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Alpine Shrubification: Juniper Encroachment into Tundra in the Ural Mountains

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Abstract: Snow cover is one of the most important factors affecting the regeneration and growth of shrubs in cold arctic and alpine ecosystems. In many of these cold regions, climate change in the last century is manifested not only in a rapid rise of temperature, but also in an increase in winter precipitation. For instance, in the Ural Mountains, winter turned warmer and more humid during the past century, leading to higher snow accumulation. We investigated how the change trends in the cold season (November to March) climate conditions affected the recruitment of the shrub *Juniperus sibirica* Burgsd., the most widespread shrub conifer in mountains of this region where it is dominant in treeless areas. Specifically, we considered seven sites located in the Southern and Northern Urals that are subjected to lower and higher continentality, respectively. We assessed how juniper recruitment changed along altitudinal gradients going from the open forest to the alpine tundra and passing by the transition zone. We found that juniper shrubs recruited at higher elevations during the 20th century in most sites, with a rapid shrub encroachment into alpine tundra (shrubification) after the 1990s. This process was especially intensive in the last decades at the uppermost parts of convex slopes where the snowpack is shallow. We found positive associations between juniper recruitment and cold-season precipitation or temperature in the Northern and Southern Urals, respectively. Shrubification is following upward treeline shifts in the Southern Urals. Our findings indicate that juniper shrubs will tend to colonize sites with low snowpack depth if winter conditions keep warm and wet enough and the snowpack allows the effective protection of shrubs.

Keywords: climate change; alpine shrubs; *Juniperus sibirica*; shrubline; Urals; winter climate conditions

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1. Introduction

Climate warming is an indisputable fact, and many of the observed changes since the 1950s are unprecedented on scales from decades to millennia. The atmosphere and ocean got warmer, Arctic sea ice and snow cover have decreased, and the global sea level has risen [1]. Climate warming is most noticeable in cold and alpine ecosystems where the temperature increase is faster and higher [2]. It is known that a change in the temperature and humidity regime in such regions may lead to shifts among ecotones separating different communities such as the treeline ecotone [3–5]. In recent decades, a large number of studies have found strong links between upward treeline shifts and climate warming [6]. However, many of these studies focused on growing-season temperatures, whereas the impacts of changing winter conditions on woody plant communities are poorly understood, despite that they have revealed important effects on treeline dynamics [5,7].

Shrubs occupy many treeless areas in cold alpine and arctic biomes, and, like trees, the dynamics of upper shrub limit are linked to climate conditions [8]. It has been shown that the radial growth of shrubs is sensitive to the climate conditions [9–12], and changes in the environmental conditions may lead to shifts in the distribution boundaries of shrubs [13]. Studies on the dynamics of shrublands were carried out mainly in Arctic areas, where there is strong evidence of shrub encroachment into the tundra [9,13–15].

In contrast, field studies on shrub dynamics across mountains as related to winter conditions are rare. In Scandinavia, an upward shrubline shift was observed [10,16] , and similar dynamics were also reported in Alaska [17–20], Canada [21], the Rocky Mountains in the USA [22], the European Alps [23,24], and the Ural Mountains [25,26]. Assessing shrub dynamics in mountains is very relevant for preserving alpine biodiversity since shrub encroachments can lead to a decrease in the richness and diversity of alpine flora [27,28], as well as to changes in the structure and carbon and water dynamics of tundra ecosystems [2,8,29,30]. Expansion of shrub vegetation can also alter the depth and features of the snow cover [31], modify soil respiration [32], and influence permafrost formation [33]. These multiple impacts of rapid shrub encroachment into alpine tundra (shrubification) demonstrate the importance of characterizing the drivers and forecasting the dynamics of shrubs in cold mountain regions [34,35]. Here we test the idea that an improvement of winter climate conditions enhances the regeneration of shrubs in mountains. Several studies have indicated that warmer and wetter climate conditions augment shrub establishment in cold biomes [10,16,24].

Currently, *Juniperus sibirica* Burgsd. is the most abundant conifer shrub in the cold areas of the Ural Mountains, where it is a dominant species of alpine communities [26]. Shrubs of *J. sibirica* may be found in gaps or open subalpine forest, in the transition zone above the treeline, and near the lowermost mountain tundra and meadows, forming thickets within the alpine tundra. In the northern Subpolar and Polar Urals, *J. sibirica* occurs sporadically, not forming a dense belt above the uppermost forest limit. Recent studies have shown that *J. sibirica* expanded into tundra of the Northern Urals [25].

In this study, *J. sibirica* dynamics are assessed in the Northern and Southern Ural Mountains by reconstructing shrub age structures and relating them to climate variables (temperature and precipitation). Our goals are: (1) to assess the extent of *J. sibirica* shrub expansion along altitudinal gradients in the Northern and Southern Urals; (2) to analyze the associations between *J. sibirica* recruitment and climate variables; and (3) to discuss and forecast how these associations would determine future shrubby vegetation encroachment into tundra. We assume that increased snow cover facilitates the recruitment of *J. sibirica* shrubs across the Ural Mountains and that wetter and warmer climate conditions have facilitated the 20th century alpine shrubification in this region.

2. Materials and Methods

2.1. Study Sites

Field sampling was conducted in the period 2016–2020. In the Northern Urals, we studied three mountains: Kvarkush, Zyryanovka, and Molebnyi Kamen' (Figure 1, Table 1). The climate of this study region is continental boreal type. According to long-term observations from the "Cherdyn'' weather station (60°24′00″ N, 56°31′00″ E, 207 m a.s.l.; period 1888–2015 for temperature and 1936–2015 for precipitation), the annual mean air temperature is 0.3 ± 1.1 °C, the mean January temperature is −16.4 ± 3.9 °C (with the absolute minimum of about −50 °C), and the mean July temperature is 17.1 ± 2.1 °C (Figure 2). Mean annual precipitation is 807.5 ± 123 mm. Snow cover in the region ranges 50–150 cm. Snow starts accumulating in mid-October and lasts until late April [36]. The substrates are shales, metabasalts, and quartzitic sandstones [37].

