



ORIGINAL ARTICLE

Upward Expansion of Trees and Shrubs Leads to Alpine Tundra Contraction and Local Extinction of Species in the Southern Urals

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ABSTRACT

Alpine tundra at the top of high mountains and the treeline ecotone are both highly sensitive to modern climate change. In the Southern Urals alpine tundra occupies relatively small areas as the mountain ranges are quite low, while the treeline there is relatively high. The summit Dalniy Taganay, due to its marginal position in the mountain range and the direct onsite long-term monitoring, gives unique data on the intensity of upward expansion of woody vegetation for the last century and its consequences on the ecosystem level. By comparing old topographic maps and satellite images, repeated landscape photographs, and ana-

lyzing the age structure of forest stands it was determined that since the 1960s the upward expansion of open and closed forests had resulted in 72% decrease of unforested areas including alpine tundra. The intrusion of junipers to alpine tundra communities has been detected as well. Since 1990 the changes in various types of alpine tundra have been revealed by repeated observations. Since 2008 at the summit of Dalniy Taganay the ground-dwelling invertebrates have shown a significant decrease in the abundance of certain species and the endemic ground beetle *Carabus karpinskii* Kryzhanovskij & Matveev has not been recorded since 2022. Only the number of red ants in alpine tundra has shown a fourfold increase and typical forest beetles appeared. We could trace in detail not only the movement of forest higher into the mountains but also the changes in alpine and treeline ecotone's vegetation and animal communities with local extinction of specific species. The presented results can be used to adjust the models of climate-driven transformation for other similar mountains, where the area of alpine meadows or tundra is critically small.

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Key words: alpine tundra; treeline ecotone; ecosystem dynamics; climate change; vascular plants; invertebrate animals.

HIGHLIGHTS

- Upward forest expansion alters abundance of alpine plant and invertebrate species
- 72% area decrease since 1960 significantly transformed alpine ecosystems
- Assessment of the upper limit of open forests shift have been significantly improved

INTRODUCTION

Mountain regions housing high biodiversity and many endemic species are among the most vulnerable ecosystems (Myers and others 2000; Schmeller and others 2018). There is a consensus that alpine habitats are the most sensitive areas to modern climate change and a number of studies predict and document changes in the distribution of plants and animals with high extinction risks (Sala and others 2000; Thomas and others 2004; Thuiller and others 2005; Araujo and others 2006; Settele and others 2008; Brunetti and others 2019). Mountainous species are often represented by small and isolated populations undergoing alarming declines in their ranges due to modern climate warming (Dirnböck and others 2011; Jacobsen and others 2012; Rossaro and others 2016). As shown for Central Europe, most endemic species are concentrated in habitats above the treeline (Hewitt 2000; Essl and others 2009), and climate-induced upward migration of woody plants reduces the area of their habitats (Theurillat and Guisan 2001; Sekercioglu and others 2008).

Monitoring the treeline dynamics in mountain regions is one of the most common and effective method to study the effects of climate change on vegetation (Gorchakovskij and Shiyatov 1985; Körner 2021). Numerous studies have provided convincing evidence of forest vegetation expanding rapidly into alpine ecosystems in recent decades and as a result the extinctions of high mountain species populations at their lower altitudinal range limit (Harsch and others 2009; Dirnböck and others 2011; Hansson and others 2021). The treelines advance in response to climate warming is a dynamic process that can be faster or slower depending on many factors (Körner 2021).

According to the calculations of Körner and Hiltbrunner (2021), climate warming of 1.1 or 2.2 °C will result in the treeline position 200–400 m higher in elevation.

Alpine tundra ecosystems are unique dry and cold habitats above the treeline, home to many relict and endemic plant and animal species. In the Urals the alpine tundra extends from north to south for about 2000 km from the Polar to the Southern Urals (Gorchakovskij 1975) and the upward movement of the treeline occurs in all natural provinces, where a climatic limit to the growth of forest vegetation exists (Gorchakovskij and Shiyatov 1985; Hagedorn and others 2014). As a result of the gradual upward shift of the treeline toward the south, the upper limit of the forests in the mountains of the Southern Urals is the highest—an average of 1300 m a.s.l. Therefore, the areas of alpine tundra communities in this natural province are extremely small. According to preliminary estimate, at all 14 mountain ranges (about 50 peaks) taken into account alpine tundra currently occupies up to 10 km² in total. Besides the fact of relatively small areas these communities are also fragmented and geographically isolated, both from each other and from other mountain regions. The nearest alpine tundra of the Northern Urals is about 400 km away. For several mountain summits of the Southern Urals it is now clear that alpine tundra has been completely replaced by forests due to the ongoing transformation of the natural environment (Shiyatov and others 2020). Yurma Mountain (1003 m a.s.l.) that can be easily seen from Dalniy Taganay summit is a vivid example. Yurma is a northern terminus of the Southern Urals facing the lower Middle Urals that has climatic treeline, but its upper part is completely covered by spruce and fir forest with only some fragments of alpine vegetation around rocky outcrops (Shabanov and others 2023).

Current modeling suggests that if forest vegetation continues to colonize treeless mountain areas at the same rate, there is a risk of extinction of alpine tundra on many relatively low peaks, especially in the Southern Urals. These processes may lead to decrease in the biodiversity of high mountain vegetation (Pauli and others 2012), in particular of alpine tundra and meadow communities, and their degradation. Furthermore, long-term monitoring studies of the vegetation dynamics in the highlands of the Urals are scarce. Prior to our study the main geobotanical and floristic works have focused mainly on the current composition and structure of mountain vegetation

(Andreyashkina 1990; Nikonova and Pustovalova 2012; Degteva and others 2014).

Some authors argue that rapid changes are normal for the conditions of high elevations (Körner and Hiltbrunner 2021). However, climate warming is considered to be the main threat to high mountain species with naturally restricted habitats as an advance of the upper forest limit and fragmentation of treeless peaks critically shrink the already limited suitable area. As estimated for the Austrian Alps (Dirnböck and others 2011) the endemic species of five taxonomic groups (vascular plants, snails, spiders, butterflies, and beetles) would experience an average loss of 77% of suitable habitat even under the weakest climate change scenario (+ 1.8 °C by 2100). The rate of expected climate change is likely to exceed the migratory capacity of many endemic species (Pearson 2006) that often have poor dispersal capabilities due to their inability to fly (Dirnböck and others 2011). However, due to the spatial heterogeneity of forest limit advance (Körner 2021), the major questions remain, when and where endemics may become locally extinct. Currently, as far as we know, there is no relevant information on time lags between climate change and species range changes and it is possible that decades might elapse to detect the difference (Thuiller and others 2005).

For many temperate mountains it has been shown that the greatest diversity of endemic species is detected on peripheral or isolated low ranges not much higher than the treeline (Tribusch 2004). Furthermore, smaller mountains with a narrow alpine belt are at a greater risk of species loss (Körner and Hiltbrunner 2021). And Dalniy Taganay is good example. It is a unique natural object of the Ural Mountains: (1) the northernmost lowest peak of the Southern Urals with preserved alpine communities including some relict and endemic species of plants and invertebrate animals; (2) peripheral location, only from the south in close proximity to other peaks with areas of alpine tundra; (3) the summit never subjected to grazing; (4) long-term observations at permanent sampling plots for alpine plant communities (> 30 years) and invertebrates (15 years); (5) the weather station operating on the summit since 1932 in the closest vicinity of the studied objects.

In the last 70–50 years, tree and shrub vegetation has been intensely expanded higher into the mountains, leading to a significant reduction of alpine tundra areas (Shiyatov and others 2020). Based on the extensive accumulated in situ data for a single mountain summit without interpolating models, as well as on a variety of dendrochronolo-

gical, geobotanical, entomological, and statistical methods, this study attempts to assess the dynamics of different ecosystem components, including trees, shrubs, alpine plant species, and invertebrates, taking into account abiotic factors.

Our objectives are: (1) to quantify the shift in the upper limit of open forests based on the comparison of historical topographic maps and satellite images; (2) to assess changes in forested areas using multi-temporal landscape photographs; (3) to reconstruct the formation of tree stands and shrubs in the transition zone from forest to alpine tundra; (4) to make a quantitative assessment of changes in the alpine tundra plant communities; (5) to assess changes in the communities of ground-dwelling invertebrates based on long-term observations; (6) to correlate these changes to climate data from weather stations located near the study sites.

