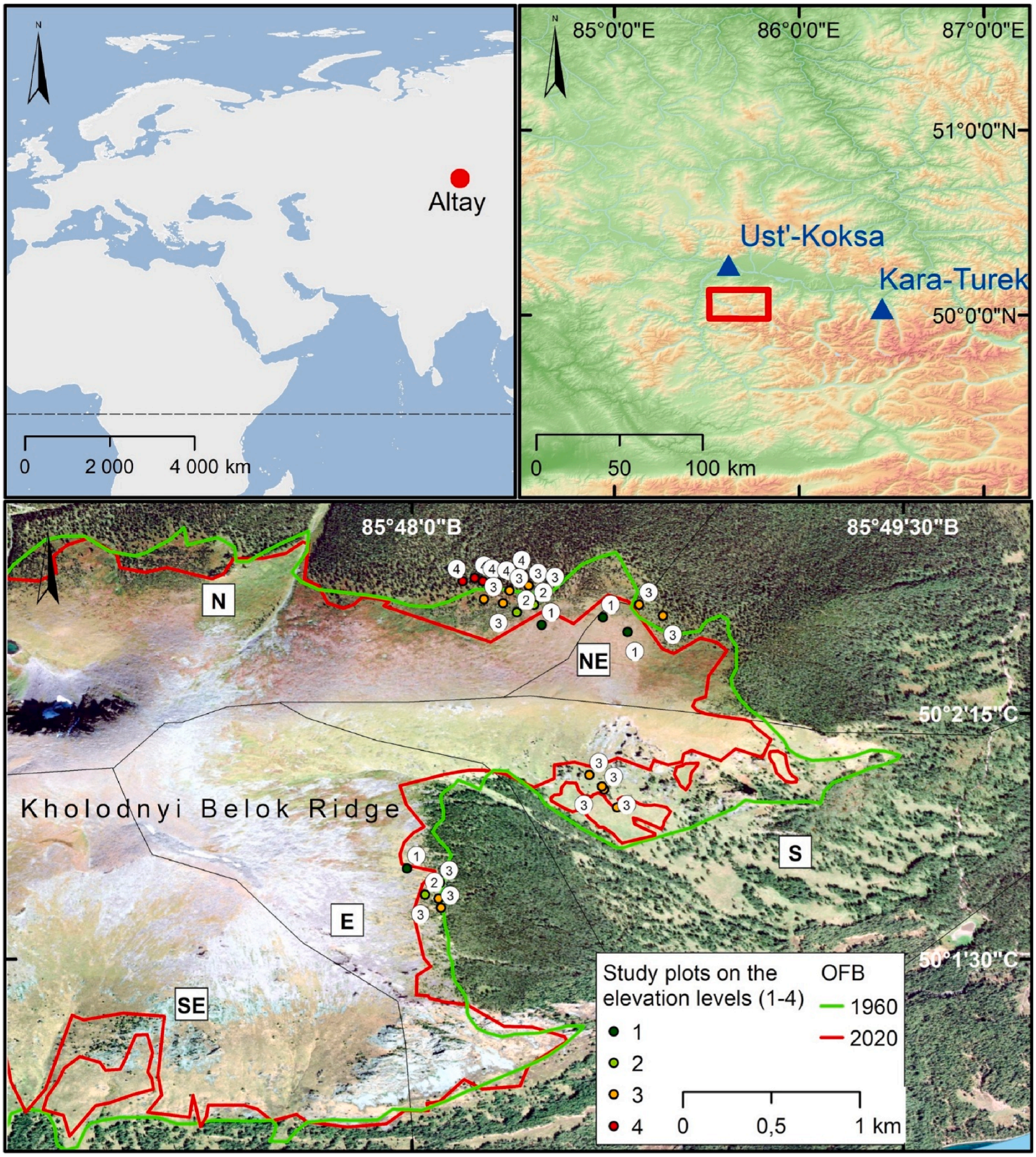

Fig. 1. Location of the study area on different exposure slopes (N: northern, NE: northeastern, S: southern, E: eastern) on the Kholodny Belok Ridge (the Central Altai Mountains). Blue triangles point to weather stations; red cycles show the levels of elevation transects.

−20.9 ± 3.8 and −16.4 ± 2.5°C, respectively (Fig. S1). In some winters, air temperatures can fall below −42 °C. The total annual precipitation is 497 ± 98 mm at 980 m a.s.l. and 623 ± 90 mm at 2,600 m a.s.l. The average wind speed at these two sites is between 2.8 and 8.6 m·s^{-1} and can reach 50 m·s^{-1} in winter. The soil surface temperature at the two weather stations drops to −19.7 ± 6.5 and −21.9 ± 9.8 °C in January and rises to 20.9 ± 11.4 and 9.8 ± 7.9 °C in July.

The treeline is located primarily within the range of 2,000 and 2,100 m a.s.l., where it is formed by stands dominated by *Pinus sibirica* Du Tour and *Larix sibirica* Ledeb. Soil formation on the slopes of the Kholodny Belok Ridge occurs on the eluvium-deluvium and colluvium of greenstone, grey-green, grey siltstone, and mudstone (Buslov et al., 2013).

The morphological structure and general patterns of spatial distribution of soils in the study area (the Kholodny Belok Ridge) are consistent with the geographical peculiarities of the soil distribution in the whole Altai region and strongly depend on elevation and slope exposure. Mountain-meadow soils are widespread under subalpine and alpine meadows on well-watered and warmer southern and western slopes. The areas of mountain-meadow soils are significantly reduced and replaced by mountain-tundra peat and humus soils beyond the belt of alpine meadows on the colder northern and eastern slopes. While forest-tundra peaty podzolized soils form a narrow band at the upper forest limit on the northern slopes. Typical brown and podzolized soils occupy the middle part of the forest belt and significant areas at the upper forest limit. Soddy-deep podzolic soils are not widespread. In the warm sites of the southern slopes, mountain meadow-steppe soils develop, which, with decreasing elevation, transform into zonal steppe soils, bypassing the forest soils (Kovalev et al., 1973).

2.2. Trees stand data sampling and calculation

In 2021–2022, four elevation transects were established on the eastern part of the Kholodny Belok Ridge on slightly stony terrain (no more than 10% of the surface area) that was not subject to visible erosion or traces of snow avalanches, with slopes of 20°–35° at four exposures (eastern, northern, northeastern, and southern) (Fig. 2). On each slope, a series of 3 to 8 study plots (8 m radius) were established at 1–4 elevation levels, depending on the presence of stands with a certain density and canopy closure. Study plots were established on the eastern and northern slopes in the following areas: sparse tree stands (level #1); open forests (level #2); in forests which are now closed (level #3), and in closed forests, as marked on topographic maps from the 1960s (level #4). On the northeastern slope, these surveys were conducted in the sparse tree stands and in the present-day closed forests, while on the southern slope, they were carried out in the present-day closed forests.

The exact location, stem diameter at breast height (DBH), crown diameter in two perpendicular directions, height, and vital status of each tree were recorded in all study plots. The age of the trees was determined by taking radial wood cores with an increment borer at the base of the stem and then processing them in a laboratory. The cores were glued to wooden bases, scraped with a hazardous blade, and pigmented with tooth powder to make the annual rings more visible. All samples were measured on LINTAB-VI semi-automatic complex (Rinntech, Germany) with an accuracy of 0.01 mm using TSAP-Win™. Further processing was carried out according to generally accepted methods of dendrochronology (Grigoriev et al., 2022; Moiseev et al., 2022). To identify false and missing rings, generalized tree-ring chronologies were constructed for larch and stone pine, against which individual tree-ring chronologies were dated. The growth patterns of tree saplings were examined to determine a correction for drilling height (Hagedorn et al., 2014). Examination of radial wood cores and visual inspection of tree trunks indicated that the study stands had not been subjected to intense fire in the last 500 years, as there were no signs of fire damage. Furthermore, visual inspection of trees revealed no substantial stem or branch damage caused by snow abrasion or wind. In total, morphometric parameters were determined for 1,478 trees (including saplings), and age was estimated for 1,032 trees over a total area of 1.14 ha. For each elevation level of the transects, standard statistical values were calculated for the morphometric and area parameters of the tree stands.

2.3. Soil sampling and analysis

Soil researches were carried out on the same study plots of four elevation transects established for the stand surveys, where soil profiles were examined for diagnostic and general characteristics (description of soil morphology, depths, soil sampling according to genetic horizons, acidity, exchangeable cations, C_{org}, N_{tot}, and available phosphorus (P)) at levels #1, #2, #3, and #4. Additionally, to account for spatial heterogeneity, soil samples were collected at fixed depths on the three slopes: eastern and northern (at three levels: #1, #2, and #3) and the southern (at one level). At each elevation level, 6 additional pits were dug—3 under crowns and 3 in open areas between trees. Soils were sampled from the depths of 0–5, 5–10, 10–20, and 20–40 cm, and, if possible, from 40 cm to the bedrock; total C, total N, and available P were analyzed.

Samples were air dried, crushed, and sieved through a 2-mm sieve (IKA MF 10 basic). The pH (water) was measured using an ion meter (I-160MI, Russia) at a substrate-to-water ratio of 1:25 for organic horizons and 1:5 for mineral horizons. Total acidity (TA; cmol·kg^{-1}) was measured by the Kappen method after treating the soil with 1 M Na-acetate (pH 8.3) at a substrate-to-extractant ratio of 1:150 for organic horizons and 1:2.5 for mineral horizons. The determination of exchangeable calcium (Ca) and magnesium (Mg) was carried out by decantation in 1 M NaCl solution, followed by complexometric titration with Trilon B. The degree of saturation of the exchange complex with bases was calculated. Available P was determined after extraction of P with 0.2 N HCl using colorimetric methods with P molybdenum blue (Vorobieva, 2006).