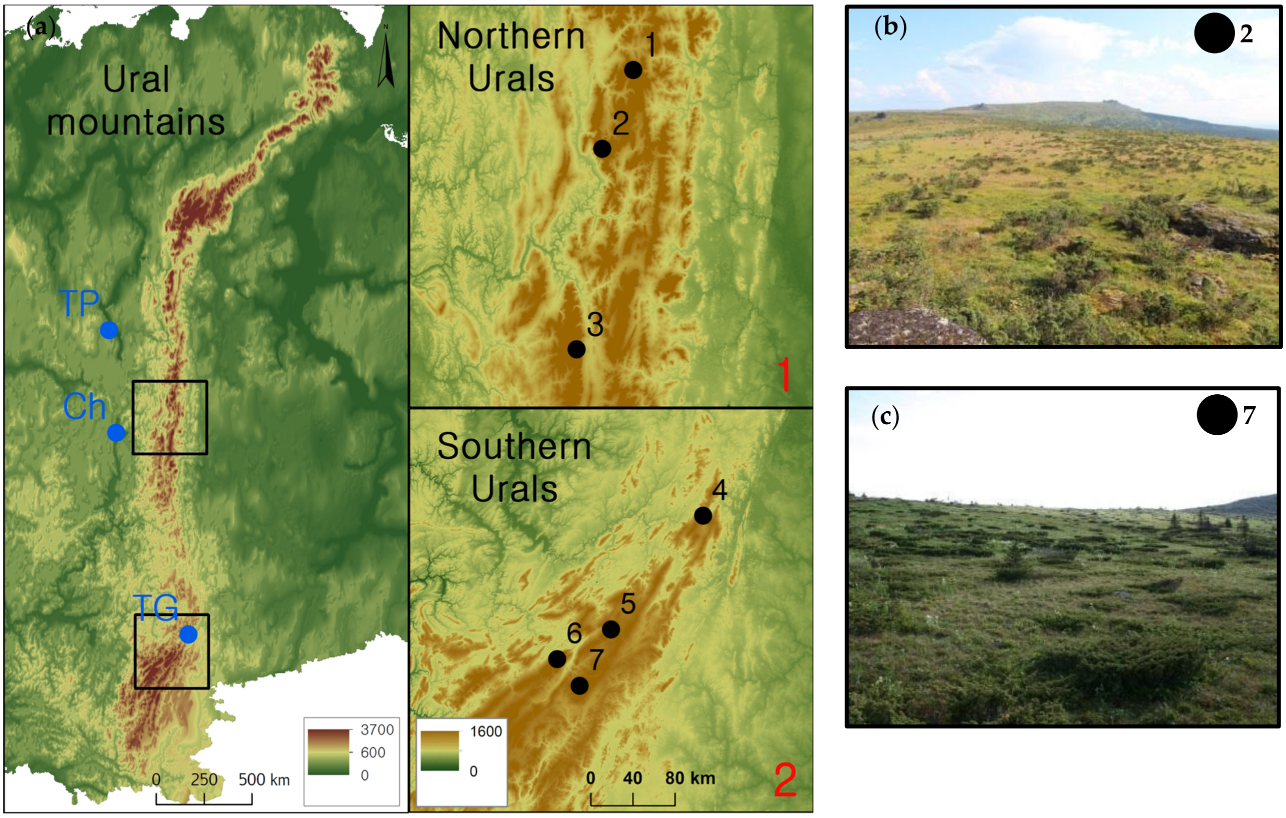


Figure 1. Study area (**a**) in the Russian Urals and views (**b**,**c**) of some studied *J. sibirica* populations. Site codes: 1—Molebnyi Kamen′; 2—Zyryanovka; 3—Kvarkush; 4—Taganay; 5—Nurgush; 6—Zigalga; 7—Iremel. Images correspond to Zyryanovka ((**b**), number 2 on the map) and Iremel ((**c**), number 7 on the map) sites, respectively. The blue circles indicate the weather stations: Troicko–Pecherskoe (TP), Cherdyn (Ch), and Taganay–Gora (TG).

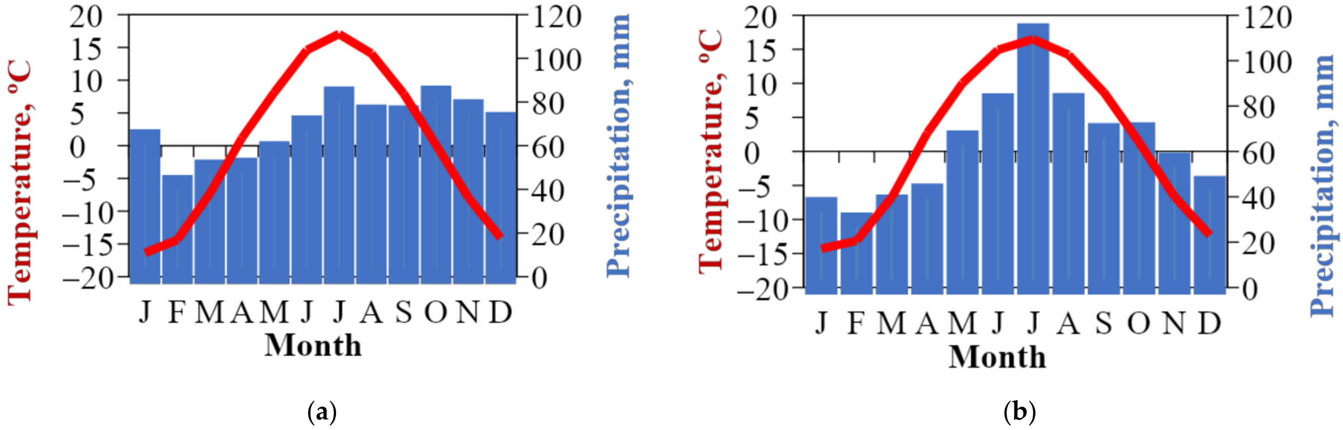


Figure 2. Climate diagrams of study regions in (**a**) Northern and (**b**) Southern Urals. The red line shows the annual dynamics of the mean monthly air temperature; the blue bars correspond to the total monthly precipitation.

Table 1. Geographical position and conditions of the study plots. Snow depth values were measured in late March (means ± SD).

Level	Variables	Northern Urals					Southern Urals			
		Molebnyi Kamen′	**Zyryanovka I**	**Zyryanovka II**	**Kvarkush I**	**Kvarkush II**	**Taganay**	**Nurgush**	**Zigalga**	**Iremel**
	Coordinates	**61°18′52″ N 59°13′51″ E**	**60°59′24″ N 58°58′05″ E**	**60°58′16″ N 58°58′23″ E**	**60°08′49″ N 58°44′56″ E**	**60°08′47″ N 58°41′51″ E**	**55°22′03″ N 59°54′30″ E**	**54°48′35″ N 59°07′18″ E**	**54°39′46″ N 58°39′47″ E**	**54°31′49″ N 58°51′16″ E**
Altitude (m a.s.l.)	High	890	835	840	907	921	1090	1240	1286	1301
	Mid	-	820	820	881	907	1080	1235	1260	1297
	Low	-	790	790	863	886	-	-	-	-
Exposition	High	summit	summit	summit	summit	NE	summit	summit	summit	summit
	Mid	-	SW	SW	NW	NE	S	SE	SE	SW
	Low	-	SW	SW	NW	NE	-	-	-	-
Snow depth (cm)	High	no date	73.8 ± 8.9	no date	no date	no date	15.1 ± 7.2	25.0 ± 9.6	21.6 ± 11.8	13.2 ± 7.3
	Mid	-	87.0 ± 17.1	no date	no date	no date	39.6 ± 23.0	111.2 ± 30.1	70.9 ± 33.0	40.9 ± 16.4
	Low	-	122.5 ± 14.2	no date	no date	no date	-	-	-	-

In the Southern Urals, studies were carried out on four areas: Bolshoi Iremel, Zigalga, Nurgush, and Taganay. According to modeled data from the "Zlatoust" weather station (55°10′00″ N, 59°40′00″ E, 537.5 m a.s.l.; period 1837–2015 for temperature and 1936–2015 for precipitation), the annual mean air temperature is 0.8 ± 1.0 °C and the mean temperatures in January and July are −15.3 ± 3.6 °C and 16.4 ± 1.7 °C, respectively (Figure 2). Mean annual precipitation is 733.0 ± 138.9 mm. Snow cover ranges 11–109 cm. Snow starts accumulating in mid-October and lasts until late April. The average wind speed increases with altitude and reaches 9.6–13 m s^{-1}, and in winter it can reach up to 40 m s^{-1} in gusts. The massif is composed of quartzitic sandstones, quartzite-sandstones, and their dark gray and black shales [38]. The soils are mountain-meadow and mountain-podzolic. Mountain-meadow soils in the goltsy altitudinal belt transform into a variety of tundra soils [39]. In both study areas, the dominant tree species is *Picea obovata* Ledeb.