MATERIALS AND METHODS

Study Area

Dalniy Taganay Mountain is a flat peak 1112 m a.s.l. (N55° 22' 10", E59° 54' 27"), a summit of the Bolshoy Taganay ridge. It is located in the northern terminus of the Southern Urals (Figure 1). Parent materials are crystalline rocks (taganaites) associated with mica and mica-garnet schist. The average January temperature on the mountain top is minus 15 °C. The total annual precipitation exceeds 800 mm. The average wind speed is from 9.6 to 13 m s⁻¹; in winter, it can rise to 40 m s⁻¹ (Moiseev and others 2016). The ground freezing temperature in open areas (alpine tundra) falls to – 20.4 °C in January and raises up to 15.6 °C in August. The snow depth in open areas is from 0 to 20 cm, in the closed forests it is up to 2 m, after snow storms it can reach 4–5 m. Alpine tundra and meadow communities develop at the top, where fine-grained soil accumulates. *Juniperus sibirica* Burgsd. grow in open areas above the upper forest limit. The dominant tree species of the treeline is *Picea obovata* Ledeb. associated with *Betula pubescens* ssp. *tortuosa* Ledeb.

Mountain regions such as the Alps and the Caucasus have been subjected to grazing for centuries. On the contrary, many summits of the Southern Urals remain undisturbed or with low human land use (Gazol and others 2017). The wild grazers such as reindeer or red deer are absent there as well. Particularly Dalniy Taganay Mountain is unsuitable for grazing. First of all, the summit has no thick grass attractive for grazing but mainly scattered alpine tundra vegetation with li-

chens, the nearest village is situated in the distance about 15 km and isolated by turbulent rivers and lack of roads. Since the building of weather station any other land use around was restricted and since 1991, when national park was established, any economic activity was stopped except only ecological tourism. Since then only hiking tourists visit the summit, but their impact on vegetation is limited by the main road to the station and paths to the rocky outcrops around.

Estimation of Elevation Changes in Upper Limit of Open Forests Using Historical Topographic Maps and Modern Satellite Images

A comparative analysis of topographic map from 1960 and satellite images of 2023 was carried out to quantify shifts in the position of the upper open forest limit (OFL) with percentage tree cover of 0.2–0.3. The position of the historical OFL was specified on the basis of landscape photographs of the 1960s–1970s. In the geographic information system ArcGIS 10.8 (ESRI Inc., USA), these data were combined with a digital elevation model with a resolution 10 m pix^{-1} created from a topographic map and the results of the lidar survey using the L-Scan system (Geomatics, Russia). The area of OFL shift was subdivided into zones with the slight and strong influence of edaphic constrains (rocky surfaces). The altitudinal position of the OFL (min, max, median) was estimated on the basis of the values obtained from the digital elevation model cells. The difference between the median values of historical and modern OFL was calculated sepa-

rately on slopes with and without wide spread of rocky surfaces. The weighted mean by area was then calculated for both zones. To analyze the horizontal shift of the OFL the Euclidean Distance Estimation was used with a starting position in the line corresponding the limit of open forests in the beginning of the study period and the resulting position in the line of the modern distribution of open forests. Thus, the median value of the shift was calculated. The 3D area of forest cover was assessed using a digital elevation model based on bilinear interpolation. The OFL shift area was divided into sections according to different gradations of exposure and slope steepness. Slope exposure was divided into gradations of 45° : north (N, $337.5\text{--}22.5^\circ$), north-east (NE, $22.5\text{--}67.5^\circ$), etc. Slope steepness was categorized from 0 to 30° in 5° increments.

Repeat Landscape Photography

For assessing changes in the upper limit of woody vegetation the repeat photographs were taken. In the high mountains the shooting point can be easily identified due to detailed images and visible landmarks (Shiyatov 2009). Clear weather and adherence to the time of year of the old and new photographs are the mandatory conditions for this work. In total, 14 repeat photographs were taken in 2022 by the first author (AAG) in the localities of the early photographs by K.N. Igoshina in 1956, by P.L. Gorchakovskiy in 1961, and by S.G. Shiyatov in 1971. All photographs are archived in the special fund of the Museum of Institute of Plant and Animal Ecology of Russian Academy of Sciences (<http://ipae.uran.ru/museum>).

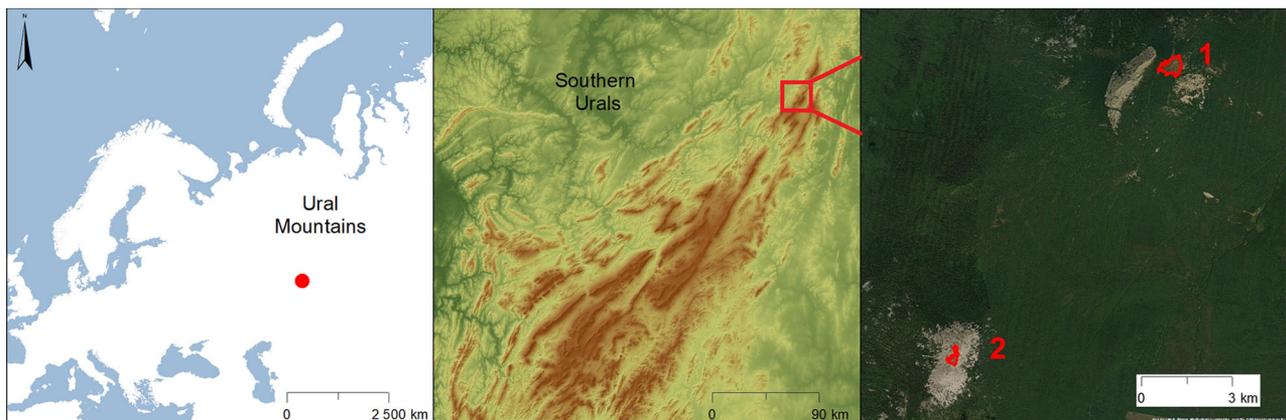


Figure 1. Study sites in the Southern Urals. **1**—Dalniy Taganay Mountain; **2**—Kruglitsa Mountain. Limits of alpine tundra domain are highlighted with red line. The satellite imagery sourced from ESRI, Maxar, Earthstar Geographics, and the GIS User Community.

Age and Morphological Structure of Forest Stands

In June 2022 two altitudinal transects were established in the treeline ecotone (the transitional zone between the upper limit of closed forests and individual trees within the alpine domain). The transect I was on southwest-facing slope; the transect II was on northwest facing slope (Figure 2). Each transect was subdivided into three altitudinal levels: the upper level—for the upper limit of occurrence of single trees, the middle level—for the upper limit of occurrence of sparse forests, and the lower level—for the upper limit of occurrence of open forests. Three to five permanent circular plots of 0.0201 ha were established at each altitudinal level. On each plot the exact location of each tree, diameter at the base and at 1.3 m height, crown diameter in two mutually perpendicular directions, age, and vital status were recorded. For each *Juniperus sibirica* the exact location, height, crown diameter in two mutually perpendicular directions, and age were recorded. The age of trees was identified by taking wood samples (cores) from its base or by taking a cross section if a diameter < 3 cm. Each sample was glued to a wooden base, cleaned with a sharp blade, and pigmented with toothpowder to make the annual rings more visible. Tree ring counting and core dating were carried out according to standard methods (Fritts 1976; Shiyatov and others 2000). All wood samples were measured using a semi-automatic Lintab 5 instrument. To identify false and dropped rings a generalized tree ring chronology was reconstructed using cores (40 pieces) specifically taken from old trees in the study area. Trees not higher than 1.5 m and not older than 30 years were classified as undergrown.



Figure 2. Location of altitudinal transects on the summit of Dalniy Taganay.

If the cores taken did not reach the center of the trunk, the missing rings were calculated using a transparent film with circle lines of different sizes to clarify the year of formation of the central ring. The age for undergrowth above 0.2 m and < 3–4 cm in diameter was determined from radial cuts taken at the root neck level. Based on the age of these trees and their trunk height the regression equation was calculated to make corrections in the calculated data and determine a more accurate age of each studied tree with the diameter > 3–4 cm. The age of *Juniperus sibirica* was determined using the previously tested methods (Grigoriev and others 2021) by taking a radial section of wood at the point where the largest branch joins the trunk. The resulting sections were polished with a specialized machine and further processed in laboratory using classical dendrochronological methods to identify the false and dropped annual rings as described above. The tree and shrub vegetation growing on both altitudinal transects has not been exposed to forest fires or other unfavorable factors at least during the last 200 years. We found neither traces of fires (dry areas) on the cross-cuts and radial cores, nor a significant number of dead trees when choosing the experimental plots. In total, the morphometric parameters of 1117 trees, including undergrowth and 199 junipers, were determined on an area of 0.96 ha.

Monitoring of Plant Communities in Alpine Tundra

In 1990 mapping of vegetation on the top of Dalniy Taganay was made by transect study using the picket survey method (scale 1:500). This method is based on dividing the study area into equal sections; the size of these sections is selected according to the complexity of vegetation and the scale of resulting map. The main line was located south from the rock (N55° 22' 09.4", E59° 54' 23"). Four stakes were placed to delimit the Sects. 50 × 50 m. Every section was divided into half using two 25 m ropes and an auxiliary peg. The vegetation map was drawn on graph paper with a cell corresponded to a square of 25 × 25 m. Plant communities were mapped within natural boundaries and classified according to standard methods (Arkhangelskij and others 1972; Mueller-Dombois 1984).