Sample preparation for carbon and N measurements included removal of small roots, crushing, and sieving through a 0.25 mm sieve. The concentration of organic carbon (C, %) was determined during high-

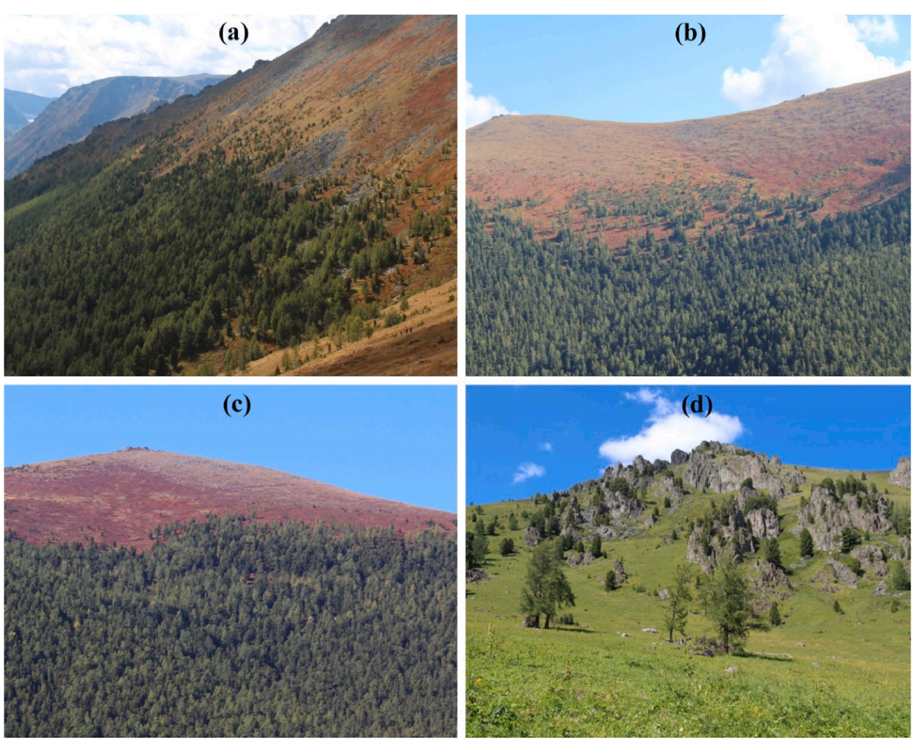

Fig. 2. General view of the studied slopes on the Kholodny Belok Ridge: **(a)** eastern, **(b)** northern, **(c)** northeastern, and **(d)** southern.

temperature combustion, followed by the determination of carbon dioxide on an infrared detector using the Multi N/C 2100 analyzer (Analytik Jena, Germany). Total N was determined by the Kjeldahl method after wet digestion of the soil in concentrated H_2SO_4 using a digester (DK20, VELP Scientifica, Italy), followed by determination on an analyzer (UDK 139, VELP Scientifica, Italy). The C/N molar ratio was calculated for each individual soil sample (soil layer), and the values obtained were then used in subsequent calculations and statistical analyses.

Soil diagnosis was performed according to the World Reference Base for Soil Resources (IUSS, 2022). Soil horizon indices were assigned according to the Guidelines for Soil Description (Jahn et al., 2006).

2.4. Estimation of regional climate changes and relation of them with tree stand dynamics

Climate conditions and their changes over 80 years in areas near the study site were assessed using mean monthly air temperature and total monthly precipitation data collected at two weather stations in the Altai Mountains: Ust'-Koksa (station index 36229, location 50°16′ N, 85°37′ E, 977 m above sea level) and Kara-Turek (station index 36442, location 50°02′ N, 86°27′ E, 2601 m above sea level) (http://meteo.ru/data, access date 23 August 2025). The obtained information was analyzed for the warm (June–July) and cold (October–April) seasons separately. Anomalies in air temperature and precipitation for each calendar year were defined by the difference between the current value and the average value in the base period (1961–1990), which is commonly used to assess the historical climate (WMO, 2017). The coefficient of determination (R^2) was used to evaluate linear regression models based on this data.

We estimated the relationships between the amount of *Pinus sibirica* trees that appeared in 5-year periods and the 5-year average air temperature and precipitation of warm and cold seasons. These calculations were done using the Spearman correlation analysis, since almost all the variables have a normal distribution according to the Shapiro-Wilk test, but the sample size is not large enough. Such analysis was not performed for *Larix sibirica* due to the low amount, which was insufficient for this investigation.

2.5. Obtaining local condition data

Regional weather station data (air temperature, precipitation, and length of the growing season) cannot be extrapolated directly for local sites and slopes in the study area. Therefore, we used the remote-sensed data on summer and winter land surface temperature (LST; June–August and LST September–May) and the normalized difference snow index (NDSI) to assess the dependence of the open forest boundary position on the local conditions. The LST is an indicator of thermal radiance or the degree of heating of objects and was defined by the NASA Earth Observatory as how hot or cold the surface of the Earth would feel to the touch in a particular location (Li et al., 2013). LST raster (50 m·pixel^{-1}) was obtained from the "ST_B10" channel of the dataset accessible on https://developers.google.com/earth-engine/datasets/catalog/LANDSAT_LC08_C02_T1_L2#description in special software on website code.earthengine.google.com as an interactive development environment (access date 23 May 2025).

The NDSI was used as an indicator of snow cover duration on different slopes of the study area. A raster of snow cover data from September 2016 to May 2023, as median NDSI was calculated from data obtained in the dataset accessible on https://developers.google.com/earthengine/datasets/catalog/LANDSAT_LC08_C01_T1_8DAY_TOA#description in the code.earthengine.google.com software environment (access date May 23 2025).

The mean duration of direct insolation during summer days was computed based on digital elevation model data in the "Potential Incoming Solar Radiation" module of SAGA GIS software (solar constant: 1,367 W·m^{-2}, time period: 15. 07. 2020, default values were used for other parameters). Using the Point Sampling Tool module in QGIS software, we extracted data from rasters of NDSI, LST (June–August and September–May), direct summer insolation, and digital elevation model in 637 points located along the open forest boundary in the 2020s (30 m·pixel^{-1}). The data was then transferred to an attribute table of point layers. Standard statistics for these parameters were calculated for slope sectors of different exposures.

2.6. Data analysis

Differences between the morphometric parameters and age of the trees were analyzed using a two way analysis of variance (ANOVA). Two factors were considered: the elevation level (#1, #2, #3, and #4) and slope expose (eastern, northern). Data on individual trees was used for calculations. This analysis could not be performed for the southern and northeastern slopes due to insufficient data. Multiple comparisons were performed using Tukey's test. The Kruskal-Wallis test was used to compare carbon, N, and P between elevations and among different slopes. Spearman correlation analysis was used to assess the relationships between tree stand characteristics and soil parameters in organic horizons Oi + Oe and in the upper 10 cm below organic horizon. The statistical unit was a sample plot (3 plots per each elevation levels: 3 levels at eastern and northern slopes, 1 level at the southern slope, $n = 20$), represented by the arithmetic means of studied parameters.

3. Results

3.1. Morphometric and areal characteristics of tree stand dynamics

We found that on all the studied transects, with increasing elevation, the average morphometric parameters of the stands decrease by a factor of 2–6 and the areal characteristics by a factor of 5–18 (Table 1). Thus, if the average stem DBH of *Pinus sibirica* is 15.3 cm on the lower level (#4) of the eastern transect, it is 5.8 cm on the upper level (#1). However, on the northern slope, these differences are more pronounced—DBH decreases from 24.6 to 3.9 cm and height from 8.4 to 2.1 m. Our data (Table 1) show that the rate of change of areal characteristics with elevation increase varies on slopes with different exposures. For example, the sum of crown projection areas decreases by a factor of 18.4 on the eastern transect and by a factor of 6.5 on the northern transect. In addition, we observed a regular decrease in the average age of the stands along the slope. The ratio of stone pine to larch by crown closure also differs significantly on slopes with different exposure. Thus, the crown cover of larch is higher than that of stone pine on the eastern slope (56%–74% vs. 26%–44%) and lower than on the northern and southern slopes (0%–52.7% vs. 47%–100%). However, on the northeastern slope, larch is absent on the upper level (#1) and dominates on the upper boundary of closed forests (61%).

Analysis of the age structure of *Pinus sibirica* stands on the northern slope of the eastern part of the Kholodny Belok Ridge showed that the first stone pines growing here today appeared in the mid-15th century at the lower elevations (data not shown in figures). Small amounts of stone pines occupied the slopes at levels #2, #3, and #4 before the mid-19th century (Fig. 3). However, it was only at the lowest level (#4) that the amount of stone pines increased most rapidly, and this continued until the end of the 19th century. The maximum established rate of stone pines at this level was observed between 1900 and 1950, after which it decreased sharply until 1980, apparently due to the strong negative impact on regeneration of the increased closure of the maternal canopy. At levels #2 and #3, stone pines began to grow actively only at the beginning of the 20th century, and this process reached its maximum between 1920 and 1940. The most active encroachment of stone pine trees at the upper level (#1) was observed since 1950, and the establishment rate reached its highest values in the period from 1995 to 2015. The eastern slope, unlike the northern slope, was not planted with stone

Table 1
Average morphometric and areal characteristics of the studied tree stands on the Kholodny Belok Ridge (the Central Altai Mountains).