2.2. Design of Field Sampling

In the Northern Urals, three altitudinal levels were recorded: low, at the upper border of closed thickets of bushes (>40% cover), mid, at the upper border of sparse thickets of bushes (20–40% cover), and high, at the border of separately growing bushes (5–20% cover) (Figure 3). In the Southern Urals, two altitudinal levels were considered: the low and high ones (Figure 3). Two transects, named I and II, were considered in Zyryanovka and Kvarkush to account for the site's spatial variability.

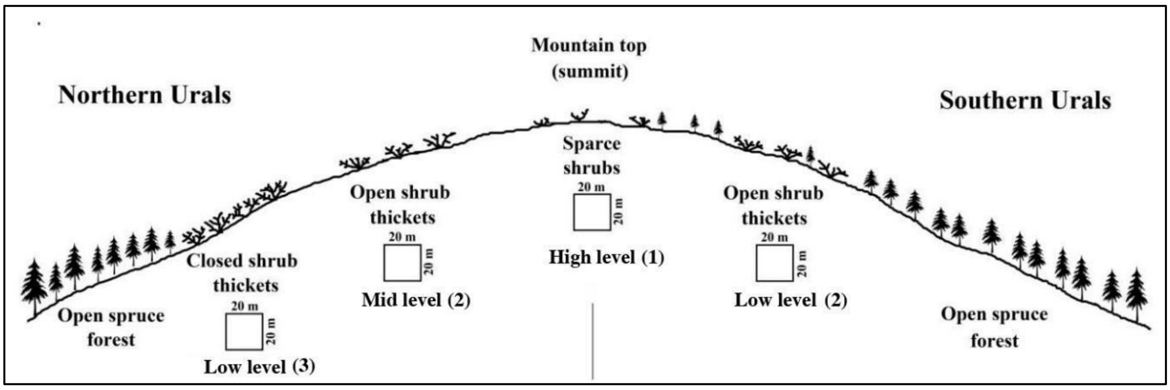


Figure 3. Scheme of changes in vegetation and sampling along altitudinal transects.

The differences between the studied regions are that in the Southern Urals, because of the higher position of the uppermost forest limit, the zone of shrub distribution in the altitudinal transect is narrower than in the Northern Urals. The location of the altitudinal levels was determined visually according to *J. sibirica* crown cover and density. At each level, two to five square test plots (20 m × 20 m) were laid on representative locations of each altitudinal level (Figure 3). In the Southern Urals, above the sparse forest boundary, there are scattered saplings of several tree species (*P. obovata*, *Betula tortuosa* Ledeb, and *Pinus sylvestris* L.). Therefore, an additional survey of these young trees was also carried out in this area.

On each test plot, for each shrub and tree, the horizontal crown diameter in two mutually perpendicular directions, height, diameter at the base (only for trees), age, and location were determined. The location of each individual plant was estimated by an aiming circle, which made it possible to measure the distance from the central pole in the test plot, and the location of this pole was fixed using GPS. The density of *J. sibirica* was calculated through the ratio of the number of individuals on the test plot to its area. The snow cover depth was measured in late March, when maximum snow accumulation occurs, using a metal avalanche probe tool with marks every 1 cm. On each plot, the snow depth was measured in at least 40 points. Snow cover in the Northern Urals was determined once. In the Southern Urals, the snow cover was measured in all test plots for several years in a row in the period 2016–2020.

For shrubs, the age was determined according to previously tested methods [25]. The only way to determine the exact age of *J. sibirica* is to extract the shrub with the root system and sample cross-sections at the hypocotyl. Since this will lead to the death of the plant, we adapted the methods [40,41]. Age was determined by finding the part of the plant where the plagiotropic branches were attached to the stem, followed by cutting off the thickest branch at the stem (Figure 4b-2). The age correction factor by the branch attachment height was established by studying the growth stages of the young individual plants of *J. sibirica* from the hypocotyl (Figure 4a-1) of the stem to the area where it splits into plagiotropic branches (Figure 4a-2) under specific conditions. If finding that area was impossible, especially in case of big, old plants, the branches were cut off at the place closest to the attachment area of plagiotropic branches to the stem (Figure 4b-3). The age of the trees was determined by taking radial wood cores at the base of the main stem using increment borers (Haglof, Långsele, Sweden). It should be noted that the age determination method used for trees by taking radial wood cores gives very low accuracy for *J. sibirica*, since their stems can have many missing rings in separate saw-cut directions.

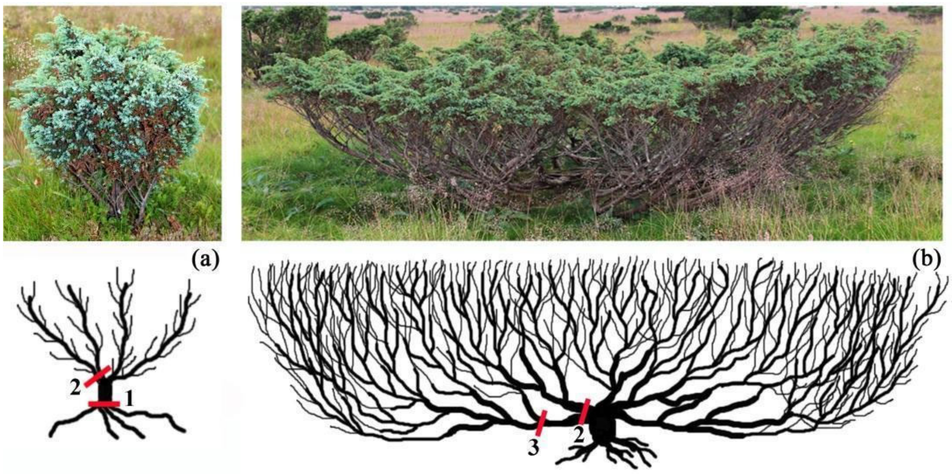


Figure 4. Age determination diagram for young (**a**) and mature (**b**) individual plants of *J. sibirica* showing the saw-cut lines: 1—near the hypocotyl, 2—in the area where the stem splits into plagiotropic branches, and 3—in other areas of the plagiotropic branch.

