Journal of Forestry Research (2024) 35:97
https://doi.org/10.1007/s11676-024-01745-3

ORIGINAL PAPER

Struggle zone: alpine shrubs are limited in the Southern Urals by an advancing treeline and insufficient snow depth

Andrey A. Grigoriev[1] · Vladimir S. Mikryukov[2] · Yulia V. Shalaumova[1] · Pavel A. Moiseev[1] · Sergey O. Vuykhin[1] · Jesús J. Camarero[3]

Received: 30 May 2023 / Accepted: 3 January 2024

Abstract In recent decades, the rapid climate warming in polar and alpine regions has been accompanied by an expansion of shrub vegetation. However, little is known about how changes in shrub distribution will change as the distribution of tree species and snow cover changes as temperatures rise. In this work, we analyzed the main environmental factors influencing the distribution and structure of *Juniperus sibirica*, the most common shrub species in the Southern Ural Mountains. Using mapping and digital elevation models, we demonstrated that *J. sibirica* forms a well-defined vegetation belt mainly between 1100 and 1400 m a.s.l. Within this zone, the abundance and cover of *J. sibirica* are influenced by factors such as rockiness, slope steepness, water regime and tree (*Picea obovata*) cover. An analysis of data spanning the past 9 years revealed an upward shift in the distribution of *J. sibirica* with a decrease in its area. The primary limiting factors for the distribution of *J. sibirica* were the removal of snow cover by strong winter winds and competition with trees. As a consequence of climatic changes, the tree line and forest limit have shifted upward, further restricting the distribution of *J. sibirica* to higher elevations where competition for light with trees is reduced and snow cover is sufficiently deep.

Keywords Juniperaceae · *Juniperus sibirica* · Snowpack cover · Shrubline · Shrub-tree competition · Southern Urals · Tree line

Project funding: This study was supported by the RSF (Grant number: 24-27-00338).

The online version is available at http://www.springerlink.com

Corresponding editor: Tao Xu.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11676-024-01745-3.

✉ Yulia V. Shalaumova
jvshalaumova@gmail.com

Andrey A. Grigoriev
grigoriev.a.a@ipae.uran.ru

Vladimir S. Mikryukov
vmikryukov@gmail.com

Pavel A. Moiseev
moiseev@ipae.uran.ru

Sergey O. Vuykhin
sergey.vyuhin@mail.ru

Jesús J. Camarero
jjcamarero@ipe.csic.es

[1] Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, St. 8 Marta 202, Ekaterinburg, Russia 620144

[2] Institute of Ecology and Earth Sciences, University of Tartu, St. Liivi 2, 50409 Tartu, Estonia

[3] Pyrenean Ecology Institute, St. Montañana 1005, 50059 Saragossa, Spain

Introduction

Shrub vegetation has expanded into the tundra and alpine ecosystems including mountainous regions and throughout the tundra biome of the circumpolar Arctic in recent decades as a result of climate change (Myers-Smith et al 2015; Myers-Smith and Hik 2018; Wang et al 2021). Shrub boundaries have shifted in Greenland (Myers-Smith et al 2015), Sweden (Hallinger et al 2010), Alaska (Dial 2007, 2016), the Alps (Wipf et al 2009), the Rocky Mountains (Formica et al

2014), the Russian Arctic (Forbes et al 2010), and the Ural Mountains (Grigoriev et al 2020). As alpine and arctic trees and shrubs have responded to environmental changes (Bret-Harte et al 2002; Tape et al 2006; Myers-Smith et al 2015), upper forest limits, treelines, and shrublines have become sensitivity indicators of climate warming (Gorchakovskiy and Shiyatov 1985; Chapin et al 2005; Shiyatov et al 2020).

Changes in climate transforms habitat conditions, affecting shrub growth and the expansion of shrub populations (Forbes et al 2010; Hallinger et al 2010; Blok et al 2011; Büntgen et al 2015), primarily driven by alterations in winter temperatures and in precipitation (Hallinger et al 2010; Hollesen et al 2015; Carrer et al 2019), but in other cases by summer temperatures (Forbes et al 2010; Blok et al 2011; Wang et al 2023). Despite the links found between the distribution and growth of alpine shrubs and climate change (Campioli et al 2012; Tape et al 2012; Boscutti et al 2018; Frost et al 2018), we still lack a good mechanistic understanding of these interactions (but see Mod and Luoto 2016). Changes in the width and structure of vegetation belts (not only in the upper boundary) also need more research attention.

This study focuses on *Juniperus sibirica* Burgsd. (Juniperaceae), the most common evergreen shrub in the Southern Urals, where it can be long-lived (Hantemirov et al 2011). The idea of the present research was triggered when color photographs from different times but the same perspective in the mountains showed that the shrubline and the treeline had shifted upward in certain areas (Fig. 1a), but in other areas, the density of the shrub cover had decreased (Fig. 1b). These dissimilarities imply that the dynamics of different vegetation types are not ubiquitously similar, and the mechanisms underlying these dynamics in changing environments need further research. We thus characterized the distribution of the species along altitudinal and slope gradients on the three highest peaks of the Southern Urals over 10 years in relation to habitat factors (tree cover, snow depth, and soil temperatures). Our aims were (1) to characterize the distribution of *J. sibirica* and the main tree species at the treeline on these peaks, (2) to estimate tree cover, snow depth, soil temperature, and wind speed at key sites that varied in percentage of *J. sibirica* cover, (3) to assess temporal changes in the species composition, morphometric and areal characteristics of *J. sibirica* and trees on a constant altitudinal transect. Based on the properties of *J. sibirica*, we tested four hypotheses. (1) *J. sibirica* is not uniformly distributed along mountain slopes but rather is concentrated at a specific altitudinal range, forming a distinct vegetation belt. (2) The lower limit of species distribution depends on the location of the upper forest limit in the region. (3) The upper distributional limit of *J. sibirica* depends on the snow cover depth related to changes in wind speed. (4) The distribution of *J. sibirica* has shifted upward in

