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Expansion of *Juniperus sibirica* Burgsd. as a response to climate change and associated effect on mountain tundra vegetation in the Northern Urals

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Abstract: Shrub expansion into arctic and alpine tundra is one of the prominent vegetation changes currently underway. We studied the expansion of shrub vegetation into high elevation tundra in the Kvarkush Range of the Northern Ural mountains, Russia. Age structure analysis of the dominant shrub *Juniperus sibirica* Burgsd. seems to support ongoing upslope advance of shrubs, a process particularly active in the second half of the 20th century. We found a close connection between the expansion of shrub vegetation and the general change in climatic conditions of the cold season (months with mean air temperature below 0°C from November to March). In general, the greatest influence on the distribution of *J. sibirica* is exerted by the climate conditions of the beginning (November-January) and the end (March) of the cold season. With increasing elevation, the correlation coefficients between the establishment of *J. sibirica* shrubs and the precipitation of the beginning of the cold season increased, and reached maximum values at the top elevation level of the study area. However, the upwards shift of *J. sibirica* into typical mountain tundra does not lead to changes in the ecological structure of vegetation at this stage, but simply a decrease in the area of mountain tundra.

Keywords: *Juniperus sibirica*; Expansion; Tundra; Vegetation; Plant communities; Climate changes; Northern Ural mountains

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Introduction

Each of the last three decades was characterized by higher temperature near the Earth's surface than any previous decade since the 1850s (IPCC 2013). Plant communities growing under conditions characterized by large amplitudes of daily temperatures and a lack of soil moisture, such as in high mountain areas, are very sensitive to climate change (Myers-Smith 2007; Seddon et al. 2016; Scharnagl et al. 2019), which can lead to significant transformations of the structure of plant communities (Gorchakovskiy and Shiyatov 1985; Pauli et al. 2001; Kullman and Öberg 2009). High-mountain and high latitude regions are therefore well suited to assess the influence of climatic changes on the formation and growth of vegetation communities (Harsh et al. 2009; Hallinger et al. 2010; Myers-Smith et al. 2015).

Of special interest is the transition between high elevation forest and alpine tundra ecosystems, the treeline ecotone, where numerous facets of spatio-temporal changes in the elevation of forest vegetation have been reported from all over the world (see the meta-analysis in Harsch et al. 2009; Chersich et al. 2015). In Russia, most large-scale studies of this kind were conducted on the eastern side of the Ural Mountains, where widespread changes in the composition, structure, and elevation of upper treeline stands from southern to polar Urals were noted (Shiyatov 1983, 1993, 2005, 2009; Moiseev 2002; Moiseev et al. 2004, 2010; Shiyatov et al. 2007; Devi et al. 2008; Kharuk et al. 2008, 2010; Hagedorn et al. 2014; Mazepa and Shiyatov 2014; Shiyatov and Mazepa 2015). These studies identified an increase in temperature and precipitation in the winter period as the main driver of ecological change.

Most research aimed at studying the expansion of shrub vegetation, which usually forms a transitional band between upper forest limit and alpine tundra, were carried out mainly in Arctic tundra ecosystems (see meta-analysis by Myers-Smith et al. 2011). In northern alpine regions, such studies are rare (but see Dial et al. 2007, 2016; Hallinger et al. 2010; Rundqvist et al. 2011; Upshall 2011; Myers-Smith and Hik 2017). Studies of shrub vegetation in the Urals were mainly dendrochronological (Hantemirov et al. 2011; Shetti et al. 2018a,b). Even though preliminary results on *J. sibirica* expansion in the southern part of the Ural Mountains exist (Grigor'ev et al. 2018), driving forces of shrub vegetation dynamics are still poorly understood (Myers-Smith and Hik 2017). Also the consequences of shrub species invasion into tundra vegetation in high mountain areas are not sufficiently established (Sturm et al. 2005; Greenwood and Jump 2014).

The influence of shrub vegetation change on Arctic and alpine tundra has been studied mainly with a focus on deciduous shrubs (*Alnus sp., Betula sp., Salix sp.*). Some studies point out that special microclimatic conditions form under shrub canopy (Walker et al. 2006; Pajunen et al. 2011; Elmendorf et al. 2012; Tsuyuzaki et al. 2012). For example, shrub invasion can lead to faster nutrient cycling (Tape et al. 2006, 2012; Vojík and Boublík 2018), plant community change (Pajunen et al. 2011; Vojík and Boublík 2018), increase in air and soil humidity due to the later snow melt, a reduction of eolian draining and insolation, and a decrease in daily and seasonal fluctuations of soil and subsoil temperatures (Elmendorf et al. 2012; Tsuyuzaki et al. 2012; Vojík and Boublík 2018).

Here we have chosen the understudied regions of the Russian Urals, especially the Kvarkush Range, to ask the following three questions: 1) Does shrub vegetation advance along elevational gradients? 2) Is there a relationship between the expansion of shrub and recent climate change? 3) Does the advance of shrub vegetation lead to a change of species composition and structure of tundra plant communities beyond the invasion of shrubs?

In this study, we did the following: 1) analysis of age structure and morphometric traits of *J. sibirica* growing at different elevations above treeline; 2) analysis of changes in climatic conditions and its connection with the expansion of shrubs; 3) an assessment of the composition and structure of mountain tundra plant communities with different percentages of *J. sibirica*.

1 Materials and Methods

1.1 Study area

The study took place in the Kvarkush Range (60.20°N, 58.73°E), one of the branches of the dividing Ural range on the western side of the Northern Urals (Figure 1). The Kvarkush Range is a 12–15 km wide flat-topped mountain range running 60 km from north to south. The summit of the range is a mountain plain at the elevation of 750–850 m above sea level. The highest peak of the range is Mount Vogulsky Kamen – 1066 m.

The climate in the region is temperate continental, with long winters and short (2 months) summer. The climate is strongly affected by winds bringing moisture from the Atlantic Ocean. The Ural Mountains act as a natural barrier affecting precipitation patterns (Belkovskaya et al. 2014). The average annual air temperature is -2.0°C, the average January temperature is -19.0°C (the absolute minimum is more below than -50°C); July temperature is about +15°C. In winter, temperature inversions are common in the mountains with the prevalence of south-west, west and south winds. Winds in summer are mainly from the north and east. The entire region is characterized by large snow packs. The total duration of the snowy period is about 200 days (Voronchikhina 2000).