Cross-sections were air dried and polished. In the case of cores, they were air dried, glued onto wooden bases and scraped off with a razor blade. For a better visualization of tree rings, all wood samples were whitened with dental powder. To determine the year of establishment and, in some cases, death, as well as the exact age of the shrub, the tree ring dating methods were used to identify false and missing rings and to associate individual chronologies with the calendar scale [42,43]. Previous studies [44] showed that spruce tree species and *J. sibirica* growing under the same conditions during the same years react similarly to both favorable and extreme climatic events. To facilitate the identification of false and missing rings in the collected samples of *J. sibirica,* a generalized tree ring chronology was prepared using core samples from live trees of *Picea obovata* Ledeb. Tree rings were measured with a 0.01 mm resolution using LINTAB (F. Rinn, Heidelberg, Germany). We decided to group age data into 5-year classes to reduce the uncertainty of age estimates. In addition, this grouping is justified because the cone formation cycle of *J. sibirica* lasts 2–3 years [45] and, because of the delay in seed germination, seedlings establish 2–3 years after seed dispersal [46].

It is worth noting that shrubby and woody vegetation growing on all altitudinal transects were not exposed to fires over the past 150 years, since we did not find any signs of fire disturbance (fire scars or soil charcoal). In addition, we did not observe dieback of sampled *J. sibirica*, and cattle grazing was also absent in the surveyed areas.

2.3. Climate Data

We used climate data (temperature and precipitation) from representative local stations. In the Northern Urals, several meteorological stations were considered: (1) Troicko–Pecherskoe (62°42′00″ N, 56°11′00″ E, 136 m; with 1888–2015 and 1936–2015 periods for temperature and precipitation data, respectively; located at about 200 km from study sites); and (2) Cherdyn (located 120 km away from study sites). In the Southern Urals, the uniqueness of the Taganay–Gora station lies in the fact that it was located on the summit of Dalniy Taganay, in the immediate vicinity of our test plots (55°22′00″ N, 59°55′00″ E, 1102 m a.s.l.; with 1837–2012 and 1876–2012 periods for temperature and precipitation data, respectively). Climate data were taken from the Russian Roshydromet database (http://meteo.ru/data accessed on 10 January 2022) and the Monthly Meteorological Tables [47]. The data on the total amount of precipitation were corrected for wetting and changing of instruments [48,49].

For the analysis of climatic data, warm (June–August) and cold (November–March) seasons were considered. The choice of the warm period corresponded to the phase of the most active growth of trees and shrubs in the study areas, when daily temperatures are above 5 °C. The cold period included months with an average air temperature below 0 °C and a relatively stable snow cover depth. Anomalies of climatic parameters in the warm and cold periods of each year were determined through the deviation of the current value from the mean in the reference period 1961–1990 and considering 5-year periods. Linear regression models were built to assess trends in climatic anomalies.

2.4. Associations between Climate and Juniper Recruitment

We analyzed the relationships between the number of *J. sibirica* appearing over the 5-year periods and the average values of climatic variables (mean temperature and total precipitation) for the current and shifted 5-year periods in different intervals of the year (separate months, warm and cold periods, and the beginning of the cold period). These analyses were carried out for each study area. The shift by 5 years means that the weather time series has been shifted relative to the time series of *J. sibirica* recruitment (for example, +5 or −5 years). The choice of the comparison period is caused by the current 5-year period corresponds to the process of seed germination and first years of growth, the previous 5 years characterizes the conditions for the cone formation cycle of the maternal individuals, the next 5 years corresponds to the most vulnerable stage for the seedling survival.

We assessed the relationships between climate and recruitment using the nonparametric Spearman correlation coefficient (*Rs*), since the distributions of data differed from a normal distribution according to Shapiro–Wilk tests.

3. Results

3.1. Altitudinal Changes in Shrub Size and Density

In total, 2262 *J. sibirica* shrubs and 804 trees were measured. There was a decrease in the height of *J. sibirica* by 1.5–2 times, whereas the diameter of the crown was reduced 1.5–3 times, as elevation increased (Table 2). The heights of *J. sibirica* ranged from 0.13–0.95 m, crown diameters ranged from 0.36–3.84 m, and *J. sibirica* density varied from 234 to 3270 ind ha^{-1}. The density of *J. sibirica* reached maximum values in the Southern Urals. In comparison, tree density in the Southern Urals varied from 775 to 3820 ind ha^{-1}. The heights of tree saplings ranged from 0.62–1.18 m.

Table 2. Structure data of *J. sibirica* sampled in the two study regions. Values are means ± SD.

Variables	Altitudinal level	Northern Urals					Southern Urals			
		Molebnyi Kamen′	Zyryanovka I	Zyryanovka II	Kvarkush I	Kvarkush II	Taganay	Nurgush	Zigalga	Iremel
Height (m)	High	0.49 ± 0.15	0.36 ± 0.02	0.39 ± 0.02	0.44 ± 0.02	0.44 ± 0.02	0.13 ± 0.01	0.15 ± 0.01	0.20 ± 0.02	0.22 ± 0.02
	Mid	-	0.56 ± 0.02	0.40 ± 0.02	0.48 ± 0.03	0.76 ± 0.04	0.31 ± 0.02	0.24 ± 0.01	0.71 ± 0.03	0.27 ± 0.01
	Low	-	0.88 ± 0.03	0.82 ± 0.02	0.66 ± 0.03	0.95 ± 0.04	-	-	-	-
Crown diameter (m)	High	1.26 ± 0.49	0.87 ± 0.05	1.18 ± 0.06	0.66 ± 0.03	1.19 ± 0.10	0.41 ± 0.02	0.36 ± 0.02	1.79 ± 0.12	1.24 ± 0.07
	Mid	-	1.55 ± 0.08	1.17 ± 0.05	0.76 ± 0.04	1.47 ± 0.11	0.75 ± 0.07	1.21 ± 0.09	3.53 ± 0.21	2.07 ± 0.12
	Low	-	3.84 ± 0.23	3.63 ± 0.17	1.26 ± 0.09	1.73 ± 0.14	-	-	-	-
Density (ind ha^{-1})	High	417	614	510	738	234	665	3270	720	625
	Mid	-	1600	1366	967	488	1300	1230	590	619
	Low	-	420	476	782	540	-	-	-	-

A decrease in the density of *J. sibirica* was observed as we moved upward in both the Northern and Southern Urals. A similar decrease in tree height and density was also observed in the Southern Urals with increasing elevation (Figure S1). At higher positions, the trees were also smaller and more sparsely distributed in the Southern Urals.

3.2. Age Structures of Shrubs and Trees

In the Northern Urals, the oldest sampled *J. sibirica* recruited in the mid-19th century at the low elevation plots of Zyryanovka, and they kept recruiting until the second half of the 20th century without pronounced peaks (Figure 5). At mid elevation, the first *J. sibirica* recruited from the second half of the 19th century until the early 20th century, and this was followed by massive recruitment in the 1940s, 1950s, 1960s, and 1980s. At the high elevation, recruitment started in the early 20th century and peaked in the 1950s and 1970s.