Level #	Exposure	Elevation (a.s.l. m)	DBH (cm)		Stem height (m)		Age (years)		Crown diameter (m)		Sum of crown cover ($m^2·ha^{-a}$)	Density ($tree·ha^{-a}$)	
			Mean	Max	Mean	Max	Mean	Max	Mean	Max		≤1.5 m	>1.5 m
Larix sibirica													
1	E	2280	12.5 ± 5.9a	21.9	4.5 ± 1.9a	7.0	68 ± 24a	109	3.1 ± 0.9a	4.7	646	1	73
2	E	2230	12.0 ± 7.3a	27.1	7.4 ± 2.9ad	12.0	70 ± 20ad	105	4.2 ± 1.8ac	6.4	2643	0	176
3	E	2200	12.9 ± 7.7ac	31.5	9.7 ± 3.2bd	15.0	70 ± 19a	127	5.8 ± 1.6bc	8.6	6585	0	264
4	E	2170	25.9 ± 11.4a	50.6	16.7 ± 3.7c	24.7	104 ± 30a	203	5.8 ± 1.9bc	10.0	13,502	0	539
1	N	2120	—	—	—	—	—	—	—	—	—	—	—
2	N	2090	18.7 ± 11.5a	50.9	6.9 ± 2.9ad	10.5	100 ± 39ae	170	3.6 ± 1.4a	7.3	2368	55	220
3	N	2060	26.5 ± 16.6a	55.0	10.0 ± 3.8bde	17.5	271 ± 187bdeh	577	4.2 ± 1.9a	7.5	4053	26	291
4	N	2030	40.6 ± 23.3bc	70.0	14.1 ± 3.4ce	20.0	367 ± 187ch	628	4.5 ± 1.3a	6.7	537	18	97
3	S	2050	33.5 ± 25.2	87.0	9.9 ± 6.3	19.0	99 ± 36	166	6.1 ± 3.4	11.0	3117	5	94
1	NE	2160	—	—	—	—	—	—	—	—	—	—	—
3	NE	2080	39.2 ± 9.5	60.0	12.5 ± 1.5	16.0	383 ± 143	558	5.5 ± 1.6	9.0	7104	0	286
Pinus sibirica													
1	E	2280	5.8 ± 2.9a	13.0	2.4 ± 0.7a	3.7	28 ± 18a	96	1.7 ± 0.5a	2.9	500	470	191
2	E	2230	7.4 ± 5.2af	22.0	3.6 ± 1.5b	7.3	38 ± 22a	116	2.0 ± 0.9b	5.7	1046	154	529
3	E	2200	12.7 ± 8.2c	34.1	5.5 ± 2.7b	13.0	48 ± 18ae	104	2.8 ± 1.3c	6.1	3001	55	760
4	E	2170	15.3 ± 8.8c	42.0	9.8 ± 4.5d	20.9	91 ± 19bd	137	3.4 ± 1.5d	6.8	7610	0	881
1	N	2120	3.9 ± 2.4a	11.0	2.1 ± 0.5a	3.4	37 ± 23a	110	1.6 ± 0.6a	3.0	1395	1894	646
2	N	2090	6.6 ± 4.5ae	25.0	3.5 ± 1.8b	12.5	74 ± 26b	171	1.8 ± 1.1b	7.2	4813	220	1806
3	N	2060	8.2 ± 5.5bef	52.0	4.4 ± 2.7b	15.0	76 ± 36be	210	1.9 ± 0.9b	5.3	3639	414	1057
4	N	2030	24.6 ± 23.9d	90.0	8.4 ± 5.4c	22.5	187 ± 140c	575	3.2 ± 2.0c	8.0	8511	476	775
3	S	2050	23.9 ± 14.2	69.0	7.8 ± 3.6	19.0	80 ± 28	130	3.9 ± 1.9	9.8	4923	11	325
1	NE	2160	4.2 ± 2.7	16.0	2.3 ± 0.6	3.7	59 ± 20	105	1.4 ± 0.5	2.7	1204	954	675
3	NE	2080	16.5 ± 11.9	54.0	6.4 ± 2.9	12.0	91 ± 32	166	2.9 ± 1.3	6.3	3348	319	440

Note: Significant differences are indicated by different letters (Tukey's test, $p < 0.05$). Non-significant differences are marked with identical letters for the northern and eastern slopes. The analysis was performed separately for *Larix sibirica* and *Pinus sibirica*.

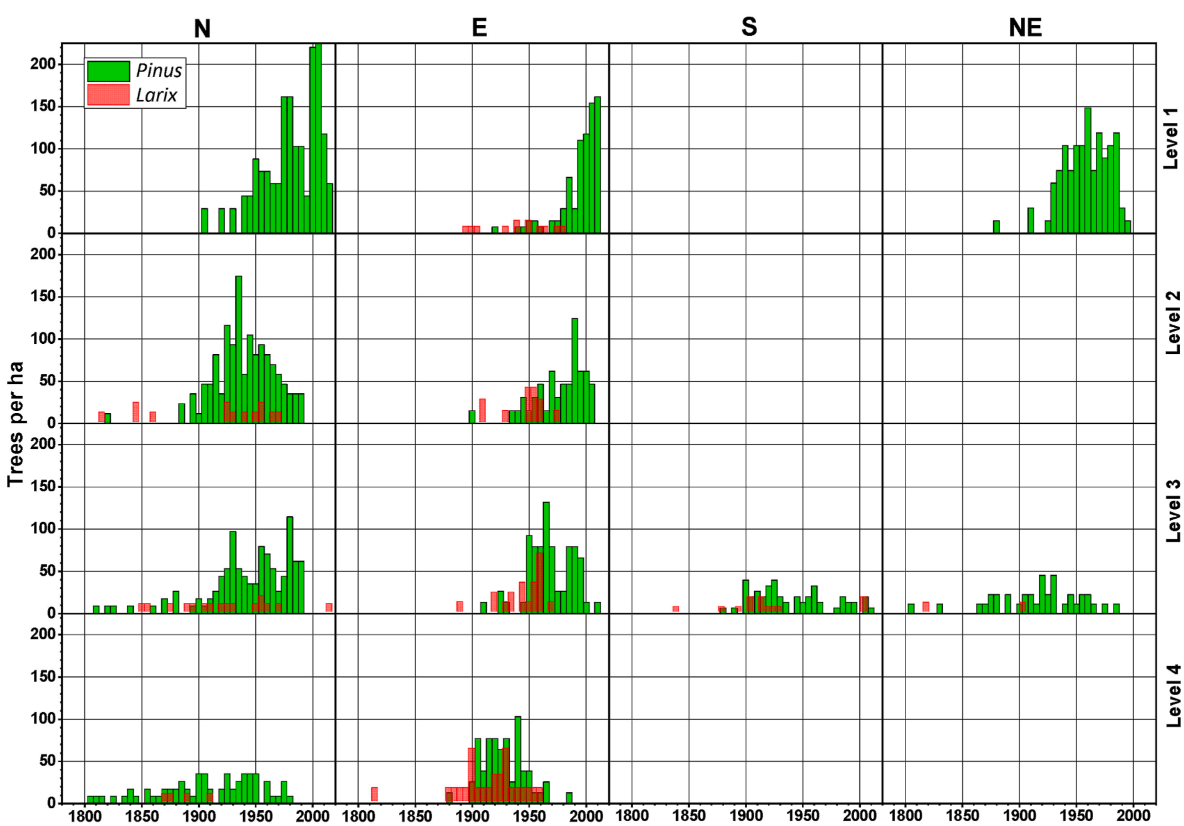

Fig. 3. Distribution of *Pinus sibirica* and *Larix sibirica* trees by periods of their appearance on the different levels of elevation transects established on the Kholodny Belok Ridge on different exposure slopes.

pine until the end of the 19th century. At the lowest level (#4), the maximum establishment rate was recorded between 1900 and 1950. At level #3, stone pine appeared most frequently between 1950 and 1990. At level #2, this was only observed after 1970, and at level #1 after 1990. On the northeastern slope at level #3, the first trees began to appear in the 17th century (data not shown), and then during the 19th and 20th centuries, the colonisation of stone pine was gradual, with no obvious peaks in amounts of established trees. At the upper elevation level, active colonisation of trees occurred after the 1930s and continued to the present day. At level #3 on the southern slope, the main period of tree establishment occurred between 1900 and 1940.

We found that the first larches (*Larix sibirica*) growing on the northern slope appeared much earlier—in the 15th century, and they continued to occupy it without obvious peaks in the form of single trees (Fig. 3). On the eastern slope at level #4, in contrast to the northern slope, the first larches did not appear until the end of the 19th century, and on levels #1, #2, and #3 until the 20th century. In general, a larch establishment rate was gradual at all elevation levels, with no obvious peaks in abundance. On the northeastern slope, the appearance of larch was similar to that on the northern slope, from the 15th century to the present. On the southern slope, larch began to appear in the mid-19th century, and this process continues to the present day through the appearance of single trees.

3.2. Soil morphology and profile structure

All studied soils were highly or very highly skeletal (stoniness in the upper 10 cm of the mineral profile is 25%–80%; in the deeper layers 60%–95%) and shallow (20–50 cm depth); most of them belong to the group of highly stony soils (Leptosols). The fine-earth fraction was represented by light and medium loams. There were no morphological signs of gleying, cryogenic pedoturbation, and permafrost.

Depending on slope exposure, soils differed markedly (Table 2). On the eastern slope, soil morphological patterns were mainly composed of organic horizons. The mean thickness of the organic horizons Oi + Oe (or OL + OF horizons), consisting of weakly decomposed plant residues, was 2.0, 4.0, and 1.9 cm at levels #3, #2, and #1, but the differences were not significant. Abundant organic powdery material with unrecognizable particles either formed a separate Oa horizon or was present as a component of mineral horizons. While the thickness of the organic horizons (Oi + Oe) was small, the thickness of the Oa horizon was considerable, reaching 5–10 cm and sometimes 15–20 cm, where it was located between stones. More developed profiles of Cambisols with structured granular mineral horizons B were formed in soils under closed forest at the level #4 and partly at the level #3 (Fig. 4).

On the southern slope, soddy soils had a dark grey colour throughout the soil profile to a depth of 60 cm and a well-defined grain and blocky subangular structure (chernozem-like pattern). The average thickness of the organic horizons Oi + Oe (or OL + OF horizons) is 3.0 cm, the Oa horizon was absent.

In the soils of the northern slope, the thickness of organic horizons (Oi + Oe) was higher than on the eastern and southern slopes and changed in the sequence of levels #3–2–1 (upper boundary of closed forest–open forest–sparse tree stands) 5.3–4.0–4.2 cm (not significant). The Oa horizon was uncommon, with a maximum thickness of 5 cm. At lower positioned levels (#2–4), the podzolic process was developed.

On the northern slope, the soil morphology noticeably changed in the transition from open forest (level #2) to the sparse tree stands (level #1), where podzolized soils are replaced by weakly developed tundra soils (constituted by O horizons and underdeveloped A horizons) and the degree of podzolisation process weakens from levels #4 to #3 and #2. On the eastern slope, soil morphology showed no distinct transitions between elevation levels. The more pronounced differences occurred at the lowest level (#4), and soils remained almost similar under closed forest, open forest, and sparse tree stands. At the same time, the distinctions between the exposures are more pronounced (Fig. 4).

3.3. Soil chemical parameters

The chemical characteristics of the soils on the different exposures were contrasting. The highest acidity was revealed in soils on the northern and northeastern slopes, while the lowest was on the southern slope. The difference in pH in the upper mineral horizons on the northern and southern slopes was about 1 unit, and in some cases reached more than 2 units (Table S2). The soils on the northern and northeastern slopes were strongly acidic in the organic (pH 3.38–4.60) and upper mineral horizons (pH 3.84–4.09), becoming less acidic with depth (up to 4.63–5.05). The opposite pattern was observed on the eastern slope. Organic horizons were less acidic than on the northern slope (pH 5.31–5.73), and acidity tended to increase with depth (pH 5.06–5.12 directly below organic horizons and up to 4.82–4.87 in the lower mineral horizons). On the southern slope, the soils were slightly acidic with weak variations throughout the soil profile (5.77–5.95, decreasing to 5.39 in the lowest horizon).