In the year 2022 a separate transect was created within the initial permanent transect to assess the changes since 1990. Within the new transect 34 sections with area 20 × 20 m were described. For every section a list of species was compiled for the tree, shrub, and herb-shrub layers, the height of

the layers was determined, and the projective species cover was noted. Species identification was confirmed in the herbarium of the Museum of the Institute of Plant and Animal Ecology of the Russian Academy of Sciences (SVER). The digital version of the map was created in the field using the graphic editor GIMP 2.10.22. The georeferencing of both maps and the orthophotomap were conducted via the geographic information system ArcGIS 10.8 using discernible landmarks including large stones and cliffs. In order to assess changes in the areas of alpine tundra communities, each community was identified as a separate polygon. For each polygon both as of 1990 and 2022 the area was calculated considering the digital elevation model. Based on these data the changes in area of plant communities for 30 years were quantified. Then the composition of dominant species in the communities registered in 1990 and 2022 were analyzed.

Dynamics of the Invertebrate Communities

The ground-dwelling invertebrates (insects, arachnids, centipedes) were collected using pitfall traps. The advantages of this method over other known ones for collecting invertebrates at high altitudes have been demonstrated in the alpine region of New Zealand (Bertoia and others 2023). The pitfall traps were installed according to the protocol from the official manual (section 7.2) of the GLORIA project (Mikhailov 2015). The summit was divided into four sectors, in each sector 20 standard 75-mm-diameter plastic cups were installed in a cross-shaped line, i.e., 10 traps placed along the main line (north, south, east, and west) at least 1 m apart, and another 10 traps were placed perpendicular to the first line. After three days, the traps were removed and their contents placed in specially marked containers. Preliminary sorting of adults and larvae was carried out in the field, and the analysis and identification of the collected material were conducted in laboratory conditions. In 2022 pitfall traps were also installed in the treeline ecotone. Two lines of 10 traps each were placed on permanent sampling plots in the upper, middle, and low levels on the southwest-facing slope.

In Dalniy Taganay the first results using this method were obtained in 2008, and the first resurvey was carried out in 2015. However before the survey period in July 2015 the weather was cool and rainy, unfavorable for invertebrate activity, so the collecting was repeated in 2016 during better weather. A second resurvey was carried out in 2022, but again unusually cold weather resulted

in poor sampling. To confirm the results, the survey was repeated in 2023 and another summit Kruglitsa (1144 m a.s.l.) of the Bolshoy Taganay ridge was surveyed simultaneously. The first data from this summit were obtained in 2016. Because according to the results of the Kolmogorov–Smirnov test the distribution in the studied groups in most cases differs from normal one, nonparametric tests were used in the analysis. The Friedman test was used for multiple comparisons of data from different years and the Wilcoxon test for pairwise comparisons.

Climate Data and Associations with Spruce and Juniper Recruitment

The climate assessment of the study area was carried out using data from the Taganay-Gora station (N55° 22', E59° 55', 1102 m a.s.l.). This weather station is located in close proximity to the test plots (from 50 to 300 m). We analyzed the dynamics of air temperature for 1837–2023 and total precipitation for 1876–2023. The missing values were reconstructed using data from the Zlatoust station (N55° 10', E59°40', 532 m a.s.l.), for which linear relationships were obtained for the parameters of

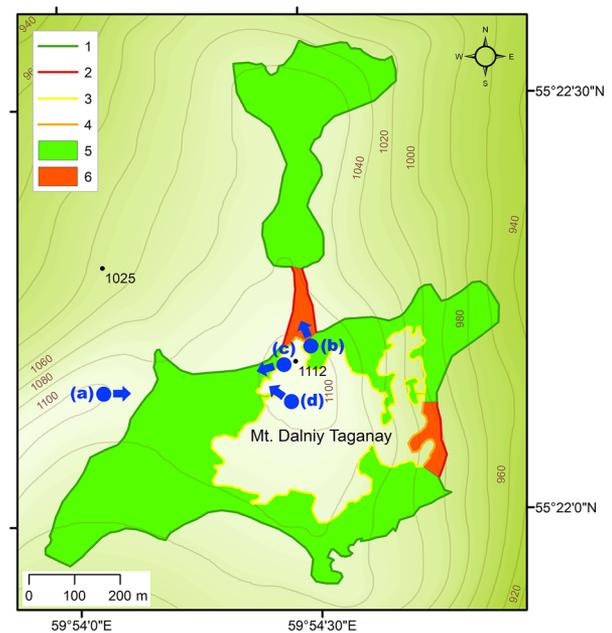


Figure 3. Position of the upper limit of open forests in 1960 (1 and 2) and 2023 (3 and 4) at the summit and area occupied by open and closed forests (5 and 6) over the 63-year period. 1, 3, 5—on slopes without wide spread of boulder fields; 2, 4, 6—on slopes with wide spread of boulder fields; **a–d**—indicate the points, from where the respective photographs in Figure 4 were taken, arrows point the direction.

Table 1. Changes of Open Forest Upper Limit on Dalniy Taganay for 1960–2023

Parameter		Type of upper limit	
		Slopes without wide spread of rocky areas	Slopes with a prevalence of rocky areas
Upward shift of the altitudinal position	Lowest position, m	59 (from 1020 to 1079)	13 (from 1015 to 1028)
	Highest position, m	3 (from 1102 to 1105)	0 (from 1102 to 1102)
	Average, m	20 (from 1057 to 1077)	14 (from 1053 to 1067)
Vertical shift	Average, m	20	15
	Rate, m per decade	3.2	2.3
	Average, m	44	10
Horizontal shift	Rate, m per decade	7.0	1.6
	Total area loss, ha	29.3	1.4
Reduction of unforested area	Rate, ha per decade	4.7	0.2

average monthly air temperature ($R^2 = 0.98$) and total monthly precipitation ($R^2 = 0.73$). We analyzed climate data from the warm (June–August) and cold (October–April) periods taken from the RosHydroMet database (<http://meteo.ru/data>) and Monthly Meteorological Tables. The warm period corresponds with the most active growth of tree and shrub vegetation in the study areas, when daytime temperatures exceed 5 °C. The cold period includes months with average air temperatures below 0 °C. Anomalies of climatic parameters in the warm and cold periods of each year were determined by the deviation of the current value from the average for the base period 1961–1990. Linear regression models were constructed to assess trends in climate anomalies. Snow depth measurements were taken during the period of maximum snow accumulation in the study area. In mid-March 2023 and 2024 snow depth was measured on each test plot using an avalanche probe with notches every 10 cm and every 1 cm in between on each test plot in two mutually perpendicular directions. At least 40 snow depth measurements were taken in each direction.

The relationships between the number of trees and shrubs establishing every 5-year period and the average values of climatic variables (average temperature and total precipitation) for the current and shifted 5-year intervals in the warm and cold periods of the year were analyzed. The shift by 5 years means that the weather time series has been shifted in relation to the time series of plant

recruitment (for example, + 5 or – 5 years). Thus, three options were studied: (1) current 5-year period matching the process of seed germination and first years of growth; (2) previous 5 years showing the conditions for the cone formation cycle of the maternal individuals; (3) next 5 years matching the most vulnerable stage for the seedling survival.

We assessed the relationships between climate and plant recruitment using the nonparametric Spearman correlation coefficient (R_s), since the distributions of data did not match with the normal distribution according to Shapiro–Wilk tests.