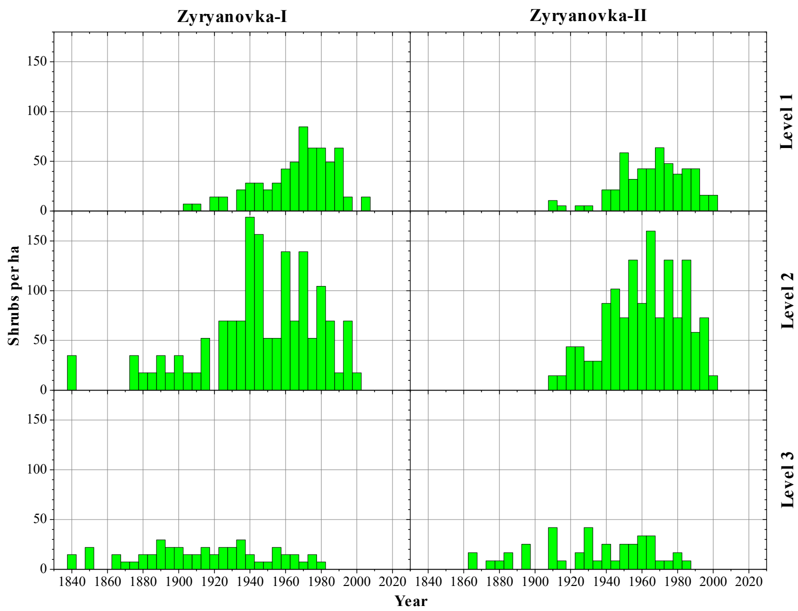


Figure 5. Age structures of *J. sibirica* at three altitudinal levels in Zyryanovka, Northern Urals. Levels 1, 2, and 3 correspond to the high, mid, and low elevations, respectively.

On the Kvarkush ridge, *J. sibirica* recruitment was first observed in the second half of the 19th century (Figure 6). Recruitment was very intense in the 1980s and 1990s, particularly in the first transect at low and mid elevation. At high elevation, recruitment also peaked in the 1980s and 1990s.

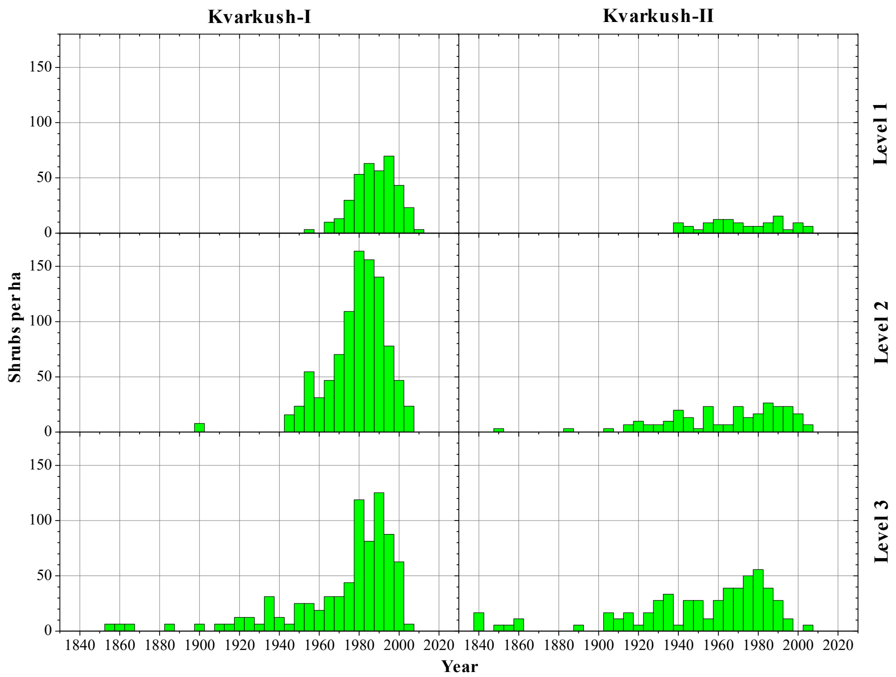


Figure 6. Age structures of *J. sibirica* in Kvarkush, Northern Urals. Levels 1, 2, and 3 correspond to the high, mid, and low elevations, respectively.

Shrubs of *J. sibirica* most intensively recruited in the uppermost parts of Molebnyi Kamen' from 1935 to 1990 (see Figure S2).

In the Southern Urals, on the Nurgush and Taganay mountains, *J. sibirica* recruitment started after the 1930s at low elevations and peaked from the 1970s to the 1990s (Figure 7). At the highest elevations, recruitment peaked from 1990 to 2005.

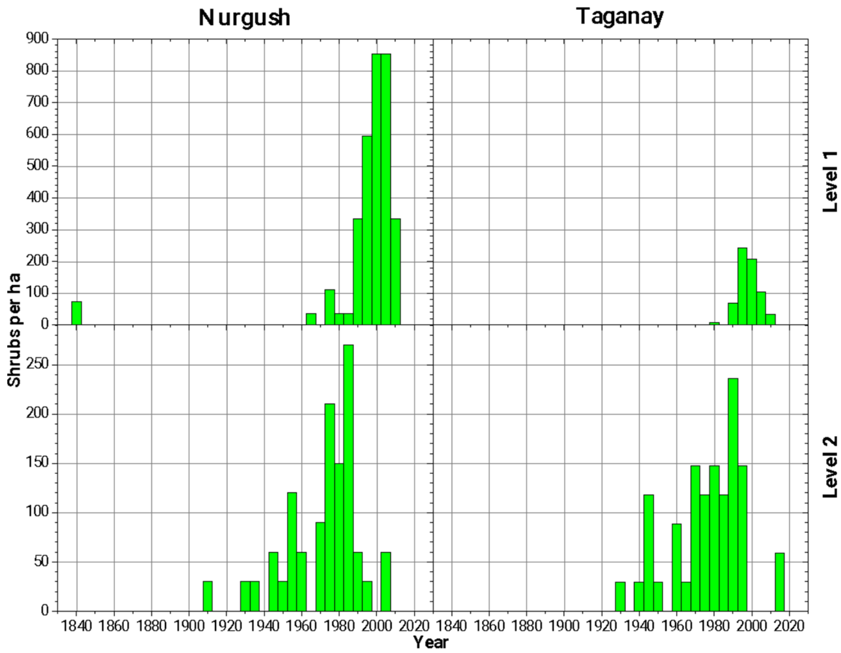


Figure 7. Age structures of *J. sibirica* on Nurgush and Taganay, Southern Urals. Levels 1 and 2 correspond to high and mid elevations, respectively.

In Iremel, recruitment peaked in the 1920s and 1950s at low and high elevations, respectively (Figure 8). The oldest *J. sibirica* shrubs were recruited in the mid-19th century and in the high elevation plots. In Zigalga, the first recruited *J. sibirica* individuals were dated from the early 19th century and were located at low elevation (Figure 8). Recruitment intensified in the 1960s at high elevations in this site.