The main high-elevation plant communities form elevational belts within the range: mountain forest, light forest with mesic meadows and mountain tundra. The upper limit of the forest consists of *Picea obovata* Ledeb. with some percentage of *Betula pubescens* Ehrh. ssp. *tortuosa* (Ledeb.) Nyman, and above, vast areas are occupied by *J. sibirica* communities (Appendix 1). The mountain tundra belt includes different types of tundras (shrub tundra, shrub-moss tundra, sedge tundra, sedge-herb tundra, dwarf shrub

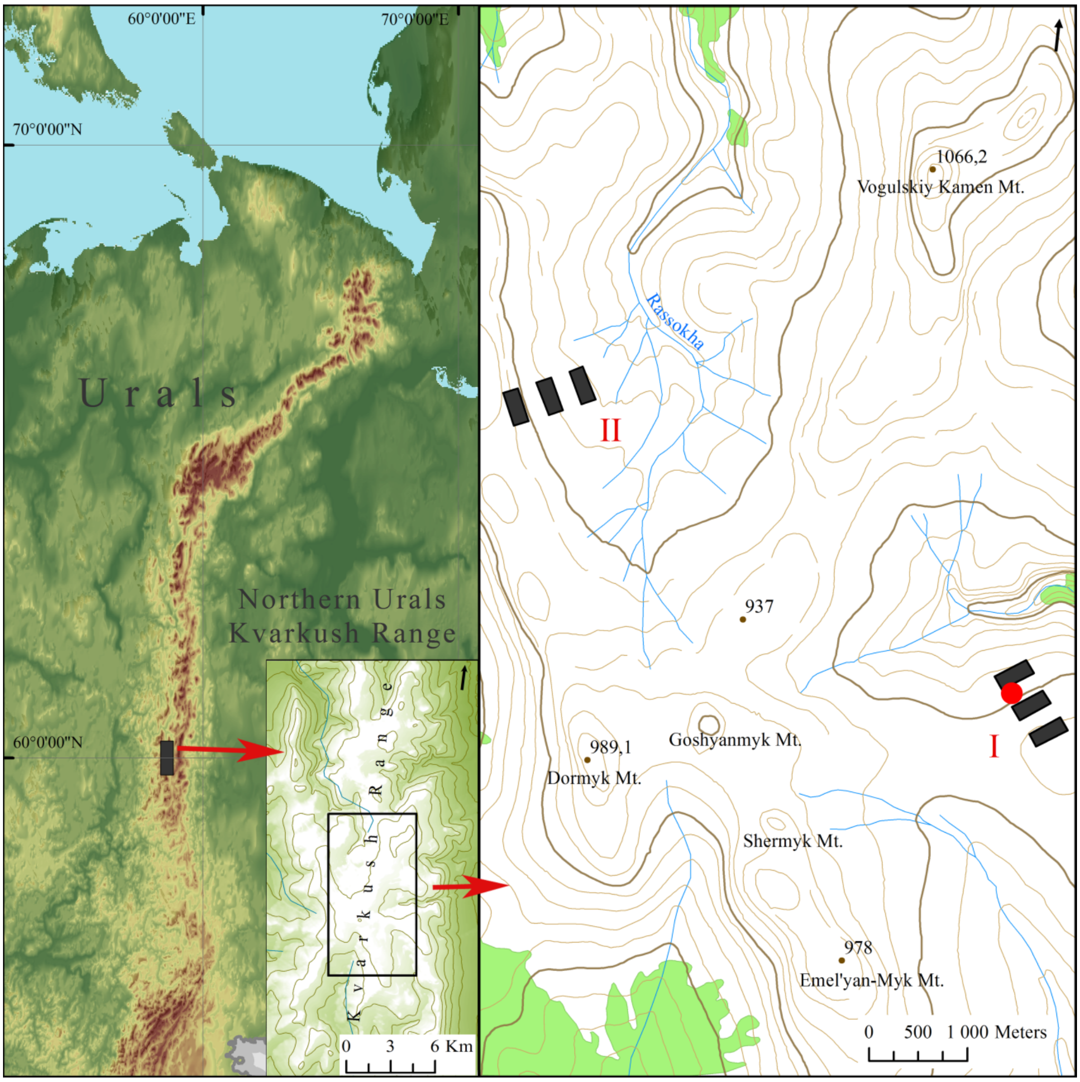

Figure 1 Schematic map of the study region indicating the location of I, II elevational transects (black rectangles) and the geobotany survey area (green oval).

tundra, moss-dwarf shrub tundra, grass-moss tundra, and stony tundra) and mountain bogs (Gorchakovskiy 1975; Ovesnov et al. 2010). In the Kvarkush Range, most often, the elevational belt of *J. sibirica* shrubs represents a transition zone between the upper boundary of the distribution of thin spruce forests and closed *J. sibirica* shrubs (in the bottom part of the belt) and individual *J. sibirica* shrubs in the tundra (in the top part of the belt).

In the study area, thin mountain-tundra soils (12–25 cm) prevail, in which the upper horizon is humus-peaty, contains skeleton elements and has a pronounced acidity. In addition, there are mountain-tundra sod soils, as well as transitional and initial soils, which are found in the mountain tundra belt. Mountain-tundra soils are characterized by a high peat content in the sod horizon, increased acidity and a small amount of absorbed calcium and magnesium (up to 2.9 mEq / 100 g) (Korotaev 1962; Gafurov 2008).

1.2 Elevational transects and morphometric traits

We used elevational transects to study the age structure of *J. sibirica*. In July 2017, two elevational transects were set up in the Kvarkush Range (near Mount Dormyk), above the upper limit of open forests, one with north-eastern and one with north-western exposure (Figure 1). Transect I covered the topmost pass part of the slope. On each elevational transect, the study plots were arranged on three levels (Figure 2): 1) the bottom level – near the upper distribution boundary of *J. sibirica* shrubs (density from 40% to 20%), 2) the middle level – near the upper boundary of sparse *J. sibirica* shrubs (from 20% to 5%), and 3) the top level – near the upper boundary of individual *J. sibirica* shrubs (< 5%).