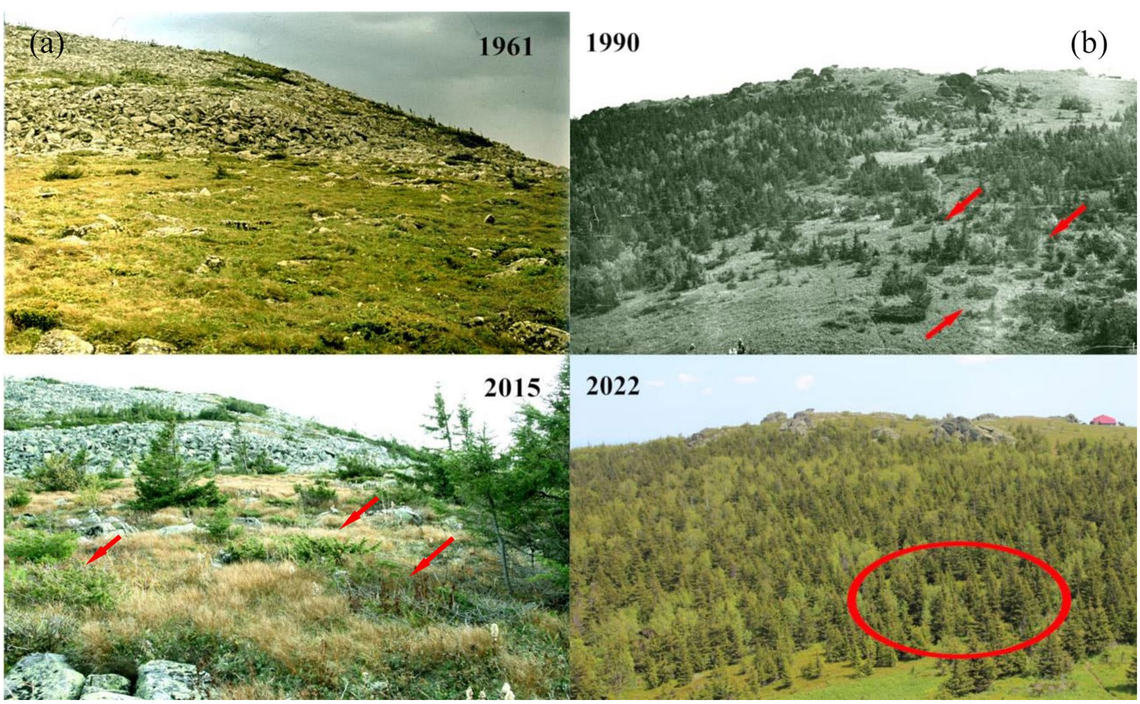

Fig. 1 Successive photos of Mt. Kruglitsa on the Bolshoy Taganay ridge (Southern Ural) showing changes in juniper cover over time (**a**, **b**). The arrows point to *Juniper sibirica*; the oval marks the area where *J. sibirica* had died

the Southern Ural Mountains, and its occupied area has decreased due to the rising upper forest limit and treeline.

Materials and methods

Study area

Three mountains in the Southern Urals were selected: Mt. Maliy Iremel and Bolshoy Iremel, massif Iremel (58°49′–58°54′ E, 54°30′–54°34′ N); Mt. Poperechnaya, Zigalga ridge (58°39′ E, 54°39′ N); Mt. Bolshoy Nurgush, Nurgush ridge (59°00′ E, 54 45′ N) (Fig. 2). The Southern Urals is up to 120 km wide and characterized by large ridges up to 1200–1600 m above sea level. In tectonic terms, this area belongs to the upper proterase, consisting of quartz sandstones, quartzite-sandstones, and dark gray and black shales (Borisevich 1968). The climate is greatly influenced by air masses coming from the Atlantic Ocean (Atlantic), the Kara Sea, Eastern Siberia (Arctic continental), and the Barents Sea (Arctic marine). Scots pine (*Pinus silvestris*) is dominant in the flat foothill areas, and *P. obovata* and *J. sibirica* are usually dominant at higher altitudes. In this region, the average temperatures of January and July are –15.3 °C and 16.4 °C, respectively (Grigoriev et al 2022). The annual precipitation is 733 mm with soils covered by snow from mid-October to late April (Grigoriev et al 2022). Snow depth varies from 4 to 260 cm according to our measurements during the period of maximum snow accumulation in early March.

Large-block stone fields occupy a significant part of individual peaks. There are thin mountain-tundra soils, soddy-meadow and soddy mountain-forest soils in the subalpine belt, and mountain-meadow podzolized soils in the upper part of the slopes (Pogodina and Rozov 1968). Along the altitudinal gradient in the study area, vegetation has a distinct zonality: mountain forest, subalpine and mountain tundra. The upper limit of tree growth (highest altitude of trees at least 2 m high) is formed by open spruce forests with an admixture of park-type birch, which is accompanied by a highly developed grass cover. The dominant shrub species is *J. sibirica*.

Field surveys of the Southern Ural Mountains

To study the localization and distribution of *J. sibirica* in the mountains of the Southern Urals we previously conducted a broader survey of the upper treeline on all the main mountain peaks of this region in 2010–2020. We covered a distance of at least 500 km and examined 27 peaks and ridges in total. The survey included ridges such as Nara, Zigalga, Mashak, Kumardak, Nurgush, Zyuratkul, Urenga, Taganay, Avalyak, Yagodny, Vorobyovy Gory, Bolshaya Suka, and such separate peaks as Bolshoy and Maliy Iremel, Uvan, Sinyak, Bolshoy and Maliy Yamantau. In almost all peaks, which are completely uncovered with forest vegetation and where a treeline is present, we traversed from the foot of the mountains to the peaks, and along the ridge axes.

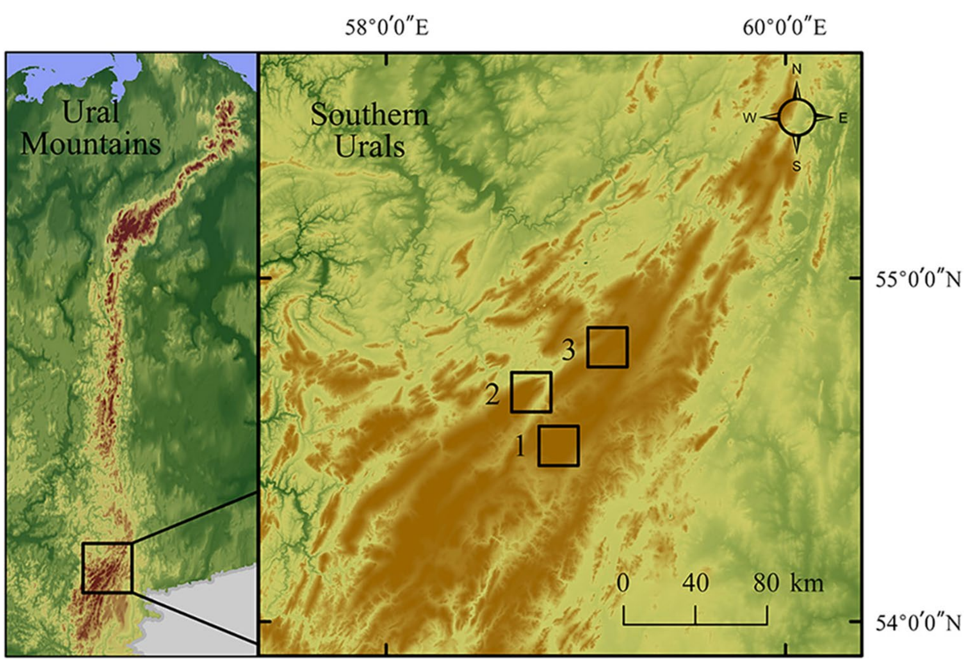

Fig. 2 Study sites in the Southern Urals. **1** Iremel massif; **2** Zigalga ridge; **3** Nurgush ridge

Vegetation mapping

We used aerial photographs, satellite images, large-scale topographic maps, and the description of 1281 study plots covering a total area of about 10,000 ha, to create maps that depict the degree of rockiness, tree layer height in the three mountain areas, and the distribution and morphometric characteristics of *J. sibirica.*

Before we began fieldwork, we used aerial and satellite images to interpret the contours of the Iremel massif, Zigalga and Nurgush ridges to identify the most favorable *J. sibirica* habitats. We marked the boundaries of study plots with different types of vegetation cover (the species composition of the forest stand, crown density) on the satellite images. However, identifying *J. sibirica* patches on photographic archives is challenging, so we determined the configuration and area of shrub cover based on results from our fieldwork.