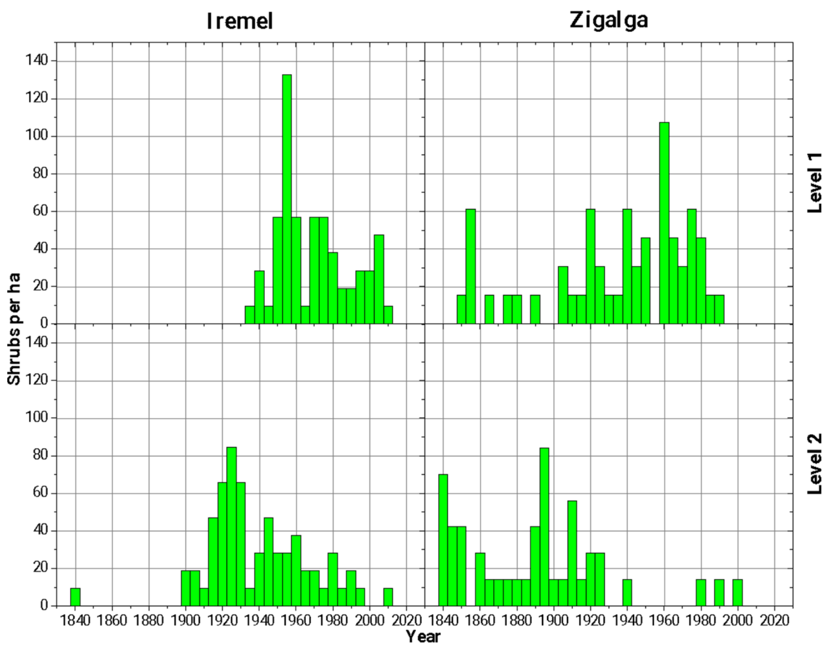
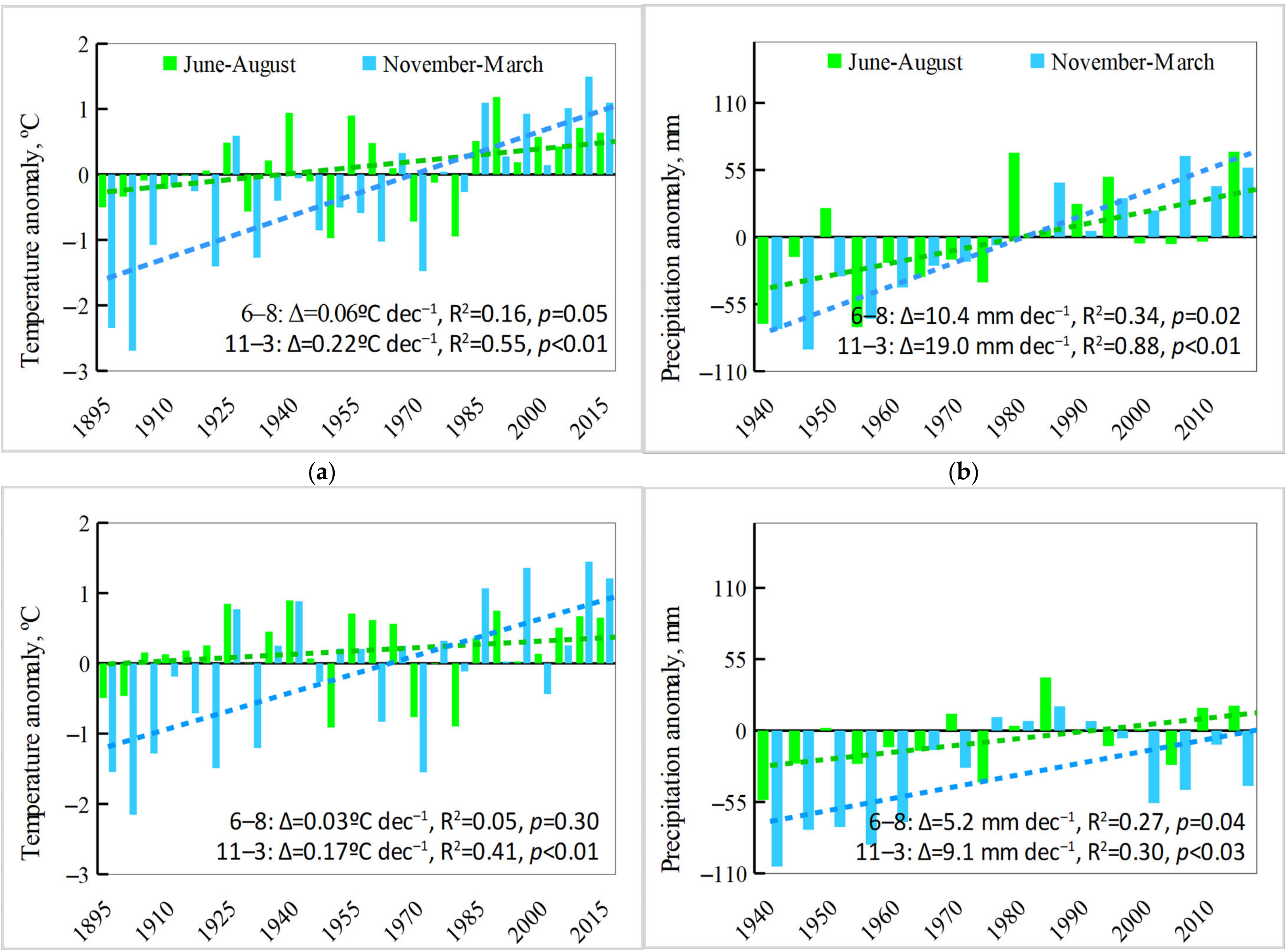


Figure 8. Age structures of *J. sibirica* on Iremel and Zigalga, Southern Urals. Levels 1 and 2 correspond to high and mid elevations, respectively.

In the Southern Urals, trees started recruiting in the second half of the 20th century and recruitment peaked in the 1990s and 2000s, particularly at high elevation; albeit, it was also observed downslope on Taganay (Figure S3).