Exchangeable Ca predominated over exchangeable Mg in the C-rich horizons, and the Mg content was comparable to that of Ca in the lower layers due to the influence of the bedrock. In organic horizons, the content of exchangeable Ca was highest in soils on the southern slope (90 $cmol \cdot kg^{-1}$), slightly lower on the eastern slope (53–84 $cmol \cdot kg^{-1}$), and minimal on the northern and northeastern slopes (22–34 $cmol \cdot kg^{-1}$); no regularities between slopes were found for Mg. In the mineral horizons on the eastern and southern slopes, the contents of Mg and Ca remained high (22.5–50.0 $cmol \cdot kg^{-1}$ Ca, 9.5–17.0 $cmol \cdot kg^{-1}$ Mg), which can be explained by the high content of OM binding Ca. On the northern and northeastern slopes, where the organic horizons transition to the mineral horizons, the content of exchangeable bases decreased sharply (Ca up to 4.5–10 $cmol \cdot kg_{soil}^{-1}$, Mg up to 1.0–9.0 $cmol \cdot kg_{soil}^{-1}$). Most soil on the eastern slope were weakly saturated with bases (61%–80%), on the southern slope were high saturated (81%–92%), and on the northern and northeastern slopes organic and podzolic horizons were not saturated (31%–53%), while in the deeper horizons saturation increased (up to 76%).

3.4. Organic carbon, total N, and available P in the soils

The depth distribution of organic carbon and total N content in all soils on the Kholodny Belok Ridge was accumulative, with the maximum concentration in the organic layer (28%–46% C_{org} and 13–23 $g \cdot (kg^{-1}$ $N_{tot})$) (Figs. 5 and 6).

On the eastern slope, below the Oi + Oe organic layer, horizons Oa were common, with carbon contents exceeding 20% and sometimes

Table 2
Typology of soils at different levels of the studied transects on the Kholodny Belok Ridge, according to the World Reference Base (IUSS, 2022).

Elevation level #	Transect			
	E	N	S	NE
1	Folic Leptosols, Someriumbric Leptosols (Hyperhumic)	Folic Leptosols (Humic)	—	Folic Leptosols, Someriumbric Leptosols
2	Folic Leptosols, Someriumbric Leptosols (Hyperhumic)	Skeletic Podzols (somewhere Folic), Skeletic Entic Podzols	—	—
3	Folic Cambic Leptosols, Folic Leptosols, Someriumbric Leptosols	Skeletic Podzols (somewhere Folic)	Skeletic Mollic Umbrisols	Skeletic Entic Podzols, Cambic Leptosols
4	Leptic Cambisols, Cambic Umbric Leptosols (Humic)	Skeletic Podzols	—	—

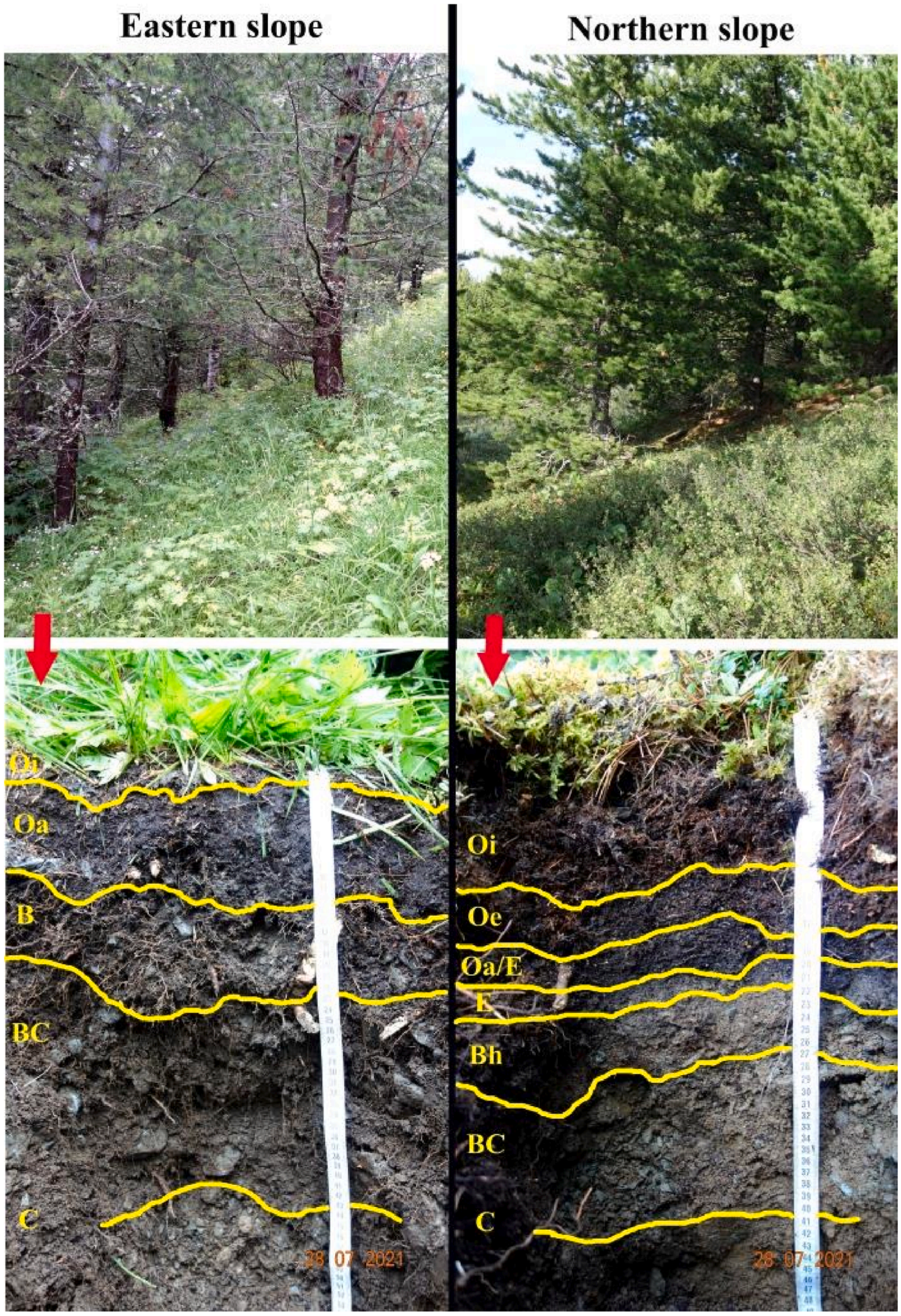

Fig. 4. Sample plots and soil profiles under closed forest (level #3) on the Kholodny Belok Ridge. Folic Cambic Leptosol on the eastern slope and Skeletic Podzol (Folic) on the northern slope (Lines show boundaries of soil horizons).

reaching 28%, extending to depths of 0–5 cm, less often 5–10 or sometimes 10–20 cm; the N content at 0–5 cm maintained the same values as in the organic horizons Oi + Oe, with mean values of 18–15–17 g·kg^{-1} N in soils on the upper boundaries of the closed forest–open forest–sparse tree stands, respectively. On the southern slope in the upper mineral horizons, the carbon content was 17%–18% and N content 6.7–16.0 g·kg^{-1}. The decrease down to the soil profile was so gradual that even at a depth greater than 20 cm, the carbon and N content in soils of the eastern and southern slopes remained very high (10.48%–8.90%–6.4% C and 8.5–8.8–5.3 g·kg^{-1} N under closed forest–open forest–sparse tree stands, respectively, on the eastern slope and 5%–7% C and 6.7–16.0 g·kg^{-1} N on the southern slope) (Figs. 5 and 6, Table S2). In the upper horizons (Oi + Oe and Oa at the depth of 0–5 cm), no differences in C and N content along the elevation gradient were found, while in deeper layers, higher C and N content was found in soils at levels #2 and #3.

Soils on the northern and northeastern slopes were characterized by lower organic carbon and total N contents and a more abrupt decline in these values down to the soil profile compared to soils on the southern and eastern slopes (Figs. 5 and 6). Carbon content in the upper soil horizons increases from tundra to forest soils. In deeper layers, carbon content shows little difference between altitude levels (and spatial variability is high). In contrast, N content tends to decrease downslope at all depths up to 20 cm.

The differences in C and N concentration on the northern, eastern, and southern slopes were significant in organic layer Oi + Oe ($H_{(2,64)} = 20.4$, $p < 0.001$, Kruskal-Wallis test for carbon, $H_{(2,64)} = 13.1$, $p = 0.0014$ for N), depth 0–5 cm ($H_{(2,44)} = 8.2$, $p = 0.016$ for C and