Two or three permanent study plots of 20 m × 20 m were arranged at each elevation level along the slope. Wooden stakes (up to 1.5 m) were driven into the soil or stone pyramids were constructed at the corners and in the center of the study plots. The exact location (using an aiming circle and a measuring tape) and the plant height were measured for every *J. sibirica* in a study area. Crown diameter of every plant was determined in two mutually perpendicular directions using a tape

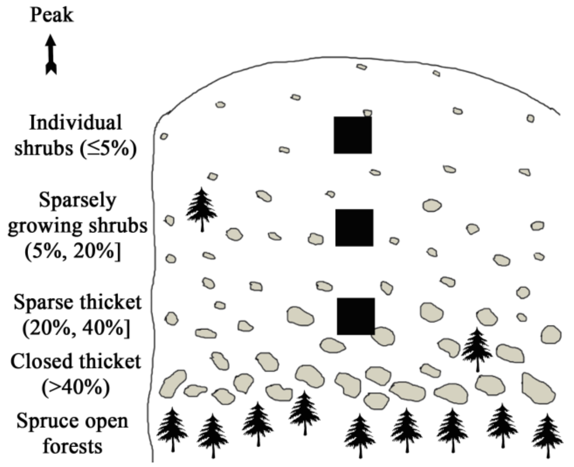

Figure 2 Arrangement diagram of an elevational transect.

measure. 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 (Korchagin 1960; Serebryakov 1962). 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 3, b-2, c-2, d-2) (Grigor'ev et al. 2018). 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 3, a-1) of the stem to the area where it splits into plagiotropic branches (Figure 3, a-2). 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 3, d-3). The shrub age correction factor was determined by studying the growth stage of plagiotropic branches under specific conditions adding a correction for the branch attachment height. In order 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 (Fritts 1976; Shiyatov et al. 2000; Vaganov et al. 2008). Previous studies (Hantemirov et al. 2011) 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

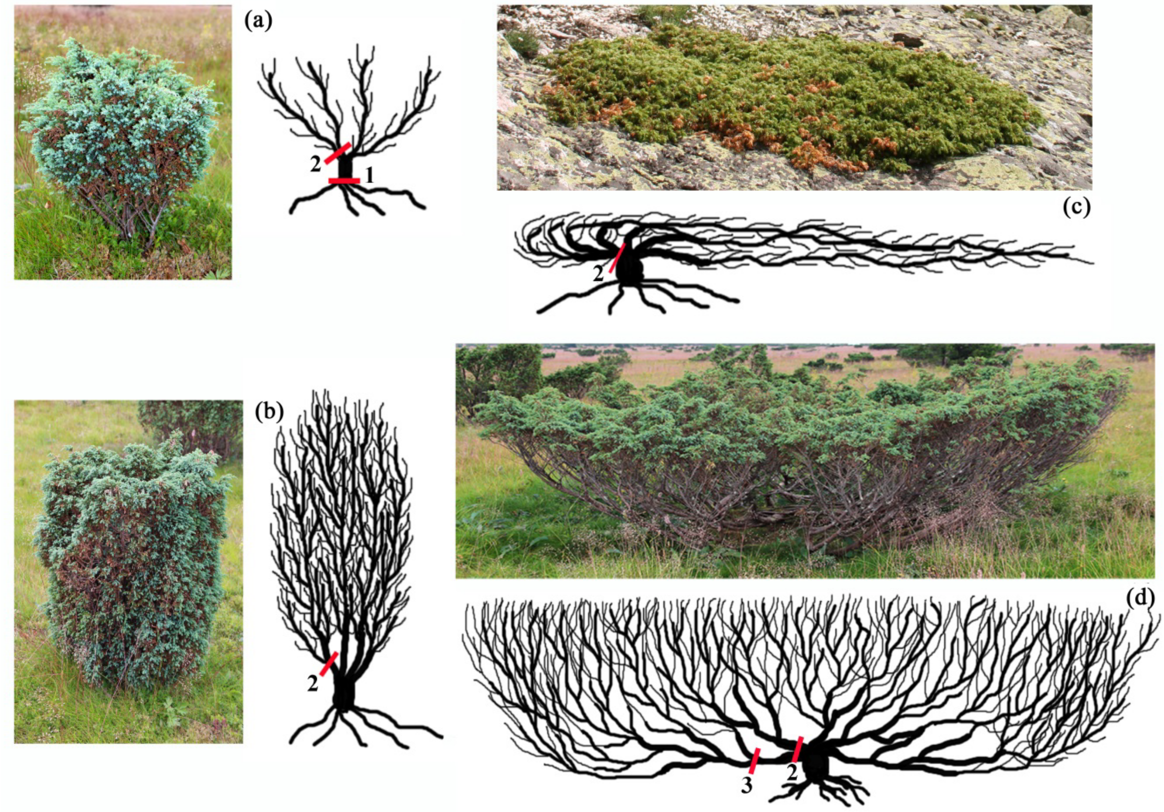

Figure 3 Age determination diagram for *J. sibirica* - young (a) and mature (b, c, d) individual plants showing the saw-cut lines: 1 –near the hypocotyl, 2 – in the area where the stem splits into plagiotropic branches, 3 – in other areas of the plagiotropic branch.

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. To ensure the possibility of comparing the periods of establishment of *J. sibirica*, all the obtained data on age were combined into 5-year groups.

Shrub vegetation growing on both elevational transects has not been exposed to any fires and any other unfavorable factors over the last 150 years (Holtmeier 2009), as we found no signs of fire (fire scars) on the transverse disks. Besides, we did not observe many dried individual plants of *J. sibirica*.

In general, the morphometric traits of 638 individual plants of *J. sibirica* were determined in the Kvarkush Range within the total area of 1.52 ha and we have established the age of 369 plants.

1.3 Climatic data and statistical analysis

We used climate data of the Cherdyn' weather station (60.40°N, 56.52°E, 208 m a.s.l.) 120 km away from the study area. This is a land (fixed) station, which began work in 1883 and is part of the Global Observing System of World Meteorological Organization (station index 23914). We used the data for the Cherdyn' station from specialized databases of Roshydromet (http://meteo.ru/data). The series of observations included: during the years of 1888 to 2015 monthly mean surface air temperature, and during the years of 1936 to 2015 monthly precipitation volume. A series of observations for precipitation was considered from a later period than for air temperature in order to preserve the homogeneity of the data, since in the 1930s Cherdyn' station (like many other weather stations in the USSR) was moved to a more open space. The data on monthly precipitation had corrections of systematic errors due to the change of equipment. The data sample contained gaps: seven values of the average monthly temperature (1899, 1919, 1920, 1948) and twelve values of the total monthly precipitation (1977).