To construct a map of the current distribution of *J. sibirica*, we used ArcGIS 10.8.1 (ESRI, Redlands, CA, USA). Topographic maps were digitized for Iremel massif, Zigalga and Nurgush ridges, and digital elevation models (10-m resolution) were built. The sections characterizing areas with different growing conditions were plotted. For each section, the ground soil, microclimatic conditions, and vegetation were described. First, height above sea level, exposure and steepness of the slope were determined by using a digital elevation model. Second, the degree of stoniness, soil moisture regime, wind conditions, forest cover and tree density (living and dead individuals), and *J. sibirica* shrubs (composition, average height, crown density) were determined in the field. The data were collected from 2012 to 2020. The area in the mapped plots was calculated using the ArcGIS Spatial Statistics module. The location of the upper limit of open forest was estimated from the corresponding values of the cells in the digital elevation model.

Resurvey of permanent plots

In 2003, we established an altitudinal transect (Fig. S1) on the southwestern slope of Maliy Iremel Mountain within a treeline ecotone as part of the international INTAS project. We defined the treeline ecotone as a transitional belt in the mountains between the upper limits of the distribution of closed forests and individual trees in the tundra. According to Gorchakovskiy and Shiyatov (1985), the ecotone of the upper limit of woody vegetation includes several categories of areas covered with woody vegetation of various densities: closed forests (crown density 0.4–0.5), open forests (crown density 0.2–0.3), sparse forests (crown density 0.05–0.1), and individual trees (crown density less than 0.05). Correspondingly, five altitudinal levels were considered along transects: level 1, at the upper border of individual trees; level 2, at upper border of sparse forests; level 3, at upper border of open forests; level 4, between the lower border of open forests and the upper border of closed forests; level 5, at the upper border of closed forests. At each level, from three to five permanent 20×20 m plots were established (Fig. S1). On each plot and for each tree, we measured the location, basal stem diameter, diameter at breast height (DBH), crown diameter in two mutually perpendicular directions, stem height (Hagedorn et al 2014; Grigoriev et al 2020). Tree age was estimated by taking radial wood cores at the base of the main stem using increment borers (Haglof, Sweden). Width of tree rings were measured with a 0.01-mm resolution using LINTAB (F. Rinn, Germany). Further processing of the cores was carried out using standard dendrochronological methods (Shiyatov et al 2000). Thereby, all trees and undergrowth were mapped on each plot. In 2012 and 2020, the surveys were repeated, and in addition, we mapped and described each *J. sibirica* plant. In total, we examined 1391 trees and 250 J. *sibirica* individuals in an area of 0.72 ha.

Temperature loggers were placed in each plot for 2 years to measure soil temperature at 10-cm depth. At the beginning of March (i.e., peak snow accumulation) in 2015 and 2018, we measured snow cover thickness with an avalanche probe (at least 40 measurements per plot in each year of the study). To assess wind speed, air temperature, precipitation, and other weather variables during 2010–2011, we set up 18 meteorological stations (Hobo, Onset, USA) along a transect on Mount Iremel between 1100 and 1450 m a.s.l.

Statistical analyses

To analyze the drivers of the distribution of *J. sibirica*, we used a generalized additive model (GAM; Wood 2017) after folded power transformation (Tukey 1977) of the cover of *J. sibirica* as the dependent variable. We used a weighted regression approach with area (in hectares) of each forest unit (a designated area characterizing localities with distinct growing conditions of vegetation) as a weight in the model (Table S1). We used thin-plate splines (bs = 'ts') with basis dimension $k = 4$ as smooth functions for all the predictors except the slope exposure (measured in degrees), for which we used the cyclic spline (bs = 'cc') function. All models were fitted in R v.4.2.2 (R Core Team 2022) using the brms package v.2.18.0 (Bürkner 2017) and Stan v.2.21.8 (Carpenter et al 2017) with 12 Markov chains of Monte Carlo simulations, 17,000 samplings and 3000 warmup iterations for each chain. Chain convergence was evaluated visually and using the R-hat statistic (Gelman-Rubin diagnostic test; Gelman 2013). To determine whether the influence of predictors varies across distinct mountain regions, we utilized Bayes factor analysis to compare models with and without interaction terms. This analysis was done using the R packages bridgesampling v.1.1–2 (Gronau et al 2020) and bayestestR v.0.13.0 (Makowski et al 2019).

Results

Shrub vigor, distribution and size changes along the altitudinal transect

In the foothill with Scots pine forests, *J. sibirica* was found in small, sparse groups, whereas it is more abundant near peaks, above the upper tree line formed by *P. obovata*. In dense stands of this spruce species, *J. sibirica* is absent, except for a few growth-suppressed individuals on bare rock in open sites (Figs. 3 and 4).

According to the mapping analyses, *J. sibirica* was present mainly between 1000 and 1400 m a.s.l., whereas the upper open forest limit was located at 1140 ± 56 m a.s.l. on Nurgush ridge, 1204 ± 50 m a.s.l. on Zigalga ridge and 1233 ± 65 m a.s.l. on Iremel massif (mean ± SD) (Fig. 4).

The relationship between altitude and *J. sibirica* cover was bell-shaped, with the maximum species abundance at 1200, 1300 and 1400 m a.s.l. on Nurgush, Zigalga and Iremel, respectively (Fig. 5). The highest density of *J. sibirica* was usually detected in areas with shallow slopes and southern exposure, covered with silt and soil, in the transitional zone between the upper border of sparse forests and mountain tundra. At the same time, the species grows in fragments on steep slopes and very stoney fields. The species is absent from high-density stands that exceed 70% cover and from heavy-sod meadows, mountain tops, and swampy areas.

The altitudinal distribution of *J. sibirica* in the forest–tundra ecotone varied according to the characteristics of each studied massif. In general, the density and cover of *J. sibirica* decreased with rockiness values > 30–40%. The highest shrub cover was observed on the Zigalga ridge, with a coverage of 14.3% ± 1.16% (mean ± SE), while the covers in Iremel and Nurgush were 12.9% ± 1.16% and 8.76% ± 1.21%, respectively.

Fig. 3 Damaged and dead *Juniper sibirica* shrubs on mountain tops (**a**, **b**) and in open forests (**c**, **d**) in the Southern Urals