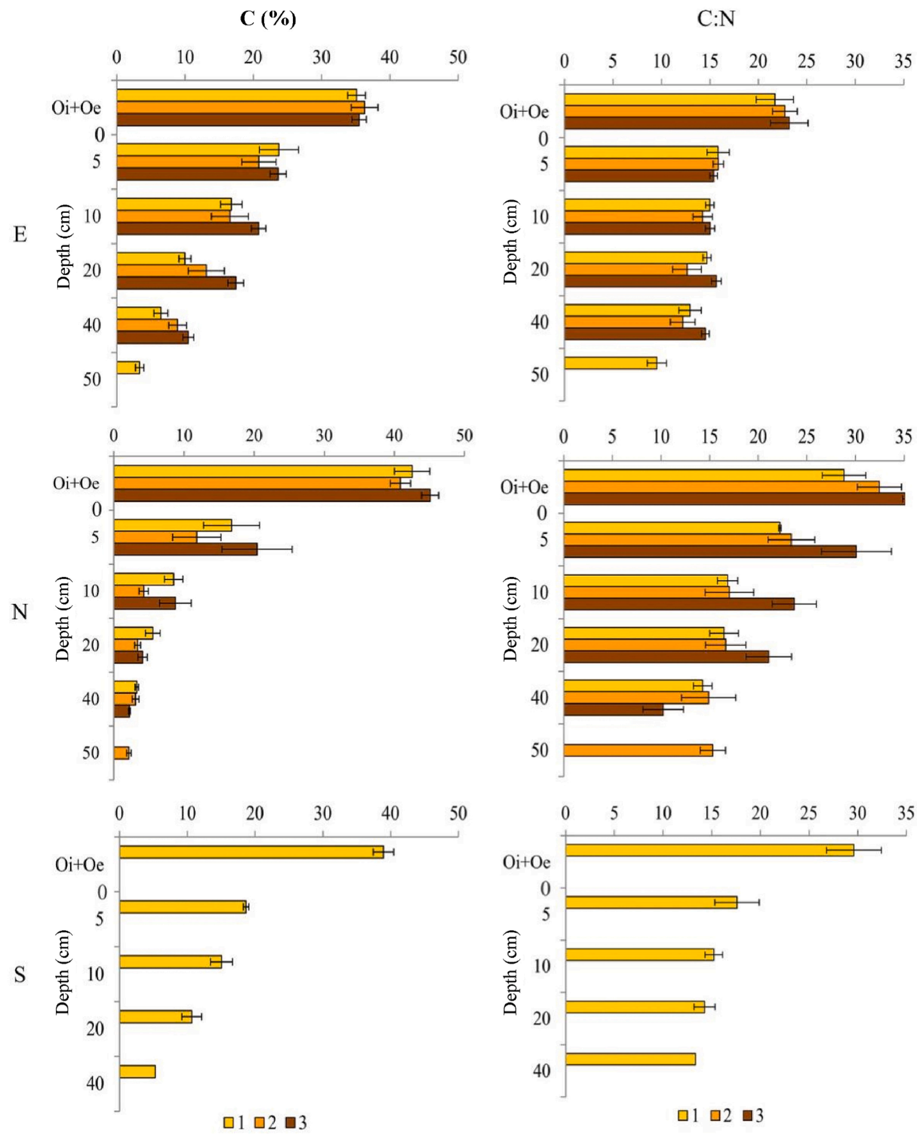

Fig. 5. Soil total carbon and C:N ratio on the Kholodny Belok Ridge (columns: mean, whiskers: standard error; #1, #2, #3: elevation levels).

$H_{(2,44)} = 27.8$, $p < 0.001$ for N), and depth 5–10 cm ($H_{(2,44)} = 24.9$, $p < 0.001$ for C and $H_{(2,44)} = 31.4$, $p < 0.001$ for N).

C:N ratio was maximal in organic horizons (Fig. 5). In the underlying layers according to the C:N values, the SOM quality on the eastern slope is very similar at all elevation levels (15.4–15.9–15.9 at the depth of 0–5 cm on levels #3–2–1, respectively) and almost did not change down to soil depth, indicating a low degree of SOM decomposition even in deep horizons, which is also consistent with soil morphology. On the southern slope, the C:N ratio varies slightly along the soil profile (the total range over 0–40 cm thickness was 13.2–18.6, and the ratio decreased to 11 deeper than 60 cm). The highest C:N values (less decomposed OM) were found in soils on the northern and northeastern slopes, where the variation of this ratio in coarse humus podzolized horizons at 0–5 cm depth was extremely high (from 12.8 to 39.8) and mean values decreased 30.0–23.4–22.1 in soils of levels #3–2–1, respectively. In deeper horizons C:N ratio decreased to values 10.1–21.5, soil on level #3 maintaining higher ratios compared to levels #1 and #2.

Available for plant nutrition P is insufficient at all slopes, except for the organic horizons. The lowest P content was found in the mineral horizons at the northern slope (Fig. 6), and the highest—at the southern slope. No significant differences were revealed in P content across the three elevation levels on both the northern and eastern slopes and between the northern, eastern and southern slopes in organic layer Oi + Oe ($H_{(2,64)} = 3.3$, $p = 0.19$), while in the deeper horizons differences on the northern, eastern and southern slopes were significant (0–5 cm $H_{(2,44)} = 7.8$, $p = 0.02$ and 5–10 cm $H_{(2,44)} = 13.4$, $p = 0.0012$).

For the organic horizon, tree age showed positive significant correlations with organic carbon ($r = 0.63$ and 0.56 for mean and maximum age, respectively) and with the C:N ratio ($r = 0.55$ and 0.47, respectively) (Table S5). A higher average age is typical for the lower level, with higher proportion of coniferous litter. The lower C:N ratio at this level could reflect either N-poor nature of coniferous litter compared to high-altitude vegetation or slower decomposition rates in the forest soils. In the upper 10 cm soil layer beneath the forest litter crown diameter showed positive significant correlations with total carbon, N, and P. DBH and stem height correlated positively only with available P. Unlike the patterns observed in the forest litter, the correlation of organic carbon with tree age was negative. Similarly, the relationship with N is negative (insignificant), and with C:N is positive (significant $r = 0.51$ and 0.47 for mean and maximum age per sample plots, respectively). This indicates that older tree stands are associated with wider C:N ratio in the upper mineral horizon.

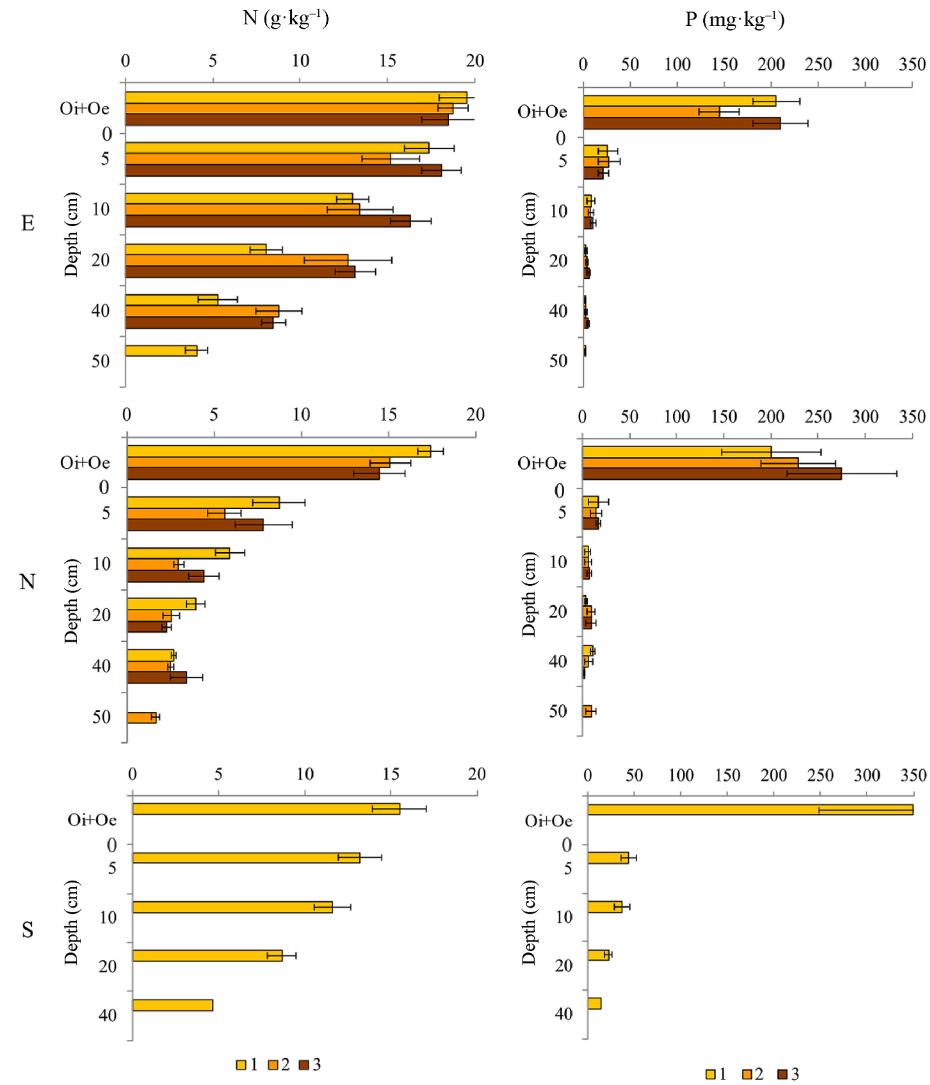

Fig. 6. Soil total nitrogen and available phosphorus on the Kholodny Belok Ridge (columns: mean, whiskers: standard error; E: eastern slope, N: northern slope, S: southern slope).

3.5. *Regional climate changes and their correlation with tree establishment rates*

The analysis of the meteorological data of weather stations located near the study area showed that the climate has become warmer in the last 80 years, with the most noticeable changes in the cold seasons in the valleys compared to the highlands (Fig. 7). In particular, in the cold period, the mean temperature increase at an elevation of 980 m a.s.l. was two times higher than at 2,600 m a.s.l. according to data collected on the Ust'-Koksa and Kara-Tyurek weather stations, where the linear trends were 0.44°C·decade^{-1} (R^2 = 0.58) and 0.21°C·decade^{-1} (R^2 = 0.46), respectively. For the warm period, a temperature increase was similar −0.18°C·decade^{-1} (R^2 = 0.47) vs. 0.15°C·decade^{-1} (R^2 = 0.41). At the same time, changes in the amount of precipitation in the cold season showed the opposite trend. There was a decrease of 4 mm·decade^{-1} (R^2 = 0.21) in the valleys and an increase of 5.7 mm·decade^{-1} (R^2 = 0.27) in the highlands. In summer, precipitation decreased insignificantly by 1.3 mm·decade^{-1} in the valleys and 0.3 mm·decade^{-1} in the highlands.

Correlation analysis found significantly high correlations between amount of *Pinus sibirica* trees established in 5-year groups on the upper part of the eastern slope (levels #1 and #2) and the mean values of climatic variables (the temperatures of cold and warm periods, as well as winter precipitation) for the first five years following after the tree appearance. These correlations were closer to temperature than to precipitation (Table S3). Additionally, a significant, but negative, correlation was obtained for northeastern slope only with the warm period temperatures. Whereas insignificant correlations were revealed with cold season temperature and precipitation for the northeastern slope and for all climatic variables for the northern slope.