RESULTS

Estimation of Elevation Changes in Upper Limit of Open Forests Using Historical Topographic Maps and Modern Satellite Images

Analysis of the upper open forest limit (OFL) shift on Dalniy Taganay showed that the proportion of areas with widespread boulder fields restricting the spread of trees is 10 and 11% in 1960 and 2023, respectively (Figure 3). On the slopes with this type of edaphic conditions the altitudinal position of OFL (min, max, median) is lower (up to 51 m) than in the areas with less or no boulder fields (Table 1). Comparison of areas with low and high distribution of rocky areas showed an excess of the values of vertical and horizontal shift of OFL by 1.3 and 4

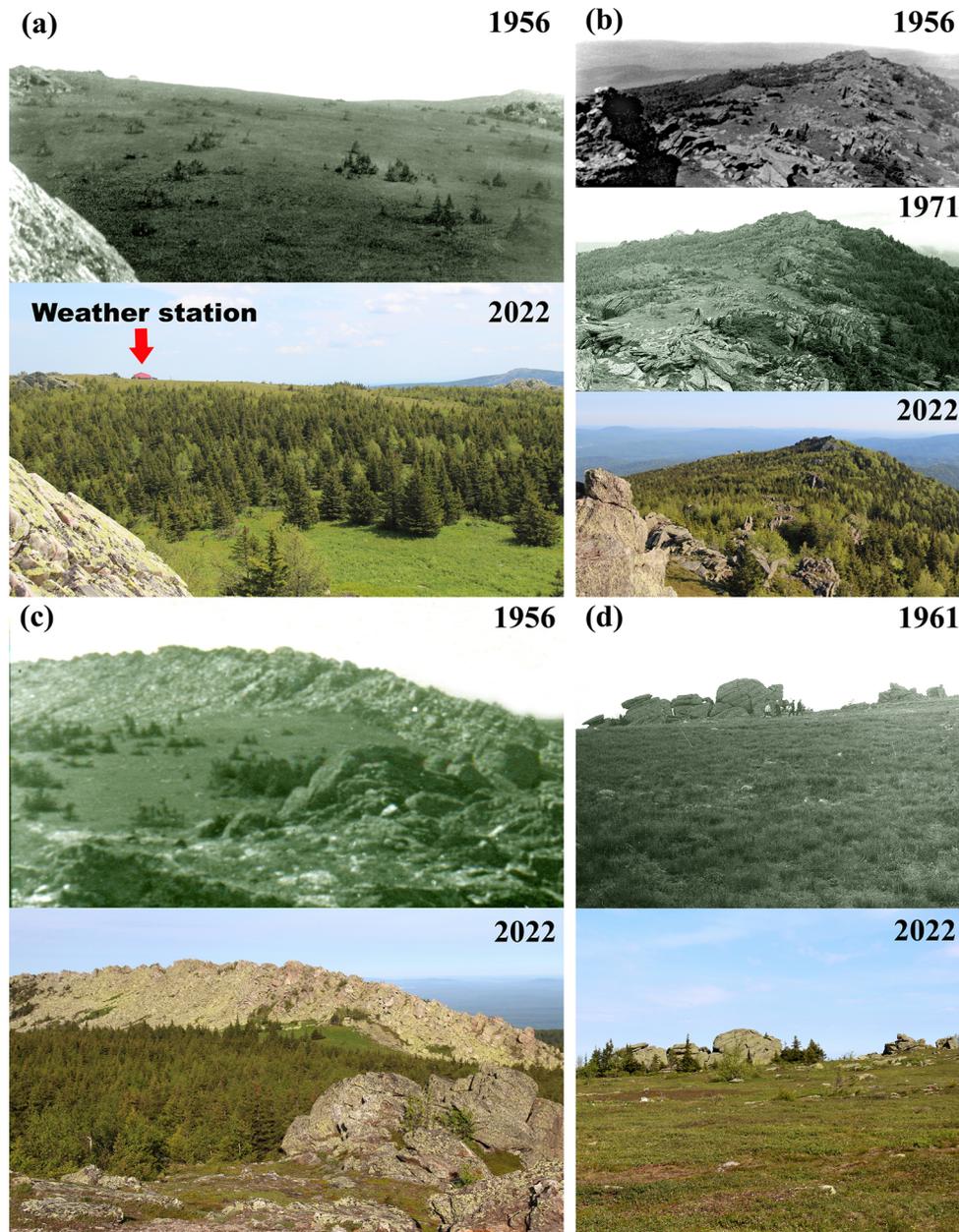


Figure 4. Repeated landscape photographs taken in the study area from the points and directions shown in Figure 3: **a–c** (1956) by K.N. Igoshina, **d** (1961) by P.L. Gorchakovskiy, **b** (1971) by S.G. Shiyatov, all from 2022 taken by A.A. Grigoriev.

times; the rates of the shift of OFL reached 3.2 and 7.0 m per decade for the areas without visible edaphic restrictions. The total area of the shift of OFL was 30.7 ha, with a reduction in the area of alpine tundra over the period under review from 42.4 (in 1960) to 11.7 ha (in 2023). Open forests moved mainly along the slopes of the eastern and the southern exposure (46%), with a steepness of 5–10° (35%) in the areas with the low distribution of boulder fields. Meanwhile, the shift of OFL in the areas with strong edaphic restrictions predom-

inated in the eastern and northeastern slopes (87%) with a greater steepness of 25–30° (43%).

Repeat Landscape Photography

The 14 repeat photographic pairs show intense expansion of forest vegetation, mainly Siberian spruce, into alpine tundra communities over the last 70–50 years. The most noticeable changes during this period have occurred on relatively flat, better-drained slopes with the presence of fine-

Table 2. Average Morphometric Indicators of Spruce Stands on the Transects

Transect and level	Exposition	Elevation, m a.s.l	Diameter at 1.3 m, cm		Trunk height, m		Age, year		Crown diameter, m		Projective crown cover, m ² ha ⁻¹	Density, ind. ha ⁻¹	
			Mean	Max	Mean	Max	Mean	Max	Mean	Max		< 1.5 m	≥ 1.5 m
1_1	SW	1090	2.8 ± 1.0	4.0	1.7 ± 0.2	2.3	15 ± 6	56	1.5 ± 1.0	4.7	264	1068	106
1_2		1080	6.2 ± 4.3	19.5	3.1 ± 1.2	6.0	22 ± 13	91	1.9 ± 0.9	5.7	2966	2805	896
1_3		1070	14.9 ± 6.4	28.0	6.6 ± 2.2	10.5	79 ± 22	115	2.9 ± 0.9	5.3	9325	15	1292
2_1	NW	1095	2.8 ± 2.4	8.6	1.9 ± 0.5	3.2	25 ± 12	55	1.4 ± 0.4	2.9	128	158	78
2_2		1090	8.6 ± 5.4	25.0	3.7 ± 1.6	7.0	40 ± 18	97	1.9 ± 0.9	5.5	5419	3700	1395
3_3		1085	14.6 ± 6.1	32.0	5.6 ± 1.5	8.6	68 ± 19	101	2.5 ± 1.1	5.5	8781	602	1541

grained soil (Figure 4a, c). Forest vegetation has not or only slightly progressed on very rocky and steep parts of the slopes and only few trees appeared closer to the summit, where the snow is blown away (Figure 4d). The resulting image (Figure 4b) shows that 50 years ago the axial part of the northern spur was partly treeless and the summit of Dalniy Taganay had larger areas of alpine tundra with only few trees of Siberian spruce growing in dwarf form.

Age and Morphological Structure of Forest Stands

With upward movement the conditions for growth become worse, so the average and maximum morphometric indicators of the trees naturally decrease (Table 2). Thus the decrease is 4–7 times for maximum trunk diameter at 1.3 m, 5 times for mean trunk diameter at 1.3 m, 3–4 times for mean height, 3–5 times for mean age, 2 times for mean crown diameter. The area of projective crown cover and the density of tree stands show the highest rate of decrease with altitude.

The colonization of the studied slope areas had different scenarios (Figure 5). At transect I, the first spruce trees appeared at lower altitudes at the beginning of the twentieth century and from 1915 to 1960 this process was quite active. Subsequently, due to the formation of closed stands, spruce regeneration practically ceased here. The first spruces in the form of single trees appeared in the middle zone between 1920 and 1985. The greatest increase occurred between 1985 and 2010, when 90% of the existing trees appeared. At the upper altitudinal level the oldest tree appeared in the 1960s, but the most massive population of trees occurred between 1995 and 2005. At transect II, at the low and middle altitudes, trees appeared in large numbers almost simultaneously. There are several peaks of mass colonization of trees: from 1920 to 1935, from 1945 to 1975, from 1980 to 1995, and from 2010 to 2015. At the upper altitudinal level there were no trees prior to the 1980s, when gradual colonization started and occurs without visible peaks in numbers up to present day.

At transect I, the first living *Juniperus sibirica* appeared in the 1940s; the period of the most massive colonization was between 1970 and 1995. In the upper altitudes the first shrubs appeared only in the 1970s. Junipers were most abundant between 1990 and 2000. At transect II the first living junipers appeared in the second half of the twentieth century in the middle level. In the upper level, the first junipers appeared a little later and continue to colonize now.