In order to analyze the data of monthly mean air temperature and monthly total precipitation over the whole period of the meteorological observations, the warm (from June to August) and cold (from November to March) seasons were selected. The duration of the warm period was determined by the duration of the active growth phase for juniper, which begins in June in the European northeast and lasts about 3 months (Gerling 2010). The cold period is months with the mean air temperature below 0°C, starting from November (-7.9°C± 3.4°C) and ending with March (-7.3°C± 3.0°C). Anomalies in the average air temperature and the total volume of precipitation in the cold and warm periods of each year were defined through the difference between the current value and the average value in the basic period (1961–1990). Linear regression models were constructed to assess the linear trend in the data on the dynamics of climatic indicators anomalies. Statistical data analysis was performed using the software package Statistica.

Correlation and regression analysis was performed to study the relationship between climatic conditions and the establishment of *J. sibirica*. To assess the strength of the relationship between the average five-year values of climatic parameters and the number of *J. sibirica* shrubs that established on the study plots in five-year periods, the Spearman correlation coefficient (R) was chosen taking into account the fact that almost all variables have normal distributions according to the Shapiro-Wilk test, but the sample size is not large enough. The coefficient of determination (R^2) was used to evaluate multiple regression models based on these data.

Five-year bins of *J. sibirica* shrub establishment is due to the fact that the cone formation cycle of *J. sibirica* is two to three years (Surso and Barzut 2010), and because of the delay in seed germination, shoots appear after another two or three years (Zyryanova et al. 2016). Likewise, temperature and precipitation parameters according to Cherdyn' station for the same or previous five-year periods were taken into account. The analyses covered the mean temperatures (over the period of 1891 to 2000) and the total precipitation (over the period of 1936 to 2000) in the warm and cold seasons of the year and in the individual months that were averaged by the five-year periods. Here we limited ourselves to the period until 2000 in order to include only mature individual plants in the analysis. For young plants, age was not determined, since they can be significantly damaged by the saw cut method.

1.4 Geobotany survey method

In the first ten days of July 2017, 12 vegetation surveys (four series, three relevés each) were made. Three percentage cover grades of *J. sibirica* (from absence to domination) were used: 0% (Group A); 30%–40% (Group B) and 80%–95% (Group C). The 10m×10m plots for geobotany survey were selected randomly and did not share any boundaries.

The survey was carried out following the standard geobotanical routines (Korchagin and Lavrenko 1964). The following parameters were registered: the number of vascular plants species and lichens within the plot; the total percentage cover of the grass and dwarf shrub layer (vascular plants), lichens and mosses; the abundance (according to the Drude scale) of each species of vascular plants and lichens. For each plot, we recorded GPS coordinates, the elevation, relief position, general percentage cover, stratification, division into sublayer and their heights. Species were identified using the Illustrated Plant Guide of Perm Region (2007) and confirmed in the Museum of the Institute of Plant and Animal Ecology (Herbarium, SVER - https://herbarium.ipae.uran. ru/).

To determine the percentage cover of different ecological and coenotic groups of plants, the Drude scale points were converted into % of cover: 0% – 0%; un – 0.1%; un-sol – 0.4%; sol-un – 0.7%; sol – 1%; sol-sp – 3%; sp-sol – 5%; sp – 7%; sp-cop1 – 11%; sp-cop1-2 – 15%; cop1 – 20%; cop1-2 – 27%; cop1-3 – 35%; cop2 – 40%; cop3 – 65%; soc – 90%. After that, the total cover of vascular plants within the area and the percentages of the species groups in the total cover were calculated.

To assess the structural similarities/ differences of the described communities with different percentages of *J. sibirica,* cluster analysis was applied using the Ward's method and the estimation of the Euclidean distance in the software package Statistica. The differences in the ecological and coenotic structure of mountain tundras with different percentages of *J. sibirica* were assessed using the Mann-Whitney test (Schmidt 1980; Vukolov 2004).

2 Results

2.1 Reconstruction of formation and structure of *J. sibirica* shrubs

Our survey results show that with increasing elevation, the mean and maximum values of morphometric traits of *J. sibirica* decrease in both transects (Table 1). Mean height and crown diameter decrease by a factor of 1.5–2. Mean age of *J. sibirica* is decreasing as well: in transect I from 54 to 29 years, and in transect II from 73 to 44 years. The maximum values of morphometric traits are 2–3 times lower in the top part of the transect. Crown cover area decreases by a factor of 5–7 with increasing elevation.

The maximum density of *J. sibirica* shrubs in transect I is observed at the middle level. In transect II, shrub density at the bottom and middle levels are very similar. In general, the density of *J. sibirica* shrubs in both elevational transects decreased with an increase in elevation. The highest overall morphometric trait valus of *J. sibirica* shrubs were observed in transect II.

The period during which *J. sibirica* shrubs populated the slopes was assessed based on age structure analysis. Individual plants of *J. sibirica* began to colonize the bottom level in transect I from the middle of the 19th century until the middle of the 20th century (Figure 4c). Within this 100 years' period, about 35% of all existent individual plants of *J. sibirica* established. Extensive distribution of shrubs at this level occurred in the period from 1970s till the 2000s. *J. sibirica* establishment at the middle level was observed at the beginning of the 20th century, while mass distribution of *J. sibirica* there took place in the second half of the 20th century (64% of existent individual *J. sibirica* plants) (Figure 4b). And as for the top elevation level, some individual *J. sibirica* shrubs established there after the 1950's, while extensive increase in shrub density began after the 1980's (96% individual *J. sibirica* plants), and has been going on ever since (Figure 4a).

Regarding transect II, the formation processes of *J.* sibirica shrubs seems different (Figure 4). The oldest existent shrubs of *J. sibirica* at the bottom elevation level date back to the middle of the 19th century (Figure 4c). Extensive distribution of *J. sibirica* took place during the periods of 1920–1950 and 1970–1990 (31% and 46% of individual *J. sibirica* plants, respectively). At the middle elevation level, individual *J. sibirica* plants began to established in the middle of the 19th century to the 1930s (Figure 4b). During the period from 1930 to 2000, the shrub density was permanent, without any discernable recruitment periods. By the end of the 20th century, the number of young individual *J. sibirica* plants increased. In total, 84% of currently growing *J. sibirica* shrubs established in the area within the time interval under consideration. At the top elevation level of this transect, first plants of *J. sibirica* began to establish in the 1940s and establishment continues to the present (Figure 4a).