3.6. *Open forest boundary elevation and local conditions*

To assess the influence of growing season length and heat supply on the elevation of the upper boundary of open forests, spatial data on summer and winter land surface temperatures and snow cover duration were analyzed on the different exposures. A comparison of these data shows that the snow melts significantly later on the northern slope than on the southern slope (Fig. 8). The eastern slope occupies an intermediate position in this regard. It has also been revealed that the land surface temperature is significantly higher on the southern slopes than on the northern slopes, and, as in the case of the duration of snow cover, the temperature on the eastern slopes has intermediate values for cold season. We found that on the eastern part of the Kholodny Belok Ridge, open forest boundary reaches maximal elevation on eastern slope (approx. 2,250 m a.s.l.), where snow cover duration and winter land

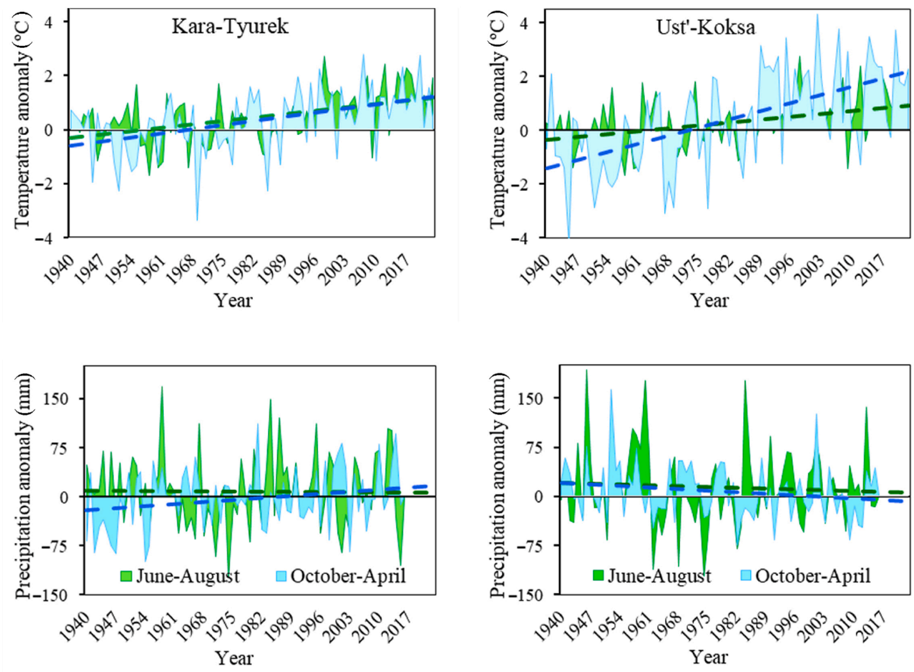

Fig. 7. Time series of mean temperature anomalies and total precipitation anomalies in warm (June–August) and cold (October–April) seasons at the Kara-Tyurek (2,600 m a.s.l.) and Ust'-Koksa (980 m a.s.l.) weather stations. Anomalies are relative to the mean values of the 1961–1990 period. The line shows the linear trend.

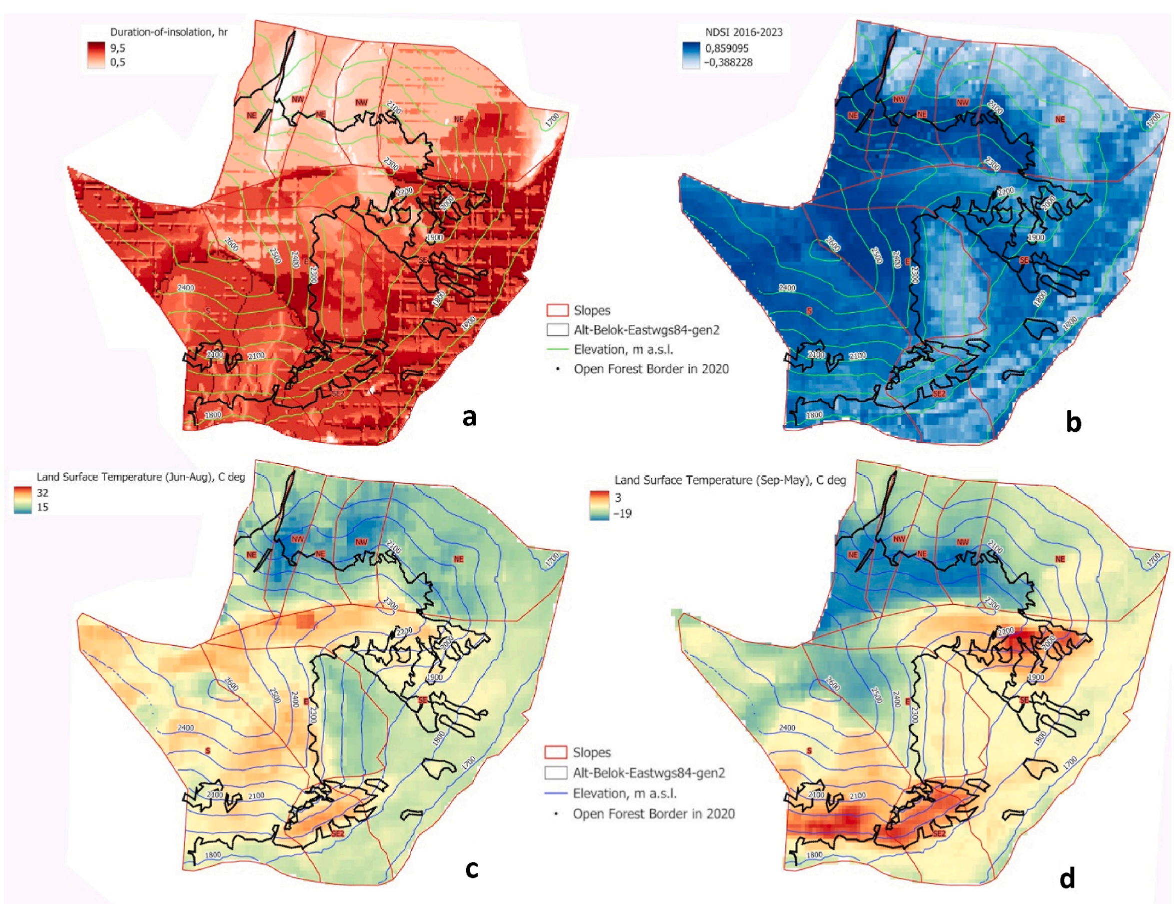

Fig. 8. Spatial distribution of sites with different **(a)** mean duration of direct insolation during summer days (h), **(b)** NDSI (0.1–0.9: earliest–latest melting of snow cover), **(c)** June–August land surface temperature: LST (°C), and **(d)** September–May LST (°C) on the different slopes (NW: northwestern, NE: northeastern, E: eastern, SE: first southeastern, S: southern, SE2: second southeastern) on the Kholodny Belok Ridge. Black line demonstrates the position of upper boundary of open forests in 2020.

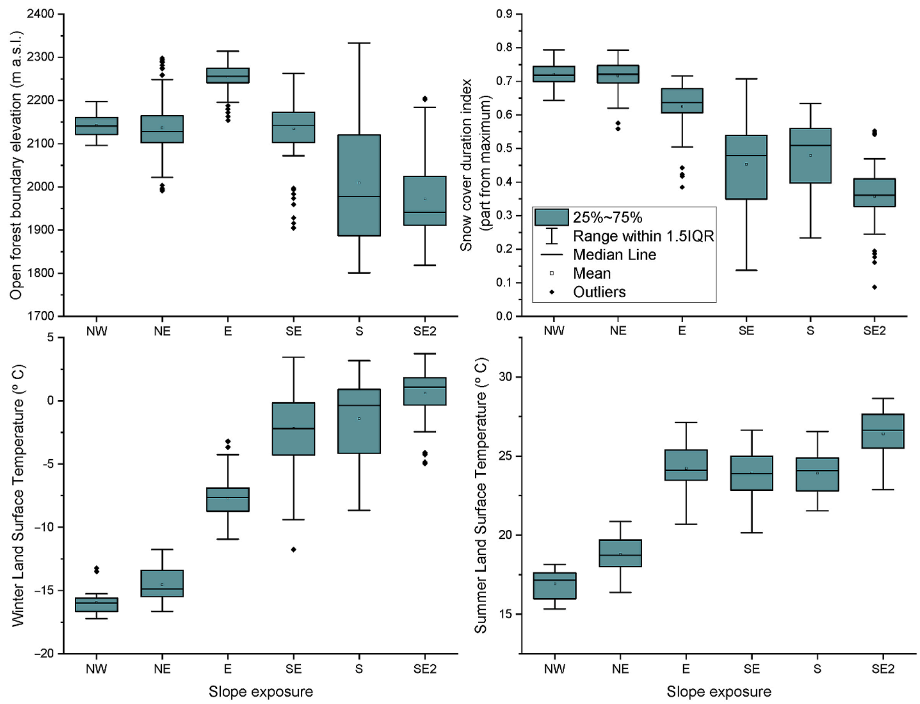

Fig. 9. Elevation of upper open forest boundary, snow cover duration index, and land surface temperature at this boundary on different exposure slopes (NW: northwestern, NE: northeastern, E: eastern, SE: first southeastern, S: southern, SE2: second southeastern) on the Kholodny Belok Ridge, where 1: 25%–75%, 2: range within 1.5 × the interquartile range (1.5IQR), 3: median line, 4: mean, 5: outliers.

surface temperature are in middle position between those observed values on northern and southern slopes (Fig. 9).

4. Discussion

4.1. Slope exposure effects on treeline ecotone structure and dynamics

Our results showed that at the Kholodny Belok Ridge (central part of Altai Mountains), the structure and dynamics of forest stands within the treeline ecotone were greatly distinguished on the slopes with different exposures. We also noted that the crown closure of larches is higher than that of stone pines on the eastern slope. The crown closure of larches on the northern and southern slopes is lower than that of stone pines.

It is well known that the wind regime (Holtmeier and Broll, 2010), the snowmelt onset and offset (Körner, 2012), the solar heating of tree trunks in spring and the subsequent cambium activation (Rossi et al., 2007), the thermal regime during the growing season (Måren et al., 2015) and dominant plant species composition (Dearborn and Danby, 2017) strongly vary with changes in slope exposure. In northern mountainous regions, increased solar radiation and warmer conditions on southern slopes favour the survival of seedlings and saplings, as well as tree growth in general (Vitasse et al., 2012). In mid-latitude forests in northwestern British Columbia, shaded, north-facing slopes had lower productivity than those on sunnier, warmer, south-facing slopes (Kuyek and Thomas, 2019). In southwestern Yukon (Canada), the range boundary of *Picea glauca* (Moench) Voss moved faster on south-facing slopes than on north-facing slopes (Danby and Hik, 2007). Comparison of the elevation of the open forest boundary on different slopes of the 30 mountains of the Altai-Sayan region (Moiseev and Nizametdinov, 2023) showed that, at latitudes lower 50°10′ N, the elevation of the upper open forest boundary was lower on the southern slopes than on the northern ones, with a ratio range from 0.79 to 0.95. A similar situation is observed in the mid-altitude mountains of the Southern Urals (Gaisin et al., 2020), which are also characterized by an extremely uneven distribution of forest areas—the slopes of the southern exposures are either treeless, or the treeline on them is located significantly lower than on northern slopes. Likewise, in Mongolia, where woody vegetation only occurs on the northern slopes of the mountains (Klinge et al., 2018). Zheng et al. (2021) quantified the subalpine population dynamics of Balfour spruce (*Picea likiangensis* var. *rubescens*) on the contrasting northern and eastern slopes of the eastern part of Tibetan Plateau. They found that the position of Balfour spruce forests has not advanced in recent decades. However, greater recruitment occurred above the current forest limit on the north-facing slope compared to the east-facing slope, indicating more favorable conditions for tree regeneration.