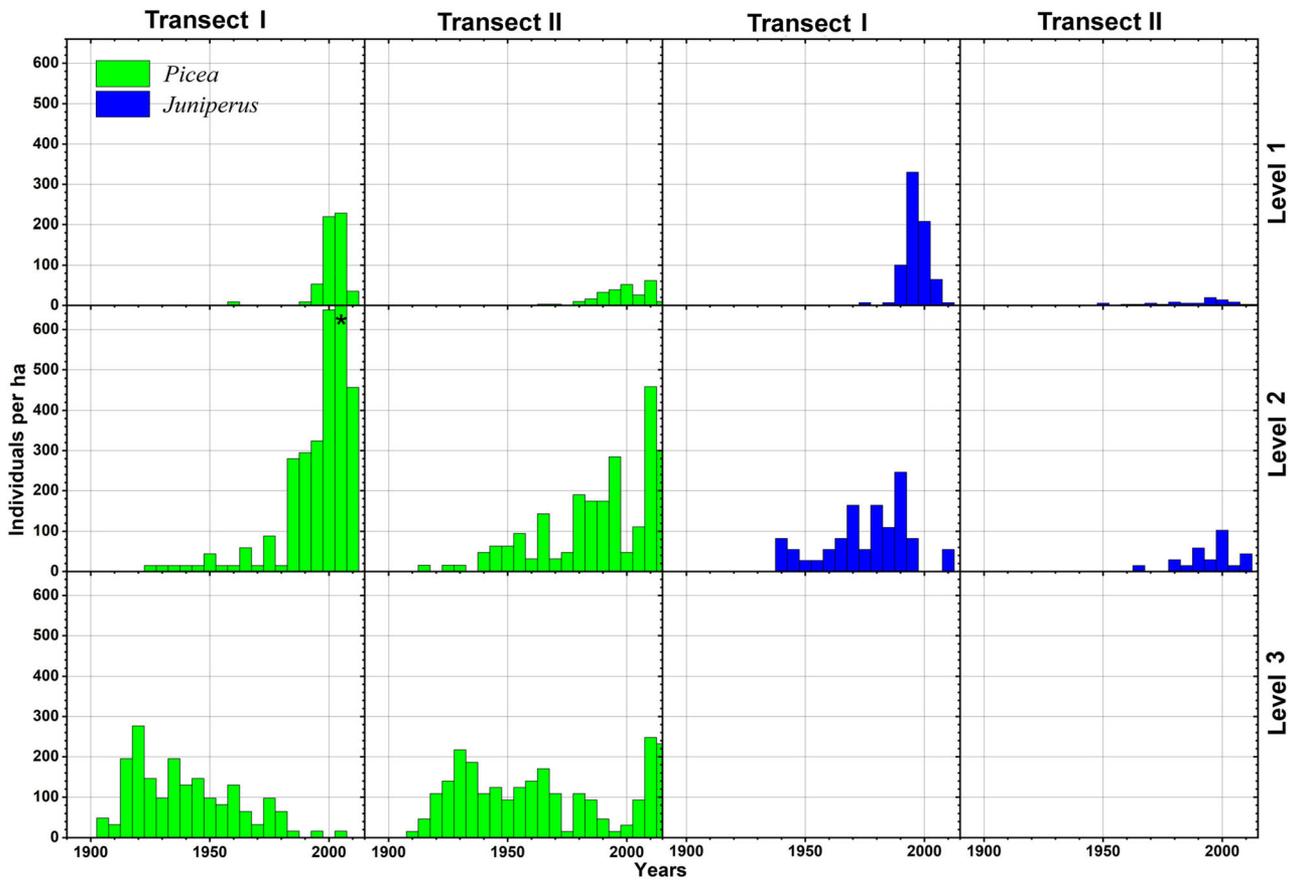


Figure 5. Distribution of Siberian spruce and Siberian juniper by periods of their establishment on the altitudinal transects. Note: * marks the column with actual value of 1356 individuals per ha.

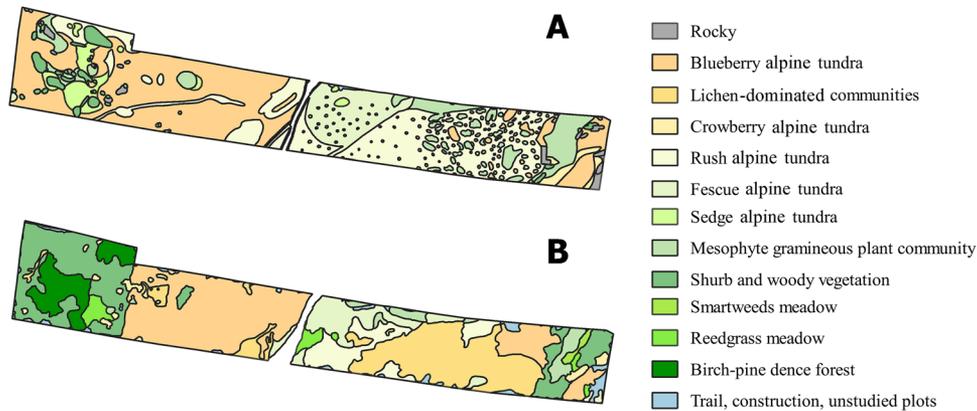


Figure 6. Plant communities of Dalniy Taganay within the transect as of 1990 (A) and 2020 (B).

Monitoring of Plant Communities in Alpine Tundra

In total, 6 types of alpine and 5 types of subalpine communities were identified within the studied transect (Figure 6). There are 3 species of trees, 6

species of bushes, 4 species of shrubs, and 27 species of herbaceous plants (Supplement Table S1). In the total number of species there are 20% of alpine, 17.5% of meadow, and 47.5% of forest species. There are 22.5% of psychrophytes and 67.5% of

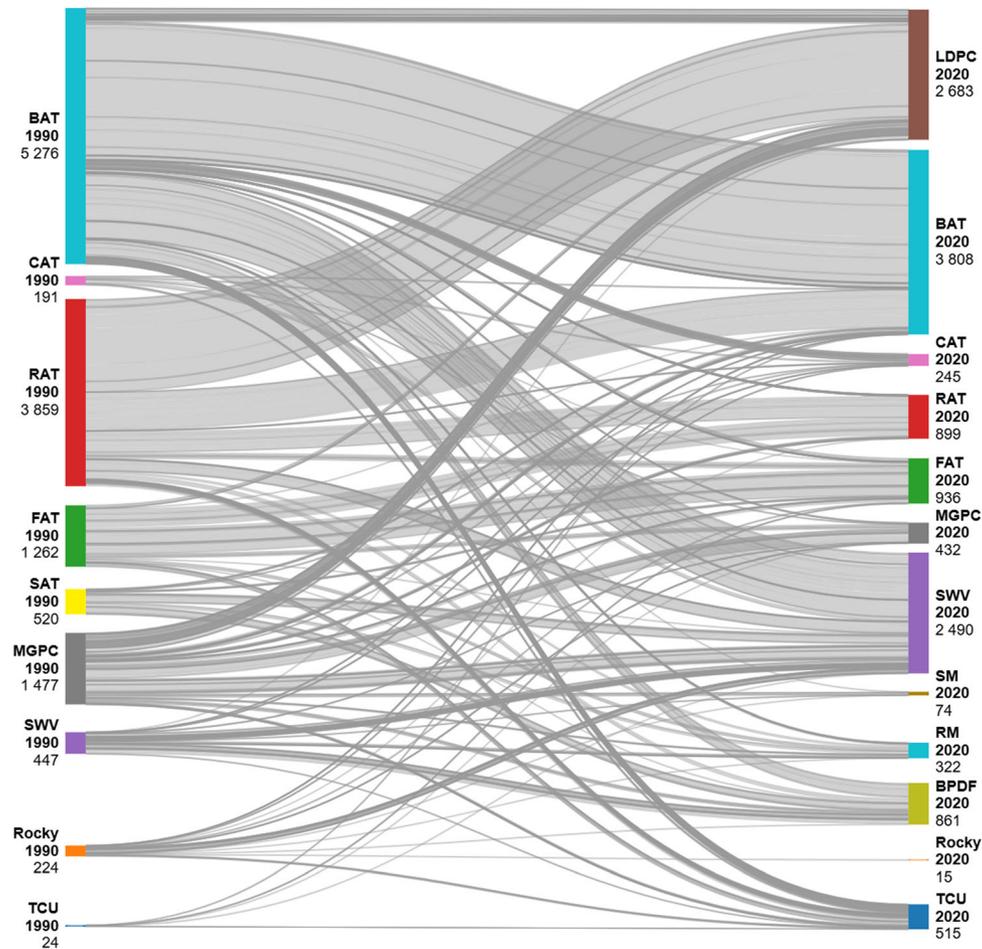


Figure 7. Changes in the area of the plant communities at Dalniy Taganay. Abbreviations used for plant communities: LDPC—lichen-dominated plant community; BAT—blueberry alpine tundra; CAT—crowberry alpine tundra; RAT—rush alpine tundra; FAT—fescue alpine tundra; SAT—sedge alpine tundra; MGPC—mesophyte gramineous plant community; SWV—shrub and woody vegetation; SM—smartweeds meadow; RM—reedgrass meadow; BPDF—birch-pine dense forest; Rocky—rocky outcrops clear of vegetation; TCU—pathways, constructions, unstudied plots.

mesophytic species. The cover of lichens within the community can reach 35% or more; they have dominant position in the communities of blueberry and rush alpine tundra. At the same time, the percentage cover of *Vaccinium uliginosum* L. decreases from 60–65 to 25–45% and *Juncus trifidus* L. from 31–50% to 20–36%.