2.2 Analysis of changes in climatic conditions and its connection with the expansion of shrubs

The data analysis of the instrumental meteorological observations (Figure 5) shows that climate in the surveyed region became warmer and more humid. The greatest changes of temperature and precipitation accumulation occurred in the cold season of the year. The time series of anomalies of the mean air temperature show a linear trend increase by 0.22°C/decade (R^2 = 0.55, p <0.001) in the cold season and 0.06°C/decade

Table 1 Morphometric and area indicators of *J. sibirica* shrubs in the elevational transects

Indicators	Elevational transect I			Elevational transect II		
Altitudinal level	Bottom	Middle	Top	Bottom	Middle	Top
Mean elevation (m a.s.l.)	862.9±1.8	881.4±2.2	907.8±3.9	886.5±3.4	906.9±2.9	921.3±0.8
Mean height (cm)	65.8±2.7	47.7±2.8	44.2±1.8	95.0±3.4	75.9±3.9	44.2±1.8
Maximum height (cm)	160	120	105	190	180	140
Mean crown diameter (cm)	126.6±8.7	76.1±3.8	66.0±2.7	172.8±14.4	147.2±11.3	119.7±10.1
Maximum crown diameter (cm)	480	240	175	935	550	265
Mean age (years)	54±4	47±2	29±1	73±4	54±4	44±3
Maximum age (years)	164	116	63	170	166	79
Density of shrubs (individual/ha)	782	967	738	540	488	234
Crown cover area (m²/ha)	1601	600	305	2203	1457	335

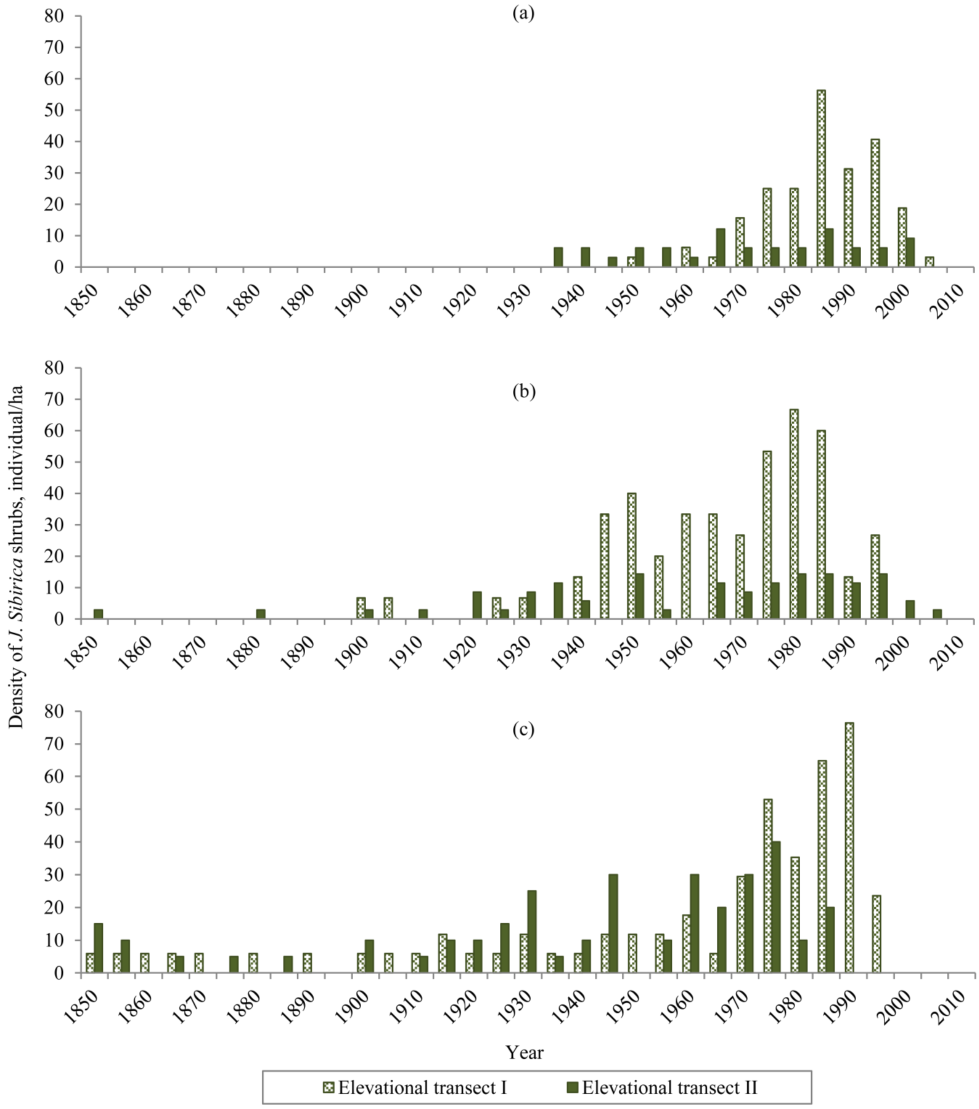

Figure 4 Establishment periods of *J. sibirica* shrubs on top (a), middle (b) and bottom (c) levels of I, II elevational transects.

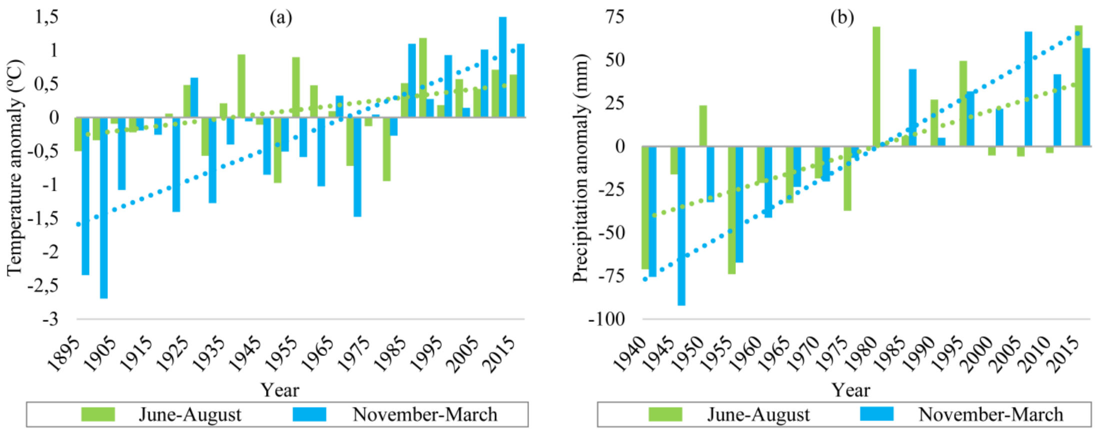

Figure 5 Time series of air temperature anomalies from 1895 to 2015 (a) and total precipitation anomalies from 1940 to 2015 (b) in warm (June-August) and cold (November-March) seasons grouped by five-year periods at the Cherdyn' weather station. Anomalies are relative to the mean of 1961–1990. The dotted line shows the linear trend of climatic indicators anomalies.