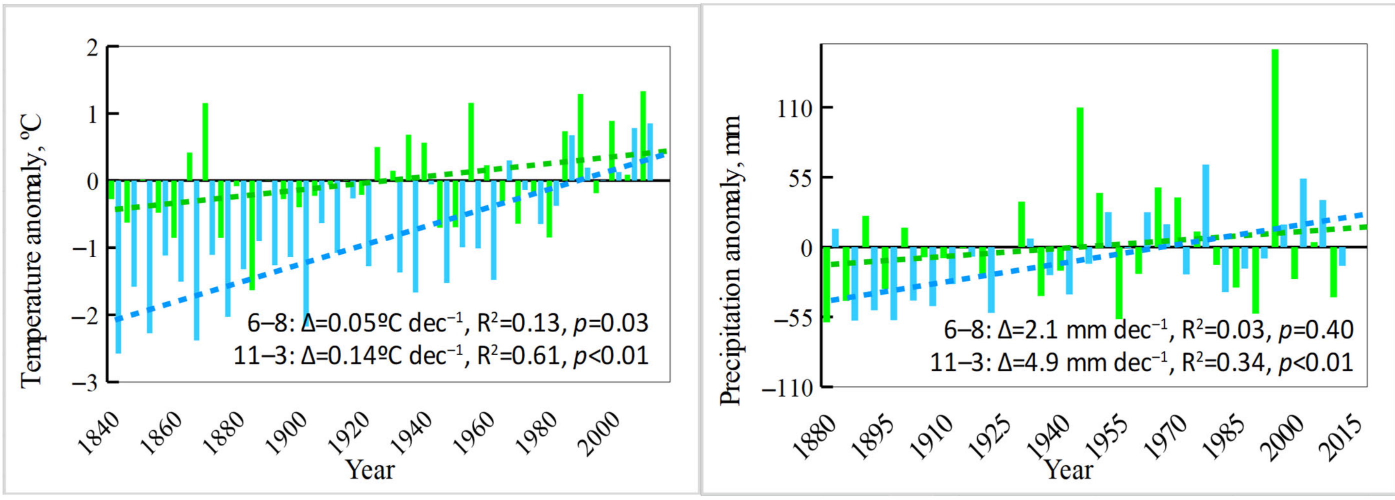
3.3. Analysis of Climate Trends

The mean air temperature of the warm season significantly increased in the Cherdyn' and Taganay–Gora stations located in the Northern and Southern Urals, respectively (Figure 9). There was also a rise of temperature in the cold season, and this rise was higher than in the warm period. The greatest warming rate was recorded for the Cherdyn' weather station, while during the months of the cold period, the increase in air temperature was three times faster compared to the warm-season warming (0.22 °C decade^{-1} vs. 0.06 °C decade^{-1}).



(**a**) (**b**)

(**c**) (**d**)



(**e**) (**f**)

Figure 9. Anomalies of mean temperature and total precipitation for warm (June–August) and cold (November–March) seasons, grouped by 5-year periods, for the following stations: Cherdyn' (**a**,**b**) and Troicko–Pecherskoe (**c**,**d**), Northern Urals, and Taganay–Gora (**e**,**f**), Southern Urals. Anomalies are relative to the mean values of the 1961–1990 period. The dotted lines show linear trends. Statistics correspond to these linear regressions.

The maximum increase in precipitation was observed in stations of the Northern Urals in the cold and warm seasons. However, the increase in precipitation was almost two times larger in the cold than in the warm season (Cherdyn' station, 19.0 mm decade $^{-1}$ vs. 10.4 mm decade $^{-1}$; Troicko–Pecherskoe station 9.1 mm decade $^{-1}$ vs. 5.2 mm decade $^{-1}$). In the Southern Urals, the cold-season precipitation also increased in the Taganay–Gora station.

3.4. Relationships between Climate Variability and Shrub Recruitment Depend on Site and Altitude

The strongest correlations between climate variables and shrub recruitment corresponded to the Northern Urals, particularly considering the cold-season precipitation (Table 3), and less often with summer (June to August) temperature. Strong correlations were also found between precipitation in the early cold season and *J. sibirica* recruitment. For instance, in Kvarkush I high-elevation plots, these correlations were significant considering current (R_S = 0.78, p = 0.001) and previous 5-year periods (R_S = 0.80, p = 0.001), respectively. Comparatively, in this site the highest significant correlation obtained with the warm-season precipitation corresponded to total *J. sibirica* recruitment regardless of altitude (R_S = 0.57, p = 0.03, current 5-year period). In Zyryanovka, Northern Urals, associations with climate variables were mainly observed in high-elevation plots.

Table 3. Spearman correlation coefficients calculated by relating the number of recruited *J. sibirica* shrubs on different altitudinal levels and climate variables. Correlations were calculated for 5-year periods in the cold (November–January) and warm (June–August) seasons. Significant values at p < 0.05 are indicated in bold.

Region	Site	Altitudinal Level	Precipitation				Temperature			
			Corresponding Period		Shifted Period		Corresponding Period		Shifted Period	
			Cold	Warm	Cold	Warm	Cold	Warm	Cold	Warm
Northern Urals	Molebnyi Kamen'	High	0.12	−0.46	0.27	0.16	0.06	−0.07	−0.07	−0.18
	Zyryanovka I	High	**0.59**	0.21	**0.71**	0.42	0.07	0.01	−0.35	**−0.46**
		Mid	−0.25	−0.15	−0.16	−0.10	**0.46**	0.09	0.17	−0.12

		Low	−0.41	**−0.68**	−0.18	−0.24	0.10	0.16	−0.06	0.02
		All	−0.11	−0.20	0.23	0.19	0.39	0.14	0.07	−0.30
	Zyryanovka II	High	0.21	0.31	**0.70**	0.44	−0.08	−0.25	−0.18	−0.28
		Mid	0.03	−0.45	0.46	−0.04	0.39	0.11	0.02	−0.35
		Low	−0.36	−0.30	−0.08	−0.29	0.21	0.05	−0.15	0.02
		All	−0.01	−0.27	**0.59**	0.09	**0.47**	0.15	0.09	−0.20
	Kvarkush I	High	**0.79**	**0.81**	**0.86** *	0.57 *	0.21	0.04	−0.05 *	0.06 *
		Mid	**0.59**	0.34	**0.63** *	0.30 *	0.16	0.11	0.04 *	−0.46 *
		Low	**0.62**	**0.60**	**0.72** *	0.42 *	0.25	0.25	0.30 *	−0.02 *
		All	**0.78**	**0.57**	**0.80** *	0.40 *	0.30	0.24	0.31 *	0.09 *
	Kvarkush II	High	−0.07	−0.34	0.24 *	−0.04 *	−0.25	**0.61**	**0.69** *	0.00 *
		Mid	0.26	0.13	**0.64** *	0.53 *	0.20	0.43	0.40 *	−0.02 *
		Low	0.18	0.12	−0.11 *	−0.45 *	−0.08	−0.43	−0.02 *	−0.24 *
		All	0.23	0.13	0.17 *	−0.27 *	0.02	−0.01	0.28 *	−0.06 *
Southern Urals	Taganay	High	0.77	0.60	0.60	0.49	−0.09	−0.03	0.09	−0.09
		Low	−0.36	0.27	0.38	0.23	−0.08	−0.32	0.00	−0.14
		All	0.03	0.18	0.48	0.14	0.16	−0.11	0.38	0.05
	Nurgush	High	0.66	−0.15	−0.03	−0.12	0.08	0.65	0.55	0.39
		Low	−0.20	−0.24	0.08	−0.24	0.04	−0.09	−0.01	0.13
		All	0.43	−0.13	0.24	−0.13	0.42	0.19	**0.50**	0.29
	Zigalga	High	0.03	0.27	0.11	0.24	0.01	−0.16	0.23	−0.24
		Low	**−0.50**	−0.35	−0.31	0.14	**−0.41**	−0.11	−0.28	−0.13
		All	−0.21	0.08	−0.04	0.36	−0.24	−0.20	0.05	−0.38
	Iremel	High	0.16	−0.07	0.33	−0.26	0.01	−0.07	0.06	0.07
		Low	−0.38	0.15	0.20	0.25	−0.11	−0.16	−0.38	−0.17
		All	0.14	0.05	**0.45**	−0.05	0.13	−0.05	−0.03	0.02

Note. The relationship between the number of recruited *J. sibirica* shrubs over five years and the meteorological data of the current and shifted periods is analyzed. The shift to the next five years was mainly used; * marks the calculations based on the meteorological data of the previous five years. Data from the following weather stations are used for the study sites: (i) Cherdyn for Molebnyi Kamen' and Kvarkush I–II; (ii) Troicko–Pecherskoe for Zyryanovka I–II; (iii) Taganay–Gora for Taganay, Nurgush, Zigalga, and Iremel.