We suppose that main reason for such contrasts in dominant tree species composition, treeline elevation and tree establishment patterns between north- and south-facing slopes in our study area is a couple of great differences in received solar radiation and, therefore, the heating rate of the slopes. The low level of solar radiation on the northern slopes causes a lower land surface temperature (Figs. 8 and 9, Table S4) and consequently less evapotranspiration and wetter soils than on the southern slopes, which makes them more conducive to tree growth and regeneration (Hais et al., 2016). In addition, possible limitations for tree colonisation of southern slopes are related to the negative influence of the highly developed meadow herbs on them, which form sod, absorb a large amount of soil moisture with their root systems, and constrain subsequent tree sapling establishment. In a recent literature analysis of tree seedling establishment drivers (Lett and Dorrepaal, 2018), authors noted that in many publications "graminoids and herbs were consistently associated with negative effects on seedling occurrence, possibly because of their usually high density at the ground surface". A field experiment in the French Alps (Loranger et al., 2017) showed that herbaceous alpine vegetation can negatively impact first-year survival, growth, and carbohydrate accumulation of planted seedlings of *Larix decidua* Mill. and *Pinus cembra* L. Based on these findings, we hypothesize that the presence of dense subalpine meadow vegetation can significantly limit the subsequent establishment of Siberian larch and Siberian stone pine on moisture-deficient sites of the southern slopes in the central part of the Altai Mountains, but this assumption requires future validation through measurements of sod density, fine root biomass, ground cover composition and dense, and soil moisture.

Finally, we can conclude that, while in the mountains of Eurasian Subarctic (Putorana Plateau, Polar Urals, and Kola Peninsula), the treeline reaches the highest elevation, and the greatest tree establishment are observed on the warm slopes of southern exposures (Grigoriev et al., 2022; Moiseev et al., 2022; Nizametdinov et al., 2022), in the studied part of Altai Mountains, a completely opposite pattern is revealed.

In this study, the differences in the age structure of tree stands at different elevations are consistent with results of other studies in the Altai Mountains (Volkov et al., 2021). Thus, age structure analysis identified a shift of stone pine and larch stands along the elevation gradient in the valley of the Aktru glacier, with stone pine regeneration being greater compared to larch (Timoshok et al., 2016). Gatti et al. (2019) found in the same area that only young trees grow at high elevations, and recorded a relatively rapid upward shift of the upper treeline by 150 m of altitude in the last 52 years, which rate has been accelerating to the present day. A recent study by Savchuk et al. (2023) showed that in the Central Altai, in the Akkem glacial basin, the density of tree stands at the upper limit of their growth increased from 1920 to 1970, and the amount of young trees were enlarged from 1980 to 2000. It was shown that the first trees at the upper limit of the forest appeared only 120 years ago on the eastern slope, and 110 years earlier (230 years) on the western slope.

We assume that the changes in tree establishment rate on the upper boundary of open forests and sparse tree stands (levels #1 and #2) on slopes with different exposures observed in recent centuries are caused by a general improvement of the growing conditions in the study area. This is most evident in changes in an air temperature and precipitation. Over the last 80 years, both winter and summer temperatures have increased at all elevations. However, precipitation did not change in summer and had opposite trends in the valleys and at high altitudes in winter. Thus, there was a decrease in precipitation at 980 m a.s.l. and an increase at 2,600 m a.s.l. We inferred that the climate at the studied slopes (1,950–2,100 m a.s.l.) has become sufficiently warmer in all seasons and slightly wetter only during winters. Our analysis aligns with the results of other publications on the Altai region (Bezuglova et al., 2012; Malygina et al., 2017).

The analyzed relationship between tree amounts in 5-year age groups and climatic parameters revealed a positive effect of summer and winter temperatures and winter precipitation on the recruitment rate of stone pine at upper elevation levels (#1 and #2) on the eastern slope, while on the northern and northeastern slopes, these correlations were insignificant. Throughout the world, upward shifts of the upper treeline have occurred more often in areas where an increase in precipitation has been observed in winter (Harsch et al., 2009). This is especially important for the survival of saplings at the upper elevation level, where there is usually a minimal depth of snowpack, which performs a protective function against ice crystal abrasion, wind desiccation, and low air and soil temperatures, and sharp fluctuations. Similar relationships were obtained for shrub vegetation in the Ural Mountains (Grigoriev et al., 2021). Rochefort and Peterson (1996) found that in the western Cascades (North America), a warm, dry summer climate favours tree establishment on west-facing slopes, where snow cover is generally very high. However, a cool, wet summer climate facilitates tree establishment on east-facing slopes, where snow cover is lower (Rochefort and Peterson, 1996). They noted that the intensity of tree establishment is significantly greater in heath-shrub (ericaceous) vegetation than in meadows. Establishment on north-facing slopes of central Cascades (North America), concentrated in heath-shrub communities, coincided with regional warming (1920–1945), when snowpacks were lighter and melted earlier (Miller and Halpern, 1998), but recruitment of trees onto south-facing slopes occurred later, when conditions were wetter (1945–1985).

Obtained data demonstrate that a deviation (decrease or increase) of NDSI and land surface temperature during the cold period on the northern and southern slopes, compared to the eastern slope, coincides with a decrease in the elevation of the upper boundary of open forest on these slopes (Fig. 8). Therefore, we inferred that both the early snowmelt (low value of NDSI) and high winter temperatures (high value of land surface temperature) on the south-facing slope, as well as the late snowmelt and low winter temperatures on the north-facing slope, do not favour the tree establishment and rapid colonisation of mountain meadows and tundra, against the general background of improving climatic conditions. Evidence from western North America (Andrus et al., 2018) points to the importance of snowpack depth and summer moisture availability for tree establishment on water-limited subalpine sites. Snowpack water content and temperatures in May-June regulate the timing and rate of soil moisture loss (Harpold et al., 2015), and a deeper snowpack provides a greater water contribution to soil moisture, typically resulting in a later melt date, which can reduce the length of summer drought and seedling moisture stress (Brodersen et al., 2006).

4.2. Soils on slopes of varying exposure as indicators of differential soil formation conditions

The morphology of soil profiles and their classification into different Reference Soil Groups (IUSS, 2022) reflect significant divergence in pedogenic factors across different slope exposures of Kholodniy Belok Ridge. Based on the data obtained for soil chemical parameters, we concluded that no consistent differences in soil acidity, exchangeable cations, and degree of saturation were observed along the elevation transects, while soils on slopes with different exposures differed markedly, resulting in distinct soil conditions for vegetation.

The revealed dependence of soil acidity on slope exposure agrees with the data for soils of different mountain regions. Thus, the higher acidity (lower pH values) in soils on northern slopes compared to southern slopes was observed in the Italian Alps (Kovalev et al., 1973; Carletti et al., 2009; for pH only), Himalaya, India (Hamid et al., 2021), Himalaya, central Nepal (Begum et al., 2010), and Greater Khingan Mountains, and northeastern China (Chu et al., 2016). The mechanism of more active podzol formation on northern slopes has been discussed in detail for subalpine forests in the Alps (Chersich et al., 2015; Egli et al., 2006, 2009) and is mainly related to the type of water regime. As a result of lower evapotranspiration (due to lower solar irradiation) and generally longer-lasting and slower-melting snow cover, soil moisture content is increased on northern slopes, and the nature of the water fluxes (slow, steady, cold water) is conducive to weathering, mineral dissolution, and the transport of degradation products into illuvial horizons. The cooler and more acidic conditions also led to more pronounced weathering processes and increased clay mineral formation on the north-facing slopes (Egli et al., 2006, 2009), which improves the water-holding capacity of the soils themselves. Similar patterns have been found not only in humid but also in semi-arid regions (southwest Idaho), where soils on northern slopes tend to be deeper, contain more OM and silt, and retain more water (Geroy et al., 2011). We do not have data on soil moisture content collected directly on studied sites, but we found a higher snow cover duration index on the northern slopes (Fig. 8), indicating that the snow cover on these slopes lasts longer and melts more slowly, resulting in an excessive soil moisture regime in spring and early summer, which is reflected in the different soil formation patterns on the northern slope compared to the southern and eastern slopes. The podzolisation process, in turn, leads to the leaching of base cations and nutrients from the mineral horizons in the northern slope. The soils on the southern slope exhibit morphological characteristics similar to steppe-landscape soils (chernozem-like patterns), which correspond to drier conditions of soil formation.

SOM decomposition. The decomposition rate of plant residues is slow. While on the eastern slopes partially decomposed OM is distributed across a considerable depth (with the Oa horizon extending up to 20 cm), on the northern slope, in contrast, it is concentrated within the organic horizon at the soil surface. This profile distribution is linked to the composition of the ground cover vegetation: In herbaceous-dominated communities on the eastern slope, root input occurs throughout the soil profile, while in moss- and shrub-dwarf-dominated tundra and forests of the northern slope, surface litterfall prevails. Both soil morphology and C:N ratios indicate the slowest rate of OM decomposition on the northern slope. This is attributed to lower temperatures (Fig. 9), and hence, a shorter active season, as well as poorer residue quality. Higher temperatures on the eastern slope favour OM decomposition. However, the accumulation of incompletely decomposed plant residues suggests a shortened period of active soil biological activity. This likely results from delayed snowmelt in spring (the snow cover duration is almost the same as on the northern slope) and summer dry periods. Reduced summer moisture availability can be attributed to elevated temperatures (similar to those on the southern slope) and high stoniness, which enhances drainage and reduces soil water-holding capacity.