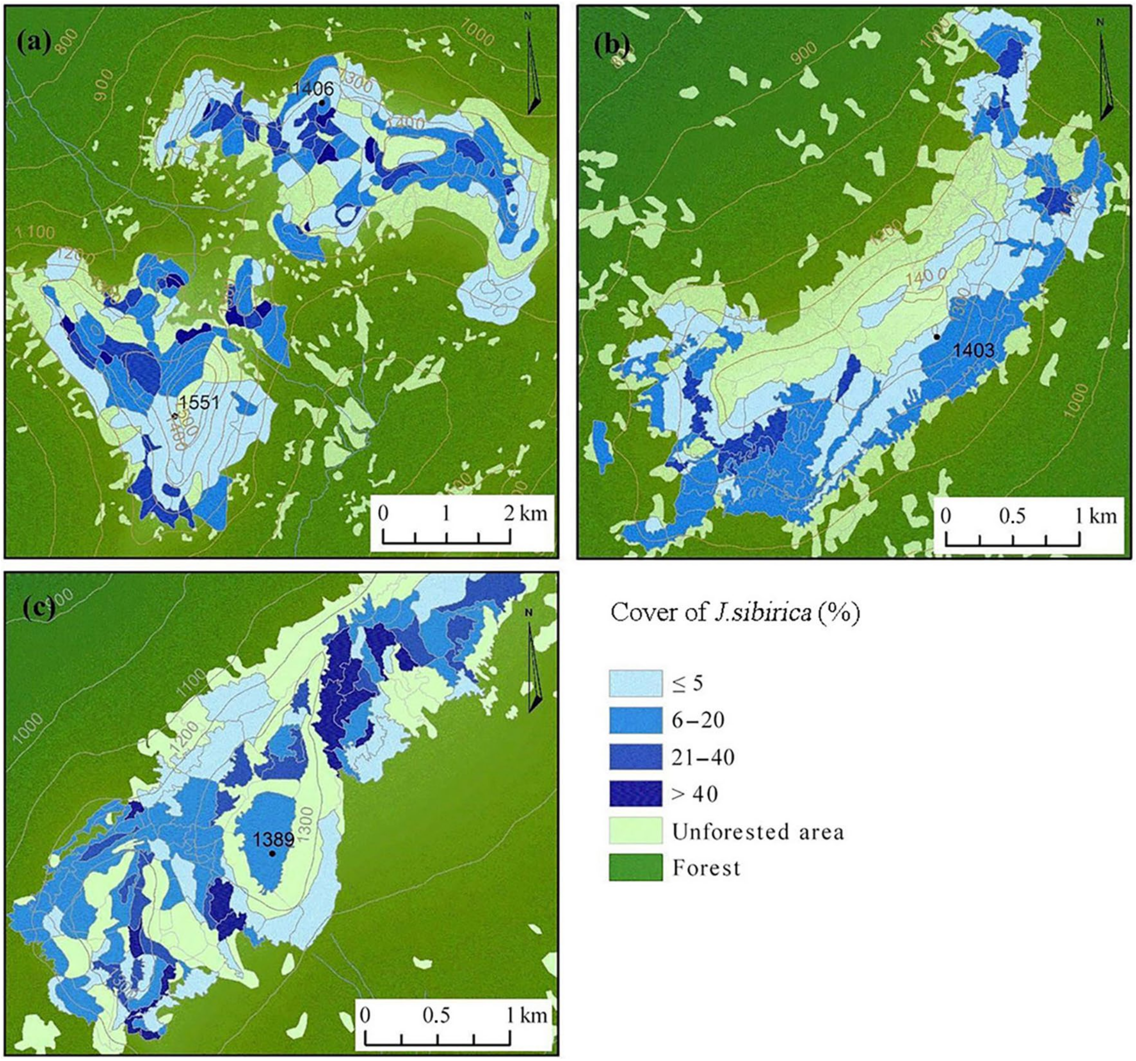

Fig. 4 Distribution maps of *Juniper sibirica* cover on **a** Iremel massif, **b** Nurgush ridge, and **c** Zigalga ridge

Relationships between forest dynamics and distribution of *J. sibirica*

Over the 9-a study, we observed changes in the stand structure of the upper forest line on the southwestern slope of the Maliy Iremel Mountain (Fig. 6). Tree data indicated a 1.5-fold increase in the average DBH, crown diameter, and height of the studied stands at all altitudinal levels from 2012 to 2020. The magnitude of the increase in tree size was less pronounced at higher altitudes. In addition, a trend toward an increase in tree cover (Fig. 6) and more dead trees (Fig. S2) and toward a decrease in tree regeneration (Fig. S3) were also observed.

Notably, the density of forest stands increased at the first, second, and third altitudes (tundra, single trees and treeline), while a decrease was observed at the lowermost fourth and fifth altitudes (open and closed forests) due to increased competition between trees caused by an increase in crown density. An increase in mortality and a reduction of undergrowth density and amount at lower levels can be attributed to this competition.

The results showed that over 9 a, the distribution of shrub vegetation in the studied area has changed significantly. In 2012, *J. sibirica* was found in the open and the closed forest with densities of 200 and 19 ind. ha^{-1}, respectively. However, currently, *J. sibirica* is absent at these lower altitudes. Additionally, the average height of *J. sibirica* increased, while the average diameter of the crowns decreased. The number of individuals only increased at the uppermost altitudine, the tundra.

Our observations indicate a positive correlation between *J. sibirica* height and snow cover depth ($R^2 = 0.54$, Fig. 7). Shrubs of *J. sibirica* did not grow in areas without snow cover or in locations with snow cover deeper than 2.0 m, as

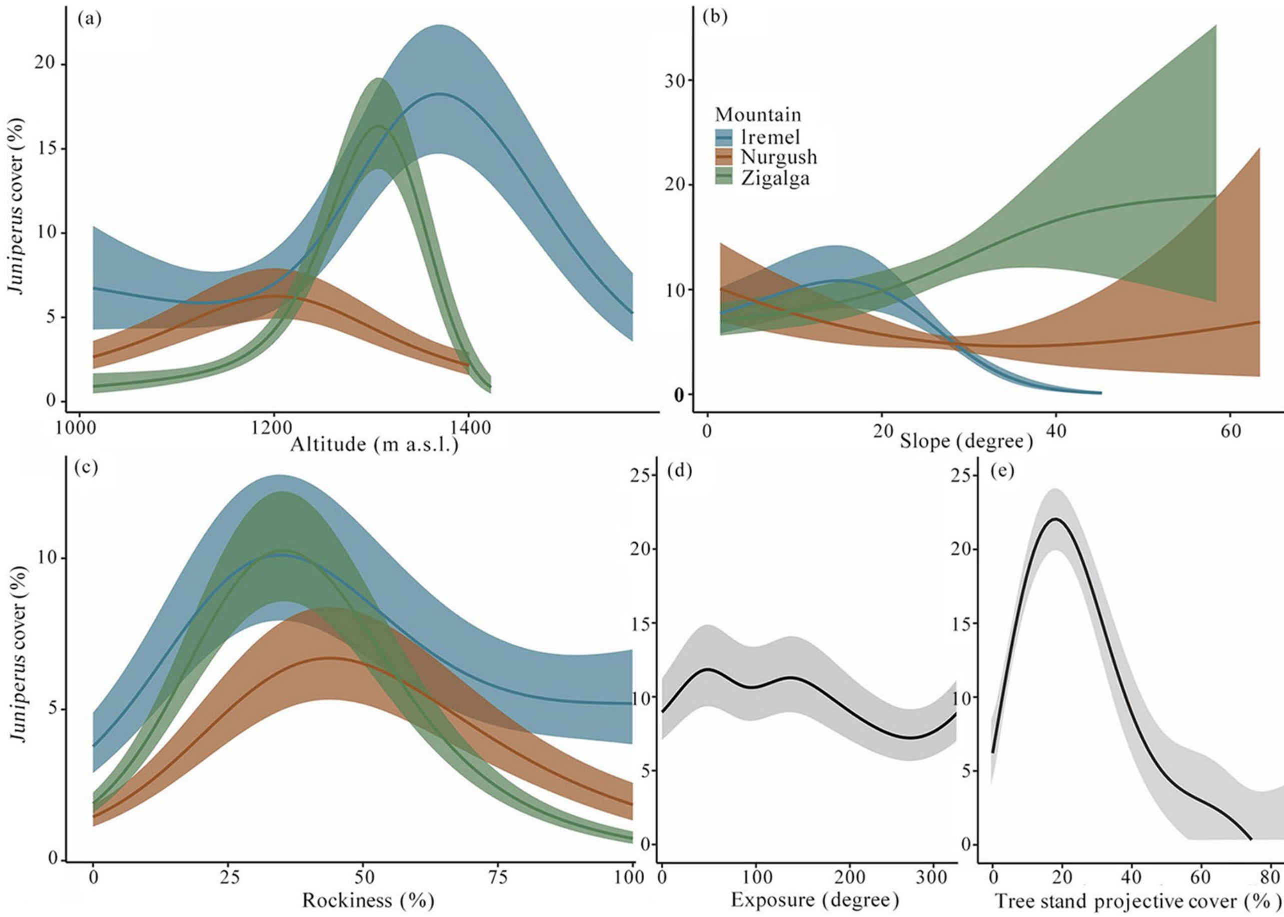

Fig. 5 The relationships between *Juniper sibirica* cover with **a** altitude, **b** slope angle, **c** rockiness of slopes, **d** slope exposure, and **e** tree cover on the three study mountains in the Southern Urals. Median and 95% credible intervals are shown. In (**d**) and (**e**) with only one curve, the interaction effect (mountain×predictor) was not statistically significant; hence, the curve represents the overall trend across all mountains

determined with winter inspections and snow measurements. The minimum soil temperature, which is logarithmically related to snow cover depth (Fig. S4), likely plays a role in this relationship.