Blueberry alpine tundra remains the dominant type of alpine plant community of Dalniy Taganay, both in 1990 and today. This community is fairly stable as blueberry plants live on average 50–60 years (Büntgen and others 2015). The largest decrease (Figure 7) was observed in rush (3022 m²) and blueberry alpine tundra (1472 m²). Fescue alpine tundra communities decreased by only 325 m² due to the distance from the upper limit of forest vegetation. The area of crowberry alpine tundra has decreased on the eastern slope due to the

development of meadow vegetation. At the same time, patches of *Empetrum hermaphroditum* Hagerup increased the area of this community type on the western slope. To specify the community type the list of dominant species is given in Table 3.

In 1990 the mountain forest communities were developed mainly in the western part of the transect. In 30 years a closed birch-spruce forest has formed; the site has been covered with dwarf trees and shrubs, represented by single and multi-stem trees of *Picea obovata* and *Betula pubescens* ssp *tortuosa* (Figure 7). Areas of tree and shrub vegetation have expanded, replacing areas of blueberry and crowberry alpine tundra. An increase in precipitation during warm and cold periods contributes to the development of meadow communities. Meadow vegetation is particularly well developed in the eastern part of the transect.

Table 3. Community Types with the List of Dominant Species

Community type	Dominant species	
	1990	2020
Sedge alpine tundra (SAT)	<i>Carex vaginata</i> Tausch, <i>Vaccinium uliginosum</i> L	–
Fescue alpine tundra (FAT)	<i>Festuca ovina</i> L., <i>Juncus trifidus</i> L	<i>Festuca ovina</i> L., <i>Juncus trifidus</i> L
Rush alpine tundra (RAT)	<i>Juncus trifidus</i> L., <i>Festuca ovina</i> L., <i>Vaccinium uliginosum</i> L	<i>Juncus trifidus</i> L., <i>Festuca ovina</i> L., <i>Vaccinium uliginosum</i> L
Crowberry alpine tundra (CAT)	<i>Empetrum hermaphroditum</i> Hagerup, <i>Vaccinium myrtillus</i> L., <i>Vaccinium uliginosum</i> L	<i>Empetrum hermaphroditum</i> Hagerup, <i>Vaccinium myrtillus</i> L., <i>Vaccinium uliginosum</i> L
Blueberry alpine tundra (BAT)	<i>Vaccinium uliginosum</i> L., <i>Cetraria</i> sp., <i>Juncus trifidus</i> L	<i>Vaccinium uliginosum</i> L., <i>Cetraria</i> sp., <i>Juncus trifidus</i> L
Lichen-dominated communities (LDPC)	–	<i>Cetraria</i> sp., <i>Vaccinium uliginosum</i> L., <i>Juncus trifidus</i> L
Reedgrass meadow (RM)	–	<i>Polygonum alpinum</i> All
Smartweeds meadow (SM)	–	<i>Galamagrostis uralensis</i> Litv., <i>Festuca ovina</i> L
Mesophyte gramineous plant community (MGPC)	<i>Vaccinium myrtillus</i> L., <i>Anemone narcissiflora biarmiensis</i> (Juz.) Jalas, <i>Maianthemum bifolium</i> (L.) F. W. Schmidt, <i>Diplazium sibiricum</i> (Turcz. ex G. Kunze) Kurata	<i>Deschampsia cespitosa</i> (L.) Beauv., <i>Diplazium sibiricum</i> (Turcz. ex G. Kunze) Kurata, <i>Chamaenerion angustifolium</i> (L.) Scop., <i>Poa pratensis</i> L., <i>Polygonum alpinum</i> All
Shrub and woody vegetation (SWV)	<i>Picea obovata</i> Ledeb., <i>Juniperus sibirica</i> Burgsd., <i>Betula pubescens</i> Ehrh., <i>Pinus sibirica</i> L., <i>Sorbus sibirica</i> Hedl	<i>Picea obovata</i> Ledeb., <i>Empetrum hermaphroditum</i> Hagerup, <i>Vaccinium uliginosum</i> L., <i>Juncus trifidus</i> L., <i>Sorbus sibirica</i> Hedl., <i>Betula pubescens</i> Ehrh., <i>Juniperus sibirica</i> Burgsd
Birch-pine dense forest (BPDF)	–	<i>Picea obovata</i> Ledeb., <i>Betula pubescens</i> Ehrh., <i>Juncus trifidus</i> L., <i>Cetraria</i> sp., <i>Vaccinium uliginosum</i> L

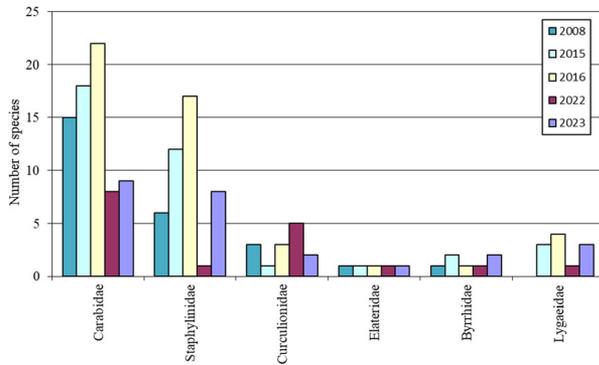


Figure 8. Changes in species richness of the main families of Coleoptera and Heteroptera on the summit of Dalniy Taganay since 2008.

Isolated patches of alpine tundra remain within the communities of dwarf trees and shrubs and birch-spruce closed forests. At the same time, the invasion of forest and grassland species can be observed. The proportion of lichens is decreasing with the formation of moss cover. The largest increase was recorded for the communities of creeping trees and shrubs (2083 m²). This led to a decrease in the area of herbaceous mesophytic communities (1060 m²) and the disappearance of the sedge alpine tundra. Some herbaceous mesophytic communities were replaced by acid grasses (78 m²) and reed grasses (326 m²). The area of closed forests formed in this territory is 865 m².

Thus, within the transect at Dalniy Taganay over a period of 30 years the development of tree, shrub, and meadow vegetation has led to a reduction in the area of alpine tundra communities by 2547 m². In the closed forests patches of alpine shrubs *Vaccinium uliginosum* and *Empetrum hermaphroditum* and single individuals of some herbaceous species remain. An endemic species *Anemone narcissiflora* ssp. *biarmiensis* (Juz.) Jalas grows well both in alpine tundra and mountain forest under the forest canopy. Blueberry alpine tundra has been very resilient for several decades.

Dynamics of the Invertebrate Communities

The insects in the samples are represented by three orders: Coleoptera, Heteroptera, and Hymenoptera, with the first being the most numerous. The alpine tundra is distinctive for a diversity of ground beetles similar to the Arctic tundra (Chernov and others 2014). Dalniy Taganay stands out among other peaks of the Southern Urals as the species *Nebria uralensis* Glasunov, 1901, and *Pterostichus kokeilii* ssp. *archangelicus* Poppius, 1907, character-

istic elsewhere, were not recorded there (Mikhailov and Ermakov 2018). *Carabus karpinskii* Kryzhanovskij and Matveev, 1993, and *Pterostichus uren-gaicus* Jurecek, 1924, although found at Dalniy Taganay, are not among the dominants. At the same time, this is the only surveyed summit, where the red forest ants *Formica aquilonia* Yarrow, 1955, and *F. fusca* Linnaeus, 1758, are dominant species. *F. aquilonia* has been observed at Dalniy Taganay since 2008 with a high abundance. The dynamic density of red ants (normalized to 100 trap-days) in 2008 was 3140, in 2016– 5820 and in 2023 was already 12 100 specimens. Much fewer ants were observed on Kruglitsa summit, where only *F. fusca* was recorded with an abundance of over 200 specimens in 2016, and around 400 specimens in 2023.

Carabus karpinskii was first collected at Dalniy Taganay by one of the authors (YEM) in 1994. With the start of regular surveys under the GLORIA project this species was recorded there in 2008, 2015, and 2016. However, no adult or larval specimens were found in 2022. In 2023, to verify the results of the previous season, soil traps were installed in parallel on the peaks of Dalniy Taganay and Kruglitsa with a difference of one day. As a result, *C. karpinskii* was not found on Dalniy Taganay, while on Kruglitsa it was recorded with the same dynamic density as in 2016.