(R^2 = 0.16, p = 0.05) in the warm season. The total precipitation increases by 19.03 mm/decade (R^2 = 0.88, p <0.001) in the cold season and 10.42 mm/decade (R^2 = 0.34, p = 0.02) in the warm season of the year.

In order to test possible connections between climate change and the expansion of *J. sibirica* shrubs, correlation and regression analyses were performed. Figure 6 shows the values of the correlation coefficient between the number of *J. sibirica* shrubs that established over five years and the average five-year values of air temperature or precipitation in different periods of the year at top, middle, and bottom elevational levels and in aggregate of all levels. Correlation scores were generally similar between both transects and all elevational levels. The results of the corresponding analysis showed the relationship between the number of establishing *J. sibirica* shrubs in total at all elevational levels and the precipitation of the first three months of the cold season (November-January) of the previous (R = 0.92, p <0.001) and corresponding (R = 0.91, p <0.001) five-year periods (Figure 6a,c). For warm period precipitation a significant correlation coefficient with data on *J. sibirica* shrub establishments in total at all elevation levels was obtained for the previous (R = 0.58, p = 0.05) and corresponding (R = 0.57, p = 0.04) five-year periods. In Appendix 2, we report the results of correlation analysis in more detail.

With increasing elevation above sea level, the relationships between precipitation at the beginning of the cold period (November-January) of the previous five years with the distribution of *J. sibirica* shrubs become stronger (Figure 6a). The highest correlation scores were found between the number of *J. sibirica* shrubs that established during the five-year period and the average total precipitation of the beginning of the cold period in the previous five-year period at highest elevation level (correlation coefficient R = 0.95, p < 0.001).

For air temperature, significant correlation

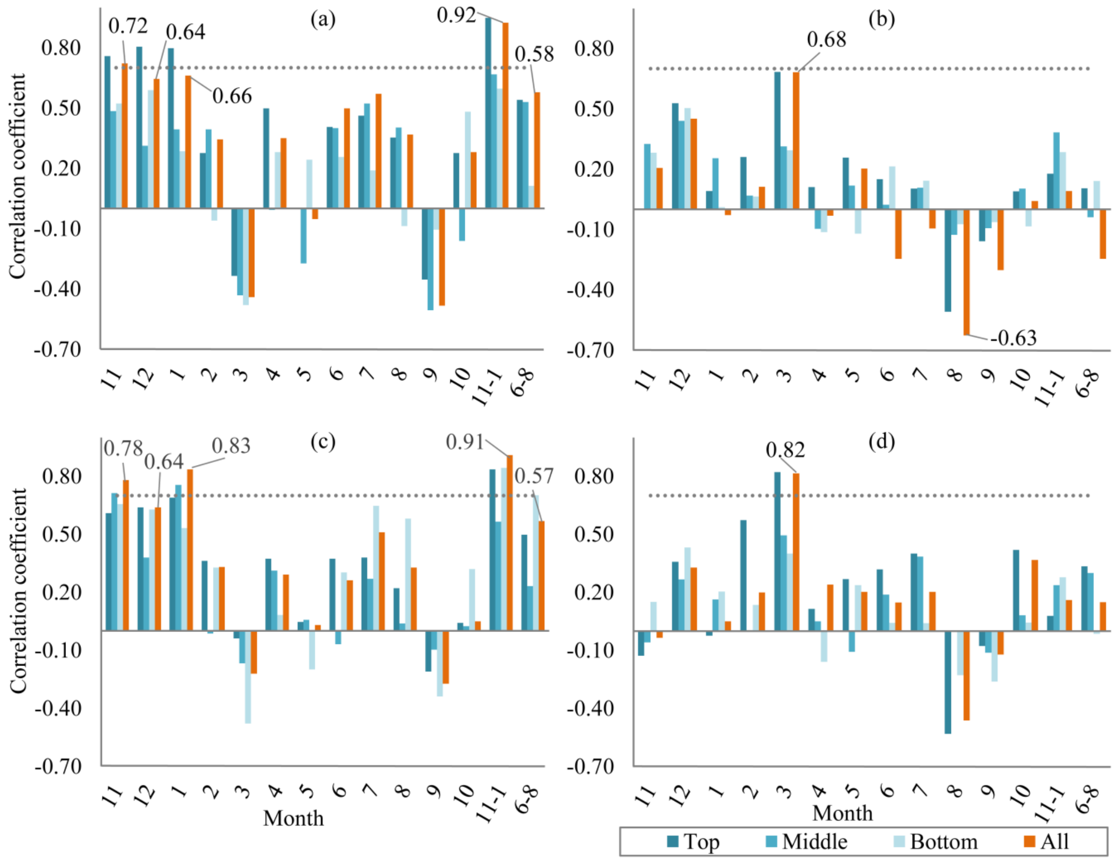

Figure 6 Correlation coefficients of the relationship between the number of established *J. sibirica* shrubs (on top, middle, bottom elevation levels and in aggregate on all of these levels) and climatic parameters grouped by five-year periods: precipitation (a) and temperature (b) of previous periods, precipitation (c) and temperature (d) of corresponding periods. Significant values at p<0.05 for data on all elevation levels are indicated.

coefficients for data on all elevation levels were obtained for March of the previous (R = 0.68, p = 0.01) and corresponding (R = 0.82, p <0.001) five-year periods (Figure 6b, d). It should be noted that for March there is a tendency for a negative correlation between the establishment of *J. sibirica* and the average total precipitation in all analyzed groups. Multiple regression analysis showed that there is a relationship between the number of *J. sibirica* shrubs, which established over a five-year period together at all elevation levels, March precipitation and March temperatures in the corresponding five-year periods at the top elevation level (the coefficient of determination R^2 = 0.78, p <0.001).

2.3 Vegetation survey

The communities we studied are moss-grass tundra with different percentages of *J. sibirica*. The structure of these communities is dominated by vascular plants and bryophytes, while lichens have low abundance (percentage cover does not exceed 15%).