On the southern slope, decomposition conditions are the most favorable, despite lower moisture content. The presence of thick, well-structured grey humus horizons (with granular and subangular blocky structure) and higher C and N content implies more intensive mineralisation and humification, with stronger binding of OM with mineral components compared to other slopes. Decomposition and humification conditions appear to be optimal on the southern slope.

The patterns of soil formation and OM decomposition clearly reflect differences in soil temperature and moisture across slopes of varying aspects. In the absence of direct measurements of these parameters, soil morphological characteristics can serve as indicators of tree growth conditions.

4.3. Soil nutrients and their link with tree stand dynamics

The degree of plant residue decomposition discussed above is closely linked to cycling of nutrient elements and their availability. Soils on the eastern slope contain high levels of total N and available P in horizons with partially decomposed OM (which extend to considerable depths). On the other hand, poorly decomposed OM in the soil profile enables to retain increased amounts of carbon, N, P, Ca, and Mg in a bound state. These nutrients are gradually released during decomposition, becoming available for plant uptake. The elevated C and N content at depths exceeding 5 cm in soils of the level #2 and #3 reflects their more developed and deeper profiles compared to those of level #1 under conditions of similar OM quality (C:N ratio).

On the northern slope, nutrient availability is likely even lower due to three reasons: (1) most elements are concentrated in the weakly decomposed forest litter (Oi + Oe horizon, thicker compared to the eastern slope) in a bound state, where the C:N ratio is maximal; (2) the low rate of OM degradation leads to a slow release of nutrients from forest litter; (3) below the forest litter, element concentrations decline sharply, and their content in mineral horizons is extremely low. Active uptake of nutrients in such soils occurs immediately at the place of their release from decomposing plant residues—in organic and upper mineral horizons. The rapid uptake of elements from litter and leaching from the mineral profile under a leaching water regime (consistent with the soil formation type, podsolisation) results in significantly lower concentrations of carbon, N, Ca, Mg, and P in the lower horizons compared to other slopes. Additionally, acidic conditions (pH 3.67–4.86; Table S2) reduce the availability of phosphate due to the formation of insoluble compounds with iron and aluminum ions.

According to available literature data, the influence of slope exposure on carbon content is uncertain and does not depend on regional climate. Some studies reported higher C contents in high altitude soils of northern slopes, for example, in Italian Alps (Carletti et al., 2009; Egli et al., 2009; Miller et al., 2004), others found no differences in Italian Alps (Egli et al., 2006), northeastern Turkey (Sariyildiz et al., 2005), northeastern China (Chu et al., 2016), and Himalayan semiarid valley (Måren et al., 2015). In other studies, the total C content was significantly higher at north-facing than at south-facing sites under forests; however, no exposure effects were found at higher altitudes under grasslands and shrubs, leading to a significant interaction between exposure and altitude (Bardelli et al., 2017). The contradictory data demonstrate the diversity of conditions and the complex interaction of various natural factors affecting soil processes and the dynamics of SOM in mountainous regions.

Our study revealed no changes in chemical parameters along the elevation gradient in the upper horizons on the eastern slope and elevated C and N concentrations in deeper horizons of forest soil compared to meadow soil. Along the northern slope, we observed increasing N content and decreasing C:N ratios with elevation (for depths up to 20 cm). These parameters contradict the widespread view that OM decomposition is more active in forest soils than in tundra soils (Kammer et al., 2009; Parker et al., 2015; Sjögersten et al., 2003; Sjögersten and Wookey, 2002, 2009), as net N mineralisation rates are also higher in forested areas compared to treeline sites (Kammer et al., 2009; Loomis et al., 2006). Generally, the faster mineralisation of OM in forests is driven by higher-quality OM input (indicated by lower C:N ratios in organic horizons under forest—a feature absent on the northern slope), combined with more favorable temperature conditions. At the same time, a review of existing literature reveals that some studies have reported increased decomposition rates and net N mineralisation with altitude (Sundqvist et al., 2013). Although direct measurements of decomposition rates are lacking in our study, we hypothesize that on the northern slope, the relatively lower N content and higher C:N ratio in forest soils compared to tundra soils result from active N uptake during plant residue decomposition coupled with leaching from mineral horizons in Podzols. More N might be bound in long-lived woody species and thus decrease long-term N turnover (Dawes et al., 2017). This process could explain the observed negative correlation between stand age and total soil N, as well as the positive correlation with the C:N ratio (Table S5). N transfer and immobilisation into biomass appear more intensive on the northern slope, likely due to its significantly greater stand age relative to the eastern slope. Consequently, the higher C:N ratios observed on the northern slope in forest soils probably indicate substantial N depletion in the soil pool, rather than reflecting the degree of decomposition.

The close correlations between stand dynamics and climatic parameters on the Kholodny Belok Ridge confirm the predominant influence of air temperatures. However, soil factors cannot be ignored even for less demanding species like larch and stone pine. For example, conditions on the eastern slope are the most optimal, not only in terms of temperature but also in nutrient content, both of which favour tree growth and relatively rapid upward expansion. In contrast, unfavorable soil parameters of the northern slope (high acidity, low content of bases, carbon, N, and P) combined with lower temperatures may contribute to the slow rate of stand formation. The significant positive correlations of DBH, crown diameter, and stem height with available P content and with N (though non-significant) support our assumption. However, definitive conclusions regarding the influence of soil nutrient content on stand formation rates need additional data.

On the southern slope, N and especially P concentrations are higher than on other slopes, suggesting that nutrient availability in the soil plays a minor role compared to soil moisture content.

Overall, on the Kholodny Belok Ridge, nutrient content interacts with other factors. Its influence can align with climatic conditions to further enhance the differential advance of woody species on slopes of varying exposure (as observed on northern and eastern slopes) or, conversely, can disagree with them (as on the southern slope) and have no predominant effect on the expansion of woody vegetation.

4.4. Coupling of vegetation and soil belts in treeline dynamics

It is generally accepted that soils respond more slowly to external drivers (e.g., climate change) compared to vegetation (Holtmeier and Broll, 2018). Our data demonstrated that soil type changes follow forest boundary shifts. On the northern slope, some morphological features of forest soils, such as podzolisation processes, begin to be recognized under the open forest (level #2: 2,230 m a.s.l.), and clear podzol profiles were already formed under the closed forest (level #3: 2,200 m a.s.l.) (Table 2). Considering that active stone pine growth on levels #2 and #3 began in the early 20th century (Section 3.1, Table 1), while larch establishment occurred much earlier, our findings suggest that approximately 100 years of forest community development are sufficient for the appearance of discernible initial podzolisation signs. A distinct podzol horizon forms within 270 years. However, this process may require more time, given that larches growing appeared much earlier (in the 15th century, though without pronounced peaks).

On the eastern slope, under open forests (level#2: 2,090 m a.s.l.), and often under closed forests (level#3: 2,060 m a.s.l.), the structure of the soil profiles does not differ from those under sparse tree stands (level#1: 2,120 m a.s.l.). Well-developed forest soils, such as Cambisols, can be found at much lower elevations (level#4: 2,030 m a.s.l., and only sometimes at level#3: 2,060 m a.s.l.). Tree establishment here occurred significantly later compared to the northern slope. The most frequent pine colonisation of level #3 was observed between 1950 and 1990. At level #2, after 1970, larch did not grow until the early 19th century. The average age difference of pine between levels #1 and #2 is only 10 and 30 years between levels #1 and #3, with larch showing similar age distributions. Clearly, the observed 50–70 year timeframe (and the 10–20 year differences in average age between levels) is insufficient for pronounced pedogenic changes. During this period, neither the degradation of the humic horizon (Oa) nor the formation of new A and B horizons in its place occurred. Additionally, there were no changes in the studied chemical parameters (in the content of N, carbon, and other elements).

The slight change in soil properties along the eastern slope's elevation gradient, contrasting with distinct pedogenic transitions on the northern slope, likely reflects differences in stand history and canopy closure. The older age of the stands on the northern slope means a longer period of soil formation under the canopy of tree species, facilitating more advanced pedogenesis. We observe that the boundaries of the vegetation and soil belts do not coincide, indicating that these high-mountain ecosystems are still developing and that a stationary state between vegetation and soil has not yet been reached. As noted previously, expected climate changes are likely to induce marked vegetation disequilibrium with climate due to lags in local population build-up and succession, in local evolutionary responses, and in ecosystem development (Svenning and Sandel, 2013). It can be specified that ecosystem development trajectories are coupled with pedogenesis, where soil formation rates mediate vegetation response dynamics to climatic changes.

5. Conclusions

Our results showed that since the beginning of the 20th century, there has been an intensive expansion of *Pinus sibirica* and *Larix sibirica* stands into the mountain tundra and meadows of the central part of the Altai Mountains. This process was most active in the last 60 years when annual air temperature and precipitation in the cold season increased. Depending on the slope aspect, we found significant differences in the composition of the dominant tree species, the morphometry, and the formation history of modern forest stands. Soils display considerable inter-slope variation in OM decomposition rates and the content of carbon, N, available P, exchangeable bases, and acidity. Our findings reveal that soil formation patterns and OM transformation dynamics directly reflect slope-specific temperature and hydrologic regimes. Nutrient content interacts with other factors and acts synergistically with climatic parameters, enhancing the differences in advance of woody species across slopes of different exposures.

The correspondence of boundaries in woody vegetation and soil cover depends on the history of tree stand formation and type of soil formation. On the eastern slope, where the advance of woody vegetation occurred over a shorter period, the soils showed only minor changes in both their morphological and chemical properties. As a result, we observe that the vegetation and soil belts have shifted at different rates, indicating that these high-mountain ecosystems are still in dynamic development. At present, a stationary state has not been achieved between woody vegetation and soil, which is a consequence of the slower response of soil properties and processes to climate change.

The results of this study underscore the significance of incorporating slope exposure characteristics, as well as the morphological and chemical parameters of soils, when developing models and predicting the transformation of high-mountain forest ecosystems under different future climate change scenarios.

CRediT authorship contribution statement

Andrey Grigoriev: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Irina Korkina:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Sergey Vyukhin:** Formal analysis, Data curation. **Yulia Shalaumova:** Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Nail Nizametdinov:** Writing – original draft, Visualization, Formal analysis, Data curation. **Dmitry Balakin:** Formal analysis, Data curation. **Dmitry Golikov:** Formal analysis, Data curation. **Pavel Moiseev:** Supervision, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

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Data availability

Data are available upon reasonable request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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