The wind velocity on Iremel massif was not correlated with altitude or stand density (Fig. 8). However, in the open areas of alpine tundra, wind velocity increased from 1 to 4 m s^{-1}, and in the highest mountain passes where woody vegetation and *J. sibirica* are absent, it reached a maximum of 5 m s^{-1}.

Discussion

The distribution of *J. sibirica* is limited by competition with trees for light at low altitudes, whereas the upper altitudinal limit seems to be more related to climatic constraints such as cold and wind. The changes in *J. sibirica* distribution and shape (increased height and reduced crown projection indicate a decline in light availability) between altitudinal zones and time periods are likely due to an increase in tree cover, leading to the competitive exclusion of *J. sibirica* by *P. obovata*. Presumably, *J. sibirica* as a shade intolerant species could not compete with *P. obovata*.

The density and condition of *J. sibirica* are influenced by various landscape features such as the degree of rockiness, steepness of slopes, water regime, and stand density. We found that soil temperature is not a limiting factor for *J. sibirica* distribution because it is found in areas with soil temperatures below – 10 °C. In our opinion, the main limiting factor for *J. sibirica* is the lack of snow cover caused by high wind speeds. The data from the portable weather stations showed that wind speed reaches its maximum values at the tops of watersheds and mountain passes where there is no *J. sibirica*. We think that the absence of *J. sibirica* in high-mountainous areas, subject to strong winds, is due to extreme conditions; the species depends on snow cover to protect it from harsh conditions caused by frost extrusion,

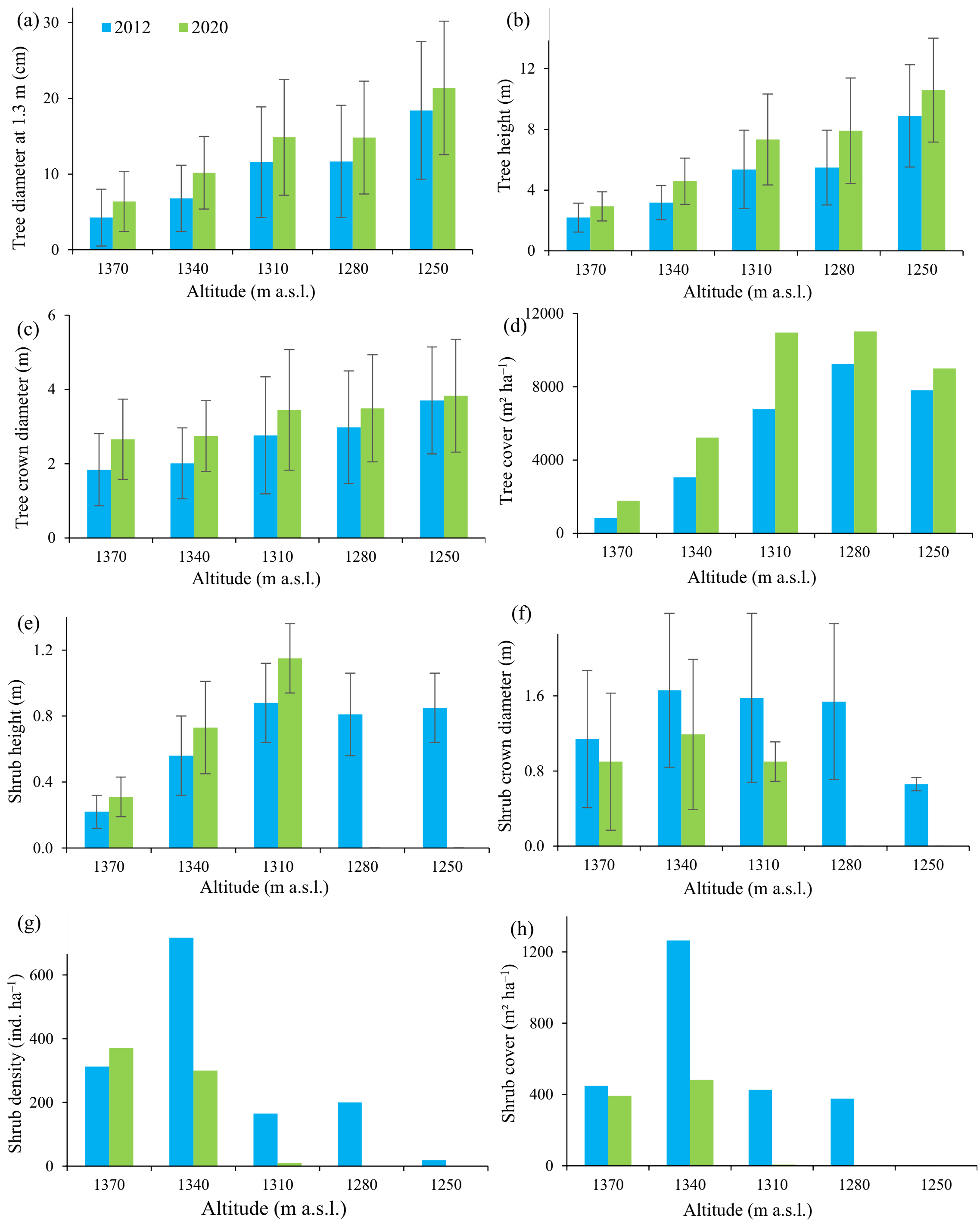

Fig. 6 Value of **a** mean DBH, **b** mean height, **c** mean crown diameter, **d** cover for trees of *P. obovate* and value of **e** mean height, **f** crown diameter, **g** density and **h** cover for shrubs of *J. sibirica* at different altitudes in the Southern Urals in 2012 and 2020. Bars on means indicate ± SD

cold air, snow abrasion, and drying frosts (Fig. 3a, b) (Grigoriev et al 2013, 2020; Hagedorn et al 2014). Snow cover strongly influences plant growth in arctic and alpine ecosystems (Schmidt et al 2006; Rixen et al 2010). As Holtmeier (2003) noted, the most crucial winter stress is not temperature but wind abrasion, snow and ice damage, and drying. Radial growth of *J. communis* in the Central and Eastern Alps also depends on the amount of winter precipitation (Pellizzari et al 2014). In previous studies on *J. sibirica* in the Urals, no shrub individuals were found with

