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# Treeline advances along the Urals mountain range – driven by improved winter conditions?

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## Abstract

High-altitude treelines are temperature-limited vegetation boundaries, but little quantitative evidence exists about the impact of climate change on treelines in untouched areas of Russia. Here, we estimated how forest-tundra ecotones have changed during the last century along the Ural mountains. In the South, North, Sub-Polar, and Polar Urals, we compared 450 historical and recent photographs and determined the ages of 11 100 trees along 16 altitudinal gradients. In these four regions, boundaries of open and closed forests (crown covers above 20% and 40%) expanded upwards by 4 to 8 m in altitude per decade. Results strongly suggest that snow was an important driver for these forest advances: (i) Winter precipitation has increased substantially throughout the Urals (~7 mm decade$^{-1}$), which corresponds to almost a doubling in the Polar Urals, while summer temperatures have only changed slightly (~0.05 °C decade$^{-1}$). (ii) There was a positive correlation between canopy cover, snow height and soil temperatures, suggesting that an increasing canopy cover promotes snow accumulation and, hence, a more favorable microclimate. (iii) Tree age analysis showed that forest expansion mainly began around the year 1900 on concave wind-sheltered slopes with thick snow covers, while it started in the 1950s and 1970s on slopes with shallower snow covers. (iv) During the 20th century, dominant growth forms of trees have changed from multistemmed trees, resulting from harsh winter conditions, to single-stemmed trees. While 87%, 31%, and 93% of stems appearing before 1950 were from multistemmed trees in the South, North and Polar Urals, more than 95% of the younger trees had a single stem. Currently, there is a high density of seedlings and saplings in the forest-tundra ecotone, indicating that forest expansion is ongoing and that alpine tundra vegetation will disappear from most mountains of the South and North Urals where treeline is already close to the highest peaks.

*Keywords:* *Betula pubescens* subsp. *tortuosa*, climate change, forest-tundra ecotone, *Larix sibirica*, microclimate, mountain ecosystem, *Picea obovata*, snow, tree establishment

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## Introduction

Global temperatures have risen during the last century, with the largest and most rapid changes occurring at high altitudes and latitudes (Arctic Climate Impact Assessment, 2005; Stocker *et al*., 2013). This warming affects the world's vegetation, particularly in cold temperature-limited ecosystems (e.g., Hudson & Henry, 2009; Pauli *et al*., 2012). One of the most striking vegetation boundaries is the upper treeline, where tree growth is thought to be primarily limited by low temperatures (Körner, 2012). Worldwide, upper treelines are confined to altitudes with mean growing season temperatures of 5–8°, strongly suggesting that the upright growth of trees is impaired if summer conditions are too cold (Körner & Paulsen, 2004). Due to this growth limitation by low temperature, treeline position is a highly responsive bio-indicator (Kullman & Öberg, 2009). Advances of woody vegetation have been reported for various arctic and alpine treeline ecotones around the world (e.g., Payette & Filion, 1985; Shiyatov *et al*., 2007; Harsch *et al*., 2009). There are a number of key factors and ecological processes that change abruptly within just a few altitudinal meters at the treeline: wind, snow cover, albedo, soil temperatures, plant productivity, biodiversity, soil development, and carbon and nutrient cycling (e.g., Holtmeier, 2003; Kammer *et al*., 2009; Loranty *et al*., 2014). As a consequence, treeline advances can have a tremendous impact on ecosystems and their functions.

Treeline shifts are usually related to climatic warming, mainly to increased temperatures during the

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growing season, because trees can adapt to very low winter temperatures (Körner, 2012). In a global meta-analysis, however, Harsch *et al.* (2009) found that treelines have advanced more strongly when they have experienced greater winter than summer warming and attributed this observation to an amelioration of harsh winter conditions. However, the most important winter 'stress' is not