In the Southern Urals, a similar pattern was found with strong associations between recruitment and cold-season precipitation; albeit, they were marginally significant (p = 0.07). For instance, this was found at the high-elevation plots in the Taganay and Nurgush sites. In Iremel, a positive association was found between the shifted cold-season precipitation and shrub recruitment considering all altitudinal positions.

4. Discussion

Our research shows evidence that there was an intensive upward expansion of the shrub *J. sibirica* during the last century on seven mountains located in the Northern and Southern Urals. This process occurred at a large geographical scale since the most distant sampled peaks were separated by 750 km. This suggests that the upslope shift of shrubs and their encroachment into tundra were driven by regional climate variability. The upward decrease in size and age of *J. sibirica* shrubs confirm that their recruitment is spatially organized with younger individuals being recruited more recently at higher elevations. Shrubs of *J. sibirica* most intensively recruited in the second half of the 20th century, particularly in the 1990s, and in the uppermost parts of the sampled mountain transects. Considering also that shrub recruitment peaks occurred in similar periods among distant mountains, particularly considering the upper parts of the slopes forming the shrubline, this further confirms that the main drivers of the observed changes in shrub dynamics were changing climatic conditions.

The analysis of data from meteorological stations, sometimes located very close to the study areas such as the Taganay–Gora station, indicates that the climate in the Northern and Southern Urals has become warmer and more humid, particularly in winter.

The research results show that, at present, there is a widespread recruitment of *J. sibirica* not only on slopes, but also on convex areas of mountains, where in winter a significant part of the snow cover is blown away by the wind (see Table 1). A similar situation was observed in north-eastern Canada [50] and in the Urals [5], and in both regions there are active processes of shrub encroachment (shrubification) into tundra [21].

Several works have shown that winter conditions drive the survival, recruitment, and growth of shrubs in cold alpine and arctic biomes [10,16,24,51,52]. Our findings concur with those studies as they confirm the high correlations detected between *J. sibirica* recruitment and current and shifted cold-season precipitation. Moreover, the highest correlation coefficients were obtained in the uppermost parts of the coldest Northern Ural sites. This indicates the importance of snow cover for the growth and survival of shrubs, as it protects needles and shoots from snow abrasion and from free-thaw embolism in these harsh environment conditions [53]. It is known that snow cover is one of the most important buffering factors that control the microclimate and may ameliorate plant growing conditions in alpine and Arctic ecosystems [54]. Snow cover protects plants from extreme winter winds and temperatures and also from sharp changes in air and soil temperature [55] (see Figure S4–S6). Even a short-term decrease in the depth of snow cover as a result of warming in the winter season can also lead to damage of shrubs [56]. We observed a similar phenomenon after the dry 2008–2019 winter with frequent freeze–thaw cycles on Dalniy Taganay (Southern Urals). Due to the lack of snow cover, *J. sibirica* underwent snow abrasion and frost desiccation, and showed extensive canopy dieback and severe damage over a large area (A. Grigoriev, *pers. observ.*, Figure S7*).* Such dieback probably leads to reduced growth in spring since most of the foliage must be rebuilt. Regarding growth, it has been shown that snow cover can influence the radial growth of deciduous shrubs (*Salix arctica*) in Greenland [57] and evergreen shrubs (*Juniperus communis*) in the Alps [52].

Snow cover increased the survival rate of shrubs, as described for willow in the Rocky Mountains [22]. In alpine ecosystems where snow is redistributed by the wind, seedlings may also be exposed to atmospheric temperatures rather than be protected by an insulating snow cover, and hence there may be an increase in winter mortality on open ridges [54,58].

Decreased snow cover can also reduce the rate of decomposition and limit N availability in the tundra [31,59]. In areas with shallow snow cover, low soil temperatures limit soil nitrogen mineralization, and in areas with high snow depth, higher winter soil temperatures increase winter nitrogen mineralization and thereby alter the amount and timing of nitrogen intake available to tundra plants [60]. Therefore, a deep snowpack can promote winter decomposition and nutrient release in spring [61]. Overall, the higher the snow depth, the lower the possibility of freezing temperature in the soil and the less damage to the shrub root system [62,63].

The high correlations found between *J. sibirica* recruitment temperature and precipitation in the cold season in the Southern Urals can be explained by the fact that the amount of precipitation is relatively low, and this may make *J. sibirica* growth more dependent on winter temperatures, snow melting, and rapid soil warming. For example, in western Greenland, *Betula nana* showed a positive growth response to both summer and winter air temperatures, and its growth was primarily enhanced by higher winter and spring temperatures, causing earlier snow melting, which allows soil to dry out and warm up faster [64]. This was also observed in other Arctic regions where willow growth increased after the 1980s because of the rise in winter temperatures [34].

In addition to upward shrubline shifts, treelines also shift upslope; albeit, we noted some time lags between starts of shrubline and treeline dynamics. This may be due to the fact that *J. sibirica* is a species that forms open, multi-stemmed horizontal crowns, which are more resistant to damage by strong winter winds as compared with the uni-stemmed, vertical crowns of tree saplings [53].

5. Conclusions

We present strong evidence of the advancement of the shrubline in the Ural Mountains where shrubs are actively encroaching into the tundra. Data based on long-term changes in weather across regional weather stations suggest that wetter and warmer cold-season conditions likely play a role in this rapid change in the shrub cover. Study of the actual climate conditions of the alpine and subalpine areas of the Urals is required to fully establish this hypothesis. If *J. sibirica* recruitment and growth continues to increase over the following decades, a more dense and closed cover of *J. sibirica* shrublands may form on selected areas of mountain peaks, mainly on convex slopes at high elevation. This can significantly affect the tundra vegetation and alter the landscape structure and ecosystem processes. The results of this study allow the reconstruction of the rates and modes of transformation of alpine and arctic woody plant communities. This is a first and necessary test to produce reliable forecasts of future environmental changes in similar cold, treeless biomes. Finally, our findings are particularly relevant given that the Arctic regions are warming at a mean rate four times higher than the rest of the world [65].

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/f13122106/s1: Figure S2: Age structures of *J. sibirica* at high altitudinal level in Molebnyi Kamen', Northern Urals.; Figure S3: Age structures of trees in the Southern Urals study areas, excepting Zigalga where no trees were found in the sampled plots. Levels 1 and 2 correspond to high and mid elevations, respectively; Figure S4: Landscape photographs taken on Zyryanovka (Northern Urals) in different seasons of the year; Figure S5: Landscape photographs taken on Zyryanovka (Northern Urals) in different seasons of the year; Figure S6: Landscape photographs taken on Zyryanovka (Northern Urals) in different seasons of the year; Figure S7: Massive dieback of J. sibirica on the convex slope of the Dalniy Taganay, Southern Urals; Table S1: Structure data of tree species sampled in in the Southern Urals. Values are means ± SD.

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