At Dalniy Taganay the maximum number of ground beetle species (22) was recorded in 2016; 19 species were recorded in a relatively unfavorable season of 2015. However, in 2022 and 2023 only 8–9 species of carabid beetles were recorded, of which only *Miscodera arctica* and *Dicheirotichus mannerheimii* can be considered as mountain specialists. *Calatus micropterus* (Duftschmid 1812), *C. melanocephalus* (Linnaeus 1758), *Amara communis* (Panzer 1797), *A. tibialis* (Paykull 1798), *A. infima* (Duftschmid 1812), and *Poecilus versicolor* (Sturm 1824) are widespread and not typical of alpine tundra. All of them have been recorded here before, but now the species composition of ground beetles in general is no more typical of alpine tundra (Figure 8).

The other beetle families are less diverse on Dalniy Taganay and represented by the same peculiar species since 2008. The tundra click beetle *Hypnoidus rivularius* Gyllenhal, 1808 (Elateridae), is an arcto-boreomontane species recorded on many peaks of the Southern Urals. From pill beetles (Byrrhidae) *Byrrhus fasciatus* (Forster 1771) is the most common. Among weevils (Curculionidae) only arcto-boreomontane species *Otiorhynchus nodosus* (O.F. Müller 1764) is constantly recorded. It is

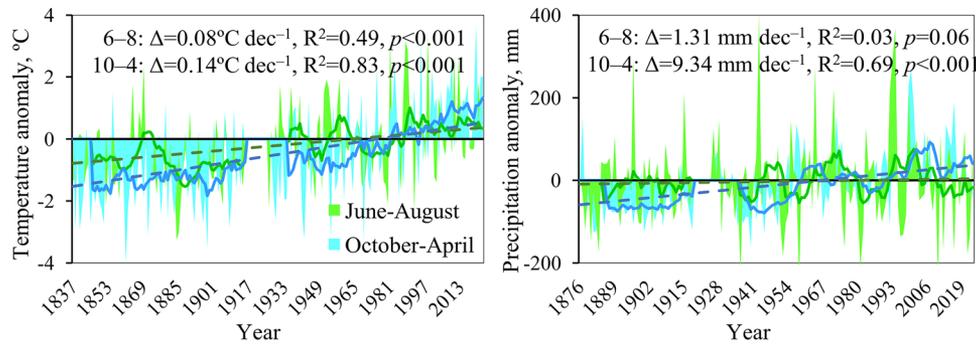


Figure 9. Anomalies of mean temperature and total precipitation for warm (June–August) and cold (October–April) periods for the weather station Taganay-Gora (a,b). Anomalies are relative to the mean values of the 1961–1990 period. The solid line indicates the 10-year moving average; the dotted line shows the linear trends. Statistics correspond to these linear regressions.

Table 4. Spearman Correlation Coefficients between the Number of Recruited *Picea obovata* Trees and *Juniperus sibirica* Shrubs on Different Altitudinal Levels on Dalniy Taganay and Climate Variables

Species	Transect	Altitudinal level	Temperature				Precipitation			
			Corresponding period		Shifted period		Corresponding period		Shifted period	
			Cold	Warm	Cold	Warm	Cold	Warm	Cold	Warm
<i>Picea obovata</i>	I	Upper	0.48	0.51	0.67	0.30	0.64	-0.16	0.46	-0.02
		Middle	0.78	0.36	0.68	0.27	0.53	0.02	0.40	-0.05
		Low	-0.74	-0.32	-0.64	-0.28	-0.34	0.11	-0.61	-0.08
	II	Upper	0.72	0.67	0.71	0.49	0.28	-0.47	0.67	0.09
		Middle	0.64	0.16	0.54	0.35	0.01	-0.03	0.35	0.02
		Low	-0.26	0.06	-0.15	0.01	-0.12	-0.14	-0.26	0.10
	All	Upper	0.60	0.64	0.80	0.48	0.48	-0.41	0.56	-0.06
		Middle	0.80	0.34	0.72	0.28	0.38	-0.06	0.45	0.00
		Low	-0.52	-0.09	-0.39	-0.05	-0.18	-0.03	-0.44	0.01
<i>J. sibirica</i>	I	Upper	0.69	0.48	0.76*	0.40*	0.56	-0.01	0.22*	-0.19*
		Middle	0.08	-0.10	0.02*	0.03*	-0.32	0.01	0.06*	-0.18*
		Low	0.35	-0.17	0.41*	0.27*	0.08	0.32	0.35*	0.07*
	II	Upper	0.64	0.37	0.71*	0.38*	0.27	-0.24	0.48*	-0.07*
		Middle	0.69	0.28	0.76*	0.32*	0.39	0.06	0.26*	-0.07*
		Low	0.26	0.04	0.42*	0.05*	-0.21	-0.07	0.08*	0.00*
	All	Upper	0.53	0.09	0.66*	0.36*	0.10	0.14	0.37*	-0.08*

Correlations calculated for 5-year periods in the cold (October–April) and warm (June–August) seasons. Significant values at $p < 0.05$ indicated in bold. Meteorological data of the current and shifted periods were analyzed, * marks the calculations based on the data of the next five years

also common on other peaks, where *Otiorynchus politus* Gyllenhal, 1834, and *Asiodonus opanassenkoi* (Legalov 1997) are often found together. These two species have not been recorded on Dalniy Taganay, but they are present on Kruglitsa. Since 2008 a typical forest species *Hylobius (Callirus) pinastri* (Gyllenhal 1813) has been recorded, feeding on pine and spruce trees. Since 2016 also the bark beetle *Hylastes cunicularius* (Erichson 1836) has

been observed, which develops in the roots and basal part of spruce trunks.

The Friedman test demonstrated differences ($p < 0.05$) between the years of sampling not only for spiders and insects separately but also for all invertebrates including centipedes (Supplement Table S2). The pairwise comparisons of the years of sampling for spiders, insects, and all invertebrates using Wilcoxon test showed similarity of the

samples from 2008 and 2015 and dissimilarity of the samples 2016 and 2023 (Supplement Table S3).

Climate Data Associated with Spruce and Juniper Recruitment

Our analysis of instrumental observations for more than 140 years showed pronounced trends in climate warming and humidification in the study area (Figure 9). In the cold season the increase in air temperature was almost twice higher in comparison with the warm season (0.14 °C per decade vs 0.08 °C per decade). An increase in precipitation is also observed in the cold period and amounts to 9.34 mm per decade, while no noticeable changes in precipitation during the warm period have been recorded. The data obtained from snow depth measurements in March 2023 and March 2024 show decreasing mean snow cover with altitude, while the maximum values vary at the middle and low elevations.

Correlation analysis (Table 4) showed that the closest connections of spruce establishment in both transects were detected with the temperature of the cold and warm periods of the current and previous five years (R_S is in the range of 0.45–0.57, $p < 0.05$). The general trend is that the relationship is stronger with higher altitude. Namely, in the upper altitudinal level the correlation coefficient of spruce establishment with temperature reaches $R_S = 0.80$ ($p = 0.003$) and the same with precipitation reaches $R_S = 0.56$ ($p = 0.07$) in the cold period for the previous 5 years, whereas, at the low altitudinal level, where intraspecific competition between juveniles and adults is more pronounced, the correlations between the appearance and survival of trees with the above mentioned climatic parameters become negative.

According to the aggregated data from both transects, the appearance of juniper shrubs demonstrates closer connections with the temperatures of the cold period of five years following their appearance ($R_S = 0.66$, $p = 0.01$) rather than with other studied indicators. The highest values were found at the upper altitudinal levels ($R_S = 0.76$, $p = 0.003$). The significant correlations of shrub recruitment with precipitation were observed only at the upper level of transect I ($R_S = 0.56$, $p = 0.04$), where, in general, less snow accumulates.

DISCUSSION

Differences in the distribution of forested areas on historical maps and satellite images as well as repeat photography of high mountain forest vegeta-

tion in the upper treeline ecotone on Dalniy Taganay give clear evidence of significant reduction of the areas of alpine tundra communities over the past 50–70 years. This process is due to the rapid advance of Siberian spruce higher into the mountains, where it begins to form closed forests. The total area without forests has decreased with 72% since 1960 to its present cover of 30.7 ha. This is also confirmed by data on age and morphological structure of spruce stands growing on the altitudinal transects. It has been shown that *Juniperus sibirica* occupies treeless areas in the upper part of the slopes, but cannot exist in the emerging closed spruce stands due to competition. Similar processes are also observed on other peaks in the Southern Urals (Grigoriev and others 2024).