Moss-grass mountain tundra without *J. sibirica* (Group A). Communities grow at elevations of 929-933 m above sea level. The plot has a slope of 0°-1° with some stone outcrops (0%-10%). The total percentage cover (TPC) varies from 50% to 80%. The percentage cover (PC) of vascular plants is about 70%. The dominating species are *Vaccinium uliginosum* L., *Poa alpigena* (Blytt) Lindm., *Aster sibiricus* L., *Juncus trifidus* L., *Anemone biarmiensis* L. PC of the moss and lichen layer is 50–80%. The layer is dominated by bryophytes with PC of 70% on average. The dominant species include *Hylocomium splendens* (Hedw.) Bruchetal., *Rhytidium rugosum* (Hedw.) Kindb, *Polytrichum commune* Hedw. Lichens grow in clumps, and do not form layers, the PC is no more than 15%. Lichens are represented by *Cetraria islandica* (L.) Ach., *Cladonia arbuscula* (Wallr.) Flot, *C. macroceras* (Delise) Hav., *C. uncialis (L.)* F. H. Wigg.

Moss-grass mountain tundra with low percentages (30%–40%) of *J. sibirica* (Group B). Communities grow at elevations of 915-928 m above sea level. The plot has a slope of 0°-1° with some stone outcrops (0%-5%). The TPC is 40%–70%. PC of vascular plants is 55%. The layer is dominated by *Vaccinium uliginosum, Poa alpigena*, *Juncus trifidus*. The PC moss-lichen layer is 50%–80%. Mosses predominate (65%): *Hylocomium splendens*, *Rhytidium rugosum*, *Polytrichum commune*. The PC of lichens does not exceed 15%. Lichens are represented by *Cetraria islandica*, *Cladonia arbuscula, C. Gracilis var gracilis* (L.) Willd, *C. uncialis*.

Moss-grass mountain tundra dominated by *J. sibirica* (85%–95%) (Group C). Communities grow at 880-931 m above sea level. The plot has a slope of 0°-2° with stone outcrops (0%-20%). TPC is 30%–40%. PC of vascular plants is on average 35%. The dominating species are *Vaccinium uliginosum, Poa alpigena*, *Juncus trifidus*. The PC of the moss and lichen layer is 30%–60%. The layer is dominated by bryophytes (PC is 40%). The dominant species include *Hylocomium splendens*, *Rhytidium rugosum*, *Polytrichum commune*. Lichens grow in clumps, PC is about 10%. The most abundant are *Cladonia arbuscula, C. gracilis, C. rangiferina* (L.) F. H. Wigg*, C. uncialis*. The PC of vascular plants and mosses decreases considerably as *J. sibirica* invades. The PC of lichens does not change.

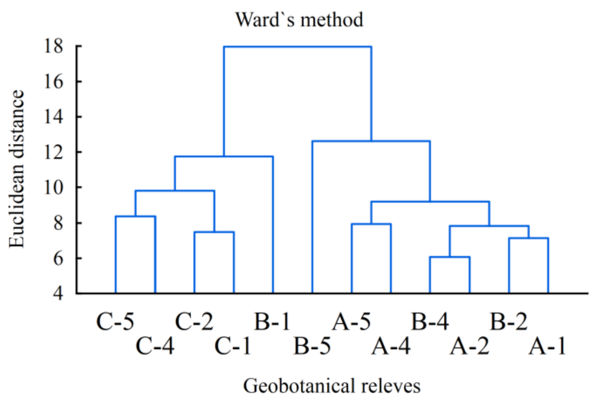

Figure 7 Dendrogram of variations of the tundra community structure in the Kvarkush Range.

To assess the differences in the structure of the studied plant communities, we performed a cluster analysis (Figure 7). All communities dominated by *J. sibirica* are grouped in the left cluster. This is evidence of the initial stage of the formation of a different typological unit, i.e., *J. sibirica* thickets on the mountain tundra area.

The transformation of vegetation communities occurring with an increase in the PC of *J. sibirica* is manifested by the changing of the ratio between ecological and coenotic plant groups (Figure 8).

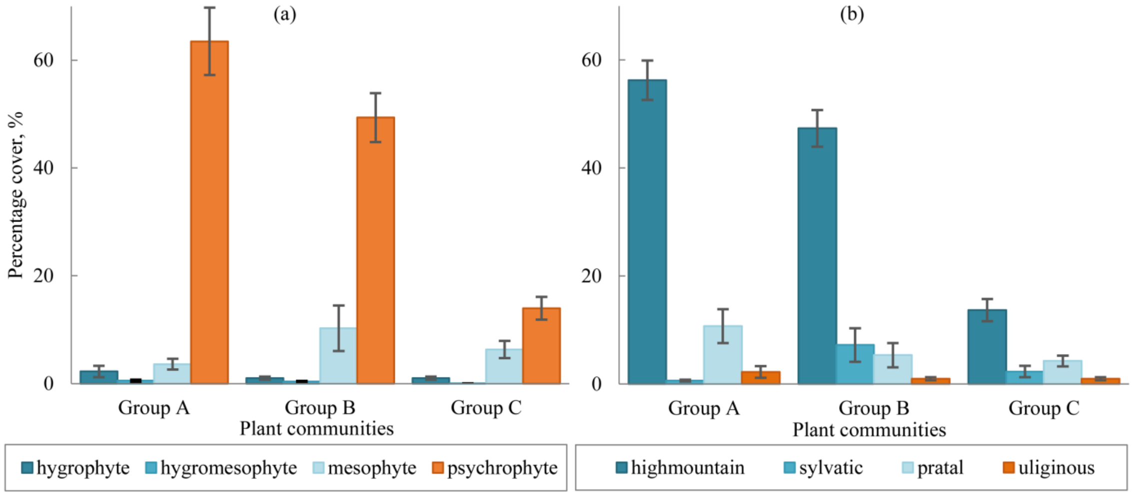

Figure 8 Structure of ecological (a) and coenotical (b) groups of vascular plants in moss-grass tundras with different percentages of *J. sibirica*: Group A, 0%; Group B, 30%-40%; Group C, 85%-95%.

In the studied communities the prevailing group is the psychrophytes, the mesophytes rank se cond, and the hygrophytes rank third. The communities are dominated by high-mountain species, next come pratal or sylvatic plants, while the cover of uliginous species is negligible. The distribution pattern is not affected by the abundance of *J. sibirica*, but the PC of psychrophytes and high-mountain species decrease dramatically.