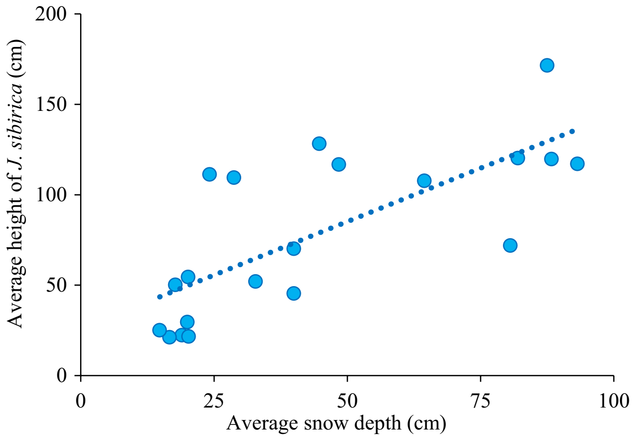

Fig. 7 *Juniperus sibirica* height was positively related to snow cover depth in the Southern Urals in 2015 and 2018

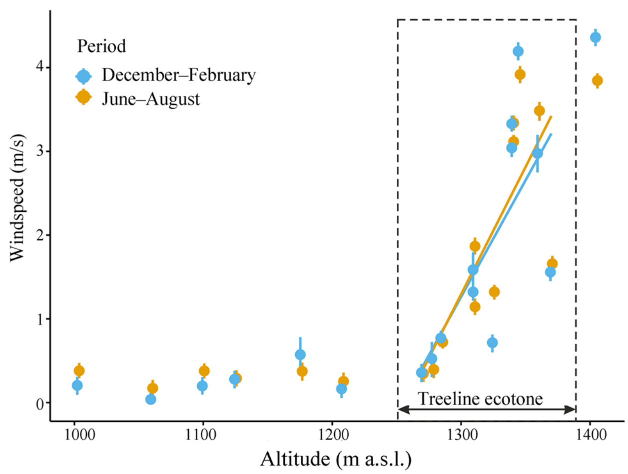

Fig. 8 Mean (± SD) wind speed measured in Iremel massif in 2010 and 2011

signs of snow damage (abrasion of the bark and breaking-off of branches under the weight of snow) on any mountain (Gorchakovskiy and Shiyatov 1985). In the study area*, J. sibirica* is always covered with snow during the winter and grows in localities where the snow cover depth ranges from 0.01 to 2.0 m. Snow cover is, therefore, the most critical factor in forming *J. sibirica* thickets in the Ural Mountains, and short-term loss of snow cover during winter thaws can seriously damage this shrubby vegetation (Bokhorst et al 2008).

Positive feedback between snow depth and plant growth rate has been identified as an essential mechanism for the large-scale increase in shrub abundance in northern Alaska and Siberia (e.g., Jia et al 2003; Sturm et al 2005; Frost and Epstein 2014). In these boreal regions, winter soil temperatures rise with increased snowfall, leading to higher nutrient availability, root growth, and greater snow retention by vegetation. The resultant increase in soil temperature also accelerates mineralization, which makes nitrogen more available for plants in tundra ecosystems with poor soils (Schimel et al 2004; Baptist et al 2010).

The obtained results and previous findings (Moiseev et al 2016; Shiyatov et al 2020) show that upward migration of *P. obovata* trees in mountains regions may either facilitate or inhibit *J. sibirica*. The presence of individual trees and tree groups in the tundra creates favorable conditions for *J. sibirica* growth and distribution, particularly in winter, as trees enhance snow retention on slopes (Moiseev 2011; Hagedorn et al 2014). Conversely, the establishment of a dense spruce forest generates extremely unfavorable conditions, such as heightened root competition, allelopathic effects, light deprivation, alterations in water relations, and dense snow accumulation, all of which inhibit the growth of *J. sibirica* (see Fig. 3c, d). In essence, *J. sibirica* is restricted to an altitudinal strip (Fig. 9), where it can struggle for existence with *P. obovata* trees, moving upslope where it is limited by harsh conditions including strong winds and lack of snow cover in winter.

Note that the study area has not been subjected in the past or present to livestock grazing; other human economic activity (including logging) is also absent here. Previous studies of trees have shown that there have been no fires in the area for at least 400 years (Hagedorn et al 2014).

Conclusion

Growth conditions of the shrub *J. sibirica* in the Southern Urals Mountains are closely linked to local environmental factors, including rockiness, slope steepness, water availability, and stand density. The altitude of the forest limit and treeline notably influences the distribution of *J. sibirica*. The primary limiting factor for *J. sibirica* upslope spread is the removal of snow cover due to high wind velocity in the highlands during winter. In contrast, downslope, dense stands of *P. obovata* outcompete *J. sibirica*, thereby defining the lower boundary of its distribution. This phenomenon suggests a potential reduction in the distribution range of *J. sibirica* due the upward shift of alpine treelines. Such range contractions of alpine shrubs are of significant concern for the conservation of alpine biodiversity.

These findings can serve as a foundation to develop models to forecast changes in the distributional range of *J. sibirica* in mountainous regions under various climate change scenarios. These models should consider a comprehensive array of factors: climatic (primarily temperature and snow depth) and topographic and edaphic characteristics, and the presence of woody vegetation. By integrating these key groups of factors, the predictive models aim to provide to help formulate effective conservation strategies.

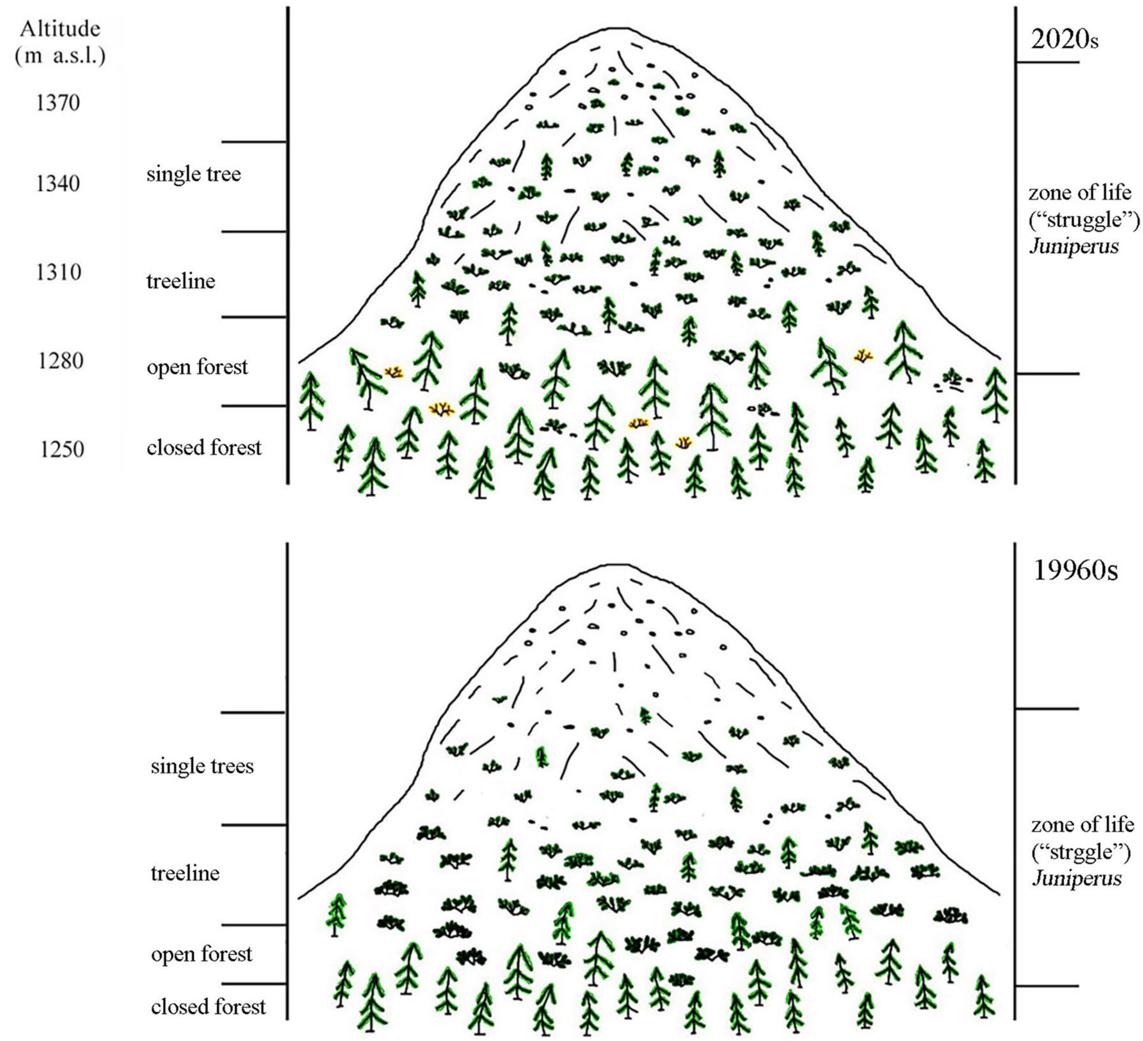

Fig. 9 Diagram of *Juniperus sibirica* distribution in the Southern Urals

Acknowledgements We are very grateful to Prof. S.G. Shiyatov for his advice during the study design and to editor.

References

Baptist F, Yoccoz NG, Choler P (2010) Direct and indirect control by snow cover over decomposition in alpine tundra along a snowmelt gradient. Plant Soil 328:397–410. https://doi.org/10.1007/s11104-009-0119-6

Blok D, Sass-Klaassen U, Schaepman-Strub G, Heijmans MMPD, Sauren P, Berendse F (2011) What are the main climate drivers for shrub growth in Northeastern Siberian tundra? Biogeosciences 8:1169–1179. https://doi.org/10.5194/bg-8-1169-2011

Bokhorst S, Bjerke JW, Bowles FW, Melillo J, Callaghan PGK (2008) Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf shrub heathland. Glob Chang Biol 14:2603–2612. https://doi.org/10.1111/j.1365-2486.2008.01689.x

Borisevich DV (1968) Relief and geological structure. Urals and Cis-Urals. Nauka, Moscow, pp 19–81

Boscutti F, Casolo V, Beraldo P, Braidot E, Zancani M, Rixen C (2018) Shrub growth and plant diversity along an elevation gradient: evidence of indirect effects of climate on alpine ecosystems. PLoS ONE 13:1–12. https://doi.org/10.1371/journal.pone.0196653

Bret-Harte MS, Shaver GR, Chapin FS (2002) Primary and secondary stem growth in arctic shrubs: implications for community response to environmental change. J Ecol 90:251–267. https://doi.org/10.1046/j.1365-2745.2001.00657.x

Büntgen U, Hellmann L, Tegel W, Normand S, Myers-Smith I, Kirdyanov AV, Nievergelt D, Schweingruber FH (2015) Temperature-induced recruitment pulses of arctic dwarf shrub communities. J Ecol 103:489–501. https://doi.org/10.1111/1365-2745.12361

Bürkner PC (2017) brms: An R package for Bayesian multilevel models using Stan. J Stat Softw 80(1):1–28. https://doi.org/10.18637/jss.v080.i01

Campioli M, Leblans N, Michelsen A (2012) Stem secondary growth of tundra shrubs: impact of environmental factors and relationships with apical growth. Arct Antarct Alp Res 44:16–25. https://doi.org/10.1657/1938-4246-44.1.16

Carpenter B, Gelman A, Hoffman MD, Lee D, Goodrich B, Betancourt M, Brubaker M, Guo J, Li P, Riddell A (2017) A probabilistic

programming language. J Stat Softw 76(1):1–32. https://doi.org/10.18637/jss.v076.i01
Carrer M, Pellizzari E, Prendin AL, Pividori M, Brunetti M (2019) Winter precipitation—not summer temperature—is still the main driver for Alpine shrub growth. Sci Total Environ 682:171–179. https://doi.org/10.1016/j.scitotenv.2019.05.152
Chapin FS, Sturm M, Serreze MC, Mcfadden JP, Key JR, Lloyd AH, Mcguire AD, Rupp TS, Lynch AH, Schimel JP, Beringer J, Chapman WL, Epstein HE, Euskirchen ES, Hinzman LD, Jia G, Ping CL, Tape KD, Thompson CDC, Walker DA, Welker JM (2005) Role of land-surface changes in arctic summer warming. Science 310:657–660. https://doi.org/10.1126/science.1117368
Dial RJ, Berg EE, Timm K, McMahon A, Geck J (2007) Changes in the alpine forest-tundra ecotone commensurate with recent warming in southcentral Alaska: evidence from orthophotos and field plots. J Geophys Res 112:G04015. https://doi.org/10.1029/2007JG000453
Dial RJ, Scott Smeltz T, Sullivan PF, Rinas CL, Timm K, Geck JE, Tobin SC, Golden TS, Berg EC (2016) Shrubline but not treeline advance matches climate velocity in montane ecosystems of south-central Alaska. Glob Chang Biol 22:1841–1856. https://doi.org/10.1111/gcb.13207
Forbes BC, Fauria MM, Zetterberg P (2010) Russian Arctic warming and "greening" are closely tracked by tundra shrub willows. Glob Chang Biol 16:1542–1554. https://doi.org/10.1111/j.1365-2486.2009.02047.x
Formica A, Farrer EC, Ashton IW, Suding KN (2014) Shrub expansion over the past 62 years in Rocky mountain alpine tundra: possible causes and consequences. Arct Antarct Alp Res 46(3):616–631. https://doi.org/10.1657/1938-4246-46.3.616
Frost GV, Epstein HE (2014) Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. Glob Chang Biol 20(4):1264–1277. https://doi.org/10.1111/gcb.12406
Frost GV, Epstein HE, Walker DA, Matyshak G, Ermokhina K (2018) Seasonal and long-term changes to active-layer temperatures after tall shrubland expansion and succession in arctic tundra. Ecosystems 21:507–520. https://doi.org/10.1007/s10021-017-0165-5
Gelman A, Carlin J, Stern H, Dunson DB, Vehtari A, Rubin DB (2013) Bayesian data analysis. Chapman and Hall/CRC, New York, p 675
Gorchakovskiy PL, Shiyatov SG (1985) Phytoindication of environmental conditions and natural processes in high mountain regions. Nauka, Moscow, p 208
Grigoriev AA, Moiseev PA, Nagimov ZY (2013) Dynamics of the timberline in high mountain areas of the nether-polar Urals under the influence of current climate change. Russ J Ecol 44:312–323. https://doi.org/10.1134/S1067413613040061
Grigoriev AA, Shalaumova YV, Erokhina OV, Sokovnina SY, Vatolina EI, Wilmking M (2020) Expansion of *Juniperus sibirica* Burgsd. as a response to climate change and associated effect on mountain tundra vegetation in the Northern Urals. J Mt Sci 17:2339–2353. https://doi.org/10.1007/s11629-019-5925-6
Grigoriev AA, Shalaumova YV, Balakin DS, Erokhina OV, Abdulmanova SY, Moiseev PA, Camarero JJ (2022) Alpine shrubification: juniper encroachment into tundra in the Ural mountains. Forests 13(12):2106. https://doi.org/10.3390/f13122106
Gronau QF, Singmann H, Wagenmakers EJ (2020) bridgesampling: an R Package for estimating normalizing constants. J Stat Softw 92(10):1–29. https://doi.org/10.18637/jss.v092.i10
Hagedorn F, Shiyatov SG, Mazepa VS, Devi NM, Grigor'ev AA, Bartysh AA, Fomin VV, Kapralov DS, Terent'ev M, Bugman H, Rigling A, Moiseev PA (2014) Treeline advances along the Urals mountain range—driven by improved winter conditions? Glob Chang Biol 20:3530–3543. https://doi.org/10.1111/gcb.12613
Hallinger M, Manthey M, Wilmking M (2010) Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. New Phytol 186:890–899. https://doi.org/10.1111/j.1469-8137.2010.03223.x
Hantemirov RM, Shiyatov SG, Gorlanova LA (2011) Dendroclimatic study of Siberian juniper (*Juniperus sibirica* Burgsd.). Dendrochronologia 29(2):119–122. https://doi.org/10.1016/j.dendro.2010.05.001
Hollesen J, Buchwal A, Rachlewicz G, Hansen BU, Hansen MO, Stecher O, Elberling B (2015) Winter warming as an important co-driver for *Betula nana* growth in western Greenland during the past century. Glob Chang Biol 21(6):2410–2423. https://doi.org/10.1111/gcb.12913
Holtmeier FK (2003) Mountain timberlines. Ecology. Patchiness, and dynamics. Kluwer, Dordrecht, p 369
Jia GJ, Epstein HE, Walker DA (2003) Greening of arctic Alaska, 1981–2001. Geophys Res Lett 30(20):1–4. https://doi.org/10.1029/2003GL018268
Makowski D, Ben-Shachar MS, Lüdecke D (2019) bayestestR: describing effects and their uncertainty, existence and significance within the Bayesian framework. J Open Source Softw 4(40):1541. https://doi.org/10.21105/joss.01541
Mod HK, Luoto M (2016) Arctic shrubification mediates the impacts of warming climate on changes to tundra vegetation. Environ Res Lett 11(12):124028. https://doi.org/10.1088/1748-9326/11/12/124028
Moiseev PA, Shiyatov SG, Grigoriev AA (2016) Climatogenic dynamics of woody vegetation at the upper limit of its distribution on the Bolshoy Taganay Ridge over the last century. Publishing house UMC UPI, Yekaterinburg, p 136
Moiseev PA (2011) Structure and dynamics of woody vegetation on the upper limit of its growth in the Urals. Dissertation, Institute of Plant and Animal Ecology, Ural Branch of Russian Academy of Sciences.
Myers-Smith IH, Hik DS (2018) Climate warming as a driver of tundra shrubline advance. J Ecol 106(2):547–560. https://doi.org/10.1111/1365-2745.12817
Myers-Smith IH, Elmendorf SC, Beck PSA, Wilmking M, Hallinger M, Blok D, Tape KD, Rayback SA, Macias-Fauria M, Forbes BC, Speed JDM, Boulanger-Lapointe N, Rixen C, Lévesque E, Schmidt NM, Baittinger C, Trant AJ, Hermanutz L, Collier LS, Dawes MA, Lantz TC, Weijers S, Jørgensen RH, Buchwal A, Buras A, Naito AT, Ravolainen V, Schaepman-Strub G, Wheeler JA, Wipf S, Guay KC, Hik DS, Vellend M (2015) Climate sensitivity of shrub growth across the tundra biome. Nat Clim Chang 5:887–891. https://doi.org/10.1038/nclimate2697
Pellizzari E, Pividori M, Carrer M (2014) Winter precipitation effect in a mid-latitude temperature-limited environment: the case of common juniper at high elevation in the Alps. Environ Res Lett 9:104021. https://doi.org/10.1088/1748-9326/9/10/104021
Pogodina GS, Rozov NN (1968) Soils. In: Komar IV, Chikishev AG (eds) Urals and the Suburals. Nauka, Moscow, pp 167–210
R Core Team (2022) A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/ [accessed on 28.03.2023].
Rixen C, Schwoerer C, Wipf S (2010) Winter climate change at different temporal scales in *Vaccinium myrtillus*, an arctic and alpine dwarf shrub. Polar Res 29:85–94. https://doi.org/10.1111/j.1751-8369.2010.00155.x
Schimel JP, Bilbrough C, Welker JM (2004) Increased snow depth affects microbial activity and nitrogen mineralization in two arctic tundra communities. Soil Biol Biochem 36(2):217–227. https://doi.org/10.1016/j.soilbio.2003.09.008
Schmidt NM, Baittinger C, Forchhammer MC (2006) Reconstructing century-long snow regimes using estimates of high arctic *Salix arctica* radial growth. Arct Antarct Alp Res 38:257–262. https://doi.org/10.1657/1523-0430(2006)38[257:RCSRUE]2.0.CO;2

Shiyatov SG, Moiseev PA, Grigoriev AA (2020) Photomonitoring of tree and shrub vegetation in the highlands of the Southern Urals over the past 100 years. Publishing house UMC UPI, Yekaterinburg, p 191

Shiyatov SG, Vaganov EA, Kirdyanov AV, Kruglov VB, Mazepa VS, Naurzbaev MM, Khantemirov RM (2000) Dendrochronological methods. Part I: Fundamentals of dendrochronology. Collection and obtaining of tree ring information. Krasnoyarskij Gosudarstvennyj Universitet, Krasnoyarsk, p 80.

Sturm M, Schimel J, Michaelson G, Welker JM, Oberbauer SF, Liston GE, Fahnestock J, Romanovsky VE (2005) Winter biological processes could help convert arctic tundra to shrubland. Bioscience 55(1):17–26. https://doi.org/10.1641/0006-3568(2005)055[0017:WBPCHC]2.0.CO;2

Tape K, Sturm M, Racine C (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Glob Chang Biol 12:686–702. https://doi.org/10.1111/j.1365-2486.2006.01128.x

Tape KD, Hallinger M, Welker JM, Ruess RW (2012) Landscape heterogeneity of shrub expansion in arctic Alaska. Ecosystems 15:711–724. https://doi.org/10.1007/s10021-012-9540-4

Tukey JW (1977) Exploratory data analysis by John W. Tukey Biometrics 33:688

Wang YF, Liang EY, Lu XM, Camarero JJ, Babst F, Shen MG, Peñuelas J (2021) Warming-induced shrubline advance stalled by moisture limitation on the Tibetan Plateau. Ecography 44:1631–1641. https://doi.org/10.1111/ecog.05845

Wang YL, Wang YF, Camarero JJ (2023) Inconsistent growth responses of alpine rhododendron shrubs to climate change at two sites on the eastern Tibetan Plateau. Forests 14:331. https://doi.org/10.3390/f14020331

Wipf S, Stoeckli V, Bebi P (2009) Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. Clim Change 94:105–121. https://doi.org/10.1007/s10584-009-9546-x

Wood S (2017) Generalized additive models: an introduction with R. CRC Press, Boca Raton, p 496