Climate warming in the study area is confirmed by the analysis of instrumental observations in the immediate vicinity of the study objects. The changes mainly occurred in the cold season as winters have become warmer and snowier. Although summer temperatures would be expected the main driver of treeline advance, Harsch and others (2009) showed that this advance is more strongly associated with increased local winter temperatures, rather than summer warming at those sites. However, these results were obtained without taking into account changes in precipitation. And this factor could be essential when warmer temperatures are combined with reduction in moisture availability (Hansson and others 2021). All this shows an important role of seedlings survival above the present treeline, and a lack of available water may prevent them from establishing, hence limiting the potential of treelines to advance (Hansson and others 2021). This is true for comparatively dry highlands with less snow where establishing and survival of seedlings may correlate with increase of summer or winter precipitation. For Dalniy Taganay mountain range moisture availability is not a limiting factor, there summer precipitation is high, and some snowbeds may persist until mid-June.

According to our results the distribution of spruce trees is closely related to temperature dynamics in both cold and warm periods of the year in previous and current five-year periods. As shown by Cannone and Malfasi (2024), warming persistence in the years before the recruitment provides suitable conditions for seed production and germination, and in the years following the recruitment it is crucial to achieve the age of reproductive maturity. The correlations between the appearance of spruce and the temperature or precipitation of the cold period in the previous five years, which characterize conditions for maternal

individuals, increase with altitude when comparing sample plots at different altitudinal levels. A similar trend is observed for the vulnerable first years of survival of juniper seedlings, showing increasing correlations with the temperatures of cold period in the next five years after the shrub establishment.

In addition to forest expansion at Dalniy Taganay the vegetation mapping has shown an increase in the number of forest and forest-meadow herbaceous species in alpine tundra over 30 years. These noticeable changes in the composition and distribution of vascular plants are observed not only under the canopy of emerging tree stands, but also in open areas with no trees at all or with only individual trees. This is one more example of thermophilization, a decrease in abundance of cold-adapted species, and increase of more-thermophilic ones (Gottfried and others 2012). *Arctous alpina* (L.) Niedenzu, 1890, a Pleistocene relict of Arctic origin that grows on the most wind-exposed sites of the Bolshoi Taganay range (Kulikov 2005), has almost expired at surveyed summit. However, some isolated remnants of major species from alpine tundra plant communities are still present in a closed forest. *Vaccinium uliginosum*, *Empetrum hermaphroditum*, and *Juncus trifidus* proved to be the most resistant.

As it was mentioned before, no grazing took place there, only some limited impact of recreation, so influence of this factor cannot be expected. In general lichen growth has been intensified with increase of precipitation (Jonson Čabrajić 2009; Borge and Ellis 2024). The pronounced increase of lichen-dominated plant communities may be associated with the successional changes, and we consider these communities as transitional stages. The rush alpine tundra makes a main contribution to the progress of lichen-dominated communities. Taking into account the high percentage cover of *Vaccinium uliginosum* in lichen-dominated plant communities we expect blueberry alpine tundra to replace them further.

The alpine flora of the Bolshoi Taganay mountain range is relatively poor in species diversity and different from the rest of the Southern Urals highlands; this may be explained by the repeated reduction of alpine vegetation area during the warmer phases of the Holocene (Kulikov 2005). As a result of such treeline fluctuations the populations of endemic leaf beetles (Chrysomelidae) may be the first to disappear. *Chrysolina lagunovi* Mikhailov, 2007, and *C. poretzkyi olschwangi* Mikhailov, 2018, two leaf beetles species common for the Southern Urals (Mikhailov 2018), were not recorded at Dalniy Taganay and Kruglitsa. However,

Anemone narcissifolia ssp *biarmiensis*, the host plant of *C. lagunovi*, is quite common and abundant throughout the mountain range.

Carabus karpinskii, although recorded at Dalniy Taganay from 1994 till 2016, was not a dominant species as on higher peaks. Since 2016 this species and another ground beetle *Pterostichus mannerheimii* have no longer been recorded in surveys and the abundance of *P. urengaicus* has significantly decreased. There is growing evidence that climate warming is leading to declines in the abundance and population size of many mountain invertebrate species (Devictor and others 2012; Platts and others 2019; Termaat and others 2019). Modeling has shown a strong relationship of low temperatures and habitat limits of *Carabus cychroides* Baudi, 1860, a local endemic of the Cottian Alps in Italy with extremely restricted habitat. Under a negative climate change scenario this can lead to its extinction by the end of this century (Anselmo and Rizzioli 2022). *Carabus karpinskii*, a local alpine endemic of the Southern Urals, represents a very similar case. The samples from two consecutive seasons 2022 and 2023, with a control taken on another peak of the same ridge, gives sufficient evidence that *C. karpinskii* has disappeared from Dalniy Taganay. The population of *C. karpinskii* from Kruglitsa therefore requires special attention as the northernmost habitat of this species.

Ground beetles are less dependent on vegetation, but the invasion of red wood ants to alpine tundra may be an important factor for them. It is known that in the territories, occupied by red ants, for example, *Formica aquilonia*, the density of active predatory invertebrates, such as ground beetles, rove beetles, and spiders, is steadily decreasing (Reznikova and Dorosheva 2004; Hawes and others 2013). *Formica aquilonia* has been observed throughout the summit of Dalniy Taganay since 2008 with high abundance, which increased almost fourfold during the observation period. Fewer ants were recorded on Kruglitsa, and these were mainly the less aggressive species *F. fusca*.

Earlier Shiyatov and others (2001) expected Dalniy Taganay to be completely covered by woody vegetation by 2040–2050. Currently, the area of alpine tundra communities excluding rocky areas is only 10.1 ha. Based on the estimated average rate of decline of the non-forested area for 1960–2023 at 4.7 ha per decade there is a possibility that complete overgrowth of Dalniy Taganay will occur by the middle of this century. However, there are some difficulties in predicting of terminal stages of woody vegetation shift on the peak, as some aspects of treeline dynamics are still not well under-

stood, first of all the role of wind. Our results demonstrate a large amount of viable undergrowth not only on the slopes but also on the convex areas and the upper levels of the altitudinal transects where snow cover is absent blown away by the wind. A similar situation is observed in northeastern Canada (Gamache and Payette 2005) and other areas of the Urals (Hagedorn and others 2014) where active processes of shrub invasion into the tundra also occur (Grigoriev and others 2022). In alpine ecosystems, where snow is redistributed by wind, seedlings may also be exposed to low temperatures rather than protected by stable snow cover. Combined with icing and wind erosion this may lead to an increased winter mortality of seedlings on exposed ridges (Wipf and Rixen 2010; Myers-Smith and Hik 2013). However, our observations on the convex slopes of Dalniy Taganay show that in the recent years juniper seedlings and maternal shrubs have managed to establish and survive in the absence of snow suggesting a change in habitat conditions.

For the treelines migrating into alpine ecosystems Hansson and others (2021) propose further studies of carbon storage capacity. Treeline advance may alter this ecosystem function, although the exact impact is likely to vary depending on the local conditions. The research in this direction has been already started in the Urals (Hagedorn and others 2014). However, our results show the need for other kind of ecosystem studies. As the typical forest beetle species feeding on spruce, the weevil *Hylobius pinastri* and the bark beetle *Hylastes cunicularius*, are regularly recorded in the treeline ecotone, the special studies of pests (insects and fungi), and their influence on survival of seedlings and larger trees, their seed production are needed. The invertebrate sampling at the altitudinal transects in 2022 discovered several species occurring both in alpine tundra and the treeline ecotone down to its lower level. These species are likely less threatened when the area of alpine tundra shrinks and is covered by forest. Although similar results can improve our understanding of upcoming changes, they are still very scarce.

CONCLUSION

A multi-level system for the long-term monitoring of climate-driven dynamics of alpine tundra and treeline ecotone vegetation was first applied for a single summit in the Southern Urals. Dalniy Taganay Mountain is a unique natural site, the lowest and northernmost peak of the Southern Urals, where alpine tundra communities and several relict

and endemic species of plants and invertebrates are preserved. And it is a mountain, where alpine tundra domain may disappear completely before our eyes. The unique data were accumulated and analyzed on the process of forest expansion and associated changes in the communities of herbaceous plants and invertebrates, when alpine species are diminishing and disappearing and forest and forest-meadow species are coming. This example of accurate quantitative assessment of changes in plant and invertebrate communities can be applied in other regions.

It is shown that climate-induced expansion of woody vegetation causes not only alpine tundra area contraction but also transformation of plant and animal communities both in forested and open areas. The environmental changes lead to decrease in abundance of certain species of vascular plants and invertebrates in the highlands. The local extinctions of one endemic ground beetle species and one vascular plant species were also recorded. The data obtained on the changes in the natural environment and the extinction of individual species on the surveyed peak improve our understanding of past and present dynamics at the treeline. It can be used to adjust the models of responses to climate change for other similar mountains, where the area of alpine meadows or tundra is critically small. In the Taganay National Park it provides useful information for the management of treeline and conservation of the alpine tundra.

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DATA AVAILABILITY

The online supplemental information includes additional data for this article.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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