3 Discussion

We have shown that since the middle of the 19th century to the present, there was an intensive expansion of shrub vegetation into the mountain tundra and meadows on the western side of the Northern Urals in the Kvarkush Range. The main evidence of this process is a decrease in mean age and morphometric trait values of *J. sibirica* shrubs with increasing elevation. The most significant changes in the distribution of shrub vegetation took place in the second half of the 20th century. The expansion of shrub vegetation in the mountain tundra and meadows of the Kvarkush Range may be due to the influence of large-scale factors, in our opinion – climate. The increase of precipitation amount in the cold period is 1.8 times higher than for the warm period. The ratio of increased rates of air temperature tends to greater warming in the cold period as well. We therefore cautiously assume that climatic conditions of the cold period became more favorable for the establishment of new *J. sibirica* individuals, as the closest relationship was found between these parameters.

Significant correlations between the establishment of *J. sibirica* and precipitation at the beginning of the cold season for the previous five-year periods can be explained by the importance of a thick snow cover (Sturm et al. 2005; Wipf et al. 2009) for protection against frost, wind damage, and abrasion and the prevention of winter desiccation of mature fertile plants (Bokhorst et al. 2009; Rixen et al. 2010), especially at the highest elevation level (where most snow is blown away by the wind). Moreover, *J. sibirica* has a long cone formation cycle of two or three years (as mentioned above) and unsatisfactory seed reproduction (or none at all) in case of unfavorable soil and climatic conditions (Ismailov 1974). Also, a more favorable microclimate under snow explains the existence of shrubs well above the treeline (Körner 2012). A number of studies point out that a change (increase) in winter precipitation has a positive effect on the growth of shrubs (Schmidt et al. 2006, 2010; Pellizzari et al. 2014; Hollesen et al. 2015; Carrer et al. 2019).

The relationship we have found between the establishment of *J. sibirica* shrubs and precipitation of the beginning of the cold period, especially in November, for the respective five-year periods may be due to having sufficiently deep snow cover for the preservation of young *J. sibirica* shrubs during the first frost, because unfavorable climatic conditions are more critical for the young plants than for the mature ones, moreover since large mature shrubs tend to accumulate snow. Similar results were obtained in the mountains of N Sweden (Hallinger et al. 2010), where younger plants of *Juniperus nana* grew at higher elevations. The authors established a positive correlation between the growth of shrubs and winter (from November) precipitation, and almost all *J. nana* plants older than 100 years had significantly increased their annual growth over the last three decades. Also, an upward shift in the upper boundary of shrubs and an increase in their density were discovered in the mountainous areas of Alaska (Dial et al. 2007, 2016) and Sweden (Rundqvist et al. 2011), making our interpretation of the results plausible.

In addition to the close relationship between the establishment of *J. sibirica* shrubs and precipitation at the beginning of the cold season, a connection was also found with the climatic conditions at the end of the winter. The obtained model, taking into account air temperature and precipitation in March of the corresponding five-year periods, may indicate that for young *J. sibirica* plants, a significant factor is the thawing time of the soil in spring, which determines the duration of the growing period (Pellizzari et al. 2014). Low average temperatures in March and large precipitation volume postpone the snow thawing time (the active stage of snowmelt begins on average in the first part of April), while an increase in the number of clear days with a positive temperature and a small amount of precipitation contributes to a faster start of the growing season. It can also be added that in our study region, the period with temperatures above 0°C in the spring advances 7.5 days/100 years, according to data for the period 1900-2007 (Ermakova et al. 2013). The influence of warm season precipitation on the establishment of *J. sibirica* shrubs in the previous and corresponding five-year periods may be explained by the sensitivity of undergrowth shrub layer to soil moistening in the mountain tundra.

However, not only do environmental conditions affect the shrub expansion, but also the increased density of shrubs leads to the formation of special microclimatic conditions under their canopy (Walker et al. 2006; Pajunen et al. 2011; Elmendorf et al. 2012; Tsuyuzaki et al. 2012). The introduction of deciduous shrubs that have a vertical growth shape and annually generate plenty of litter leads in most regions to an increase in the height and abundance of vascular plants and to a decrease of the species diversity of the community as well as to the reduction of moss and lichen abundance (Anthelme et al. 2003; Walker et al. 2006; Pajunen et al. 2011; Elmendorf et al. 2012; Scharnagl et al. 2019). However, we do not find changing species composition of mountain tundra communities with invading evergreen *J. sibirica*, which correlates with the study results of Vojík and Boublík (2018) and Scharnagl et al. (2019).

However, tundra vegetation can be characterized by considerable spatial mosaic structures, and the various mosaic parts can react to changes of environmental conditions in different ways and at different rates. In general, biotic components of ecosystems have slower reaction times to global climate changes than abiotic ones (Tape et al. 2006). This can explain the absence of any statistically relevant changes of species composition and structure of mountain tundra communities of the Northern Urals during the introduction of *J. sibirica*; which correlates with the results of several other studies (Tape et al. 2006; Kapfer et al. 2012). The absence of any relevant differences in the structure of mountain tundra communities with varying percentages of *J. sibirica* may thus simply be explained by its recent introduction (29–73 years ago).

In the long run however, the structural changes of vegetation cover we investigated in the Northern Urals have their specific features compared to the Southern Urals (Grigor'ev et al. 2018; Sokovnina et al. 2018). Mountain tundra communities dominated by *J. sibirica* are different than the communities with its low percentage in both the Southern and Northern Urals. This probably indicates the initial development stages of a new formation of plant communities – *J. sibirica* thickets replacing mountain tundra communities. However, the changes in the ecological and coenotic structure of vegetation communities are more pronounced in the Southern Urals than in the Northern Urals.

4 Conclusion

We studied age structure and morphometric traits of *J. sibirica* shrubs along elevational transects in the Northern Urals and combined this analysis with vegetation surveys. We observed a decrease in morphometric indicators and mean age of shrubs with increasing elevation, and found that the most extensive distribution of shrubs were in the second half of the 20th century. A close relation exists between the distribution of *J. sibirica* shrubs at all elevation levels and the climatic conditions in winter, particularly at the beginning (November-January) and the end (March) of the cold period. A wet (snowy) beginning of the winter and a dry and warm end seem to benefit shrub expansion. The observed shrub expansion is beginning to transform the structure of mountain tundra communities, however, no significant reorganization of the ecological and coenotic structure of moss-grass tundra communities after the introduction of *J. sibirica* is apparent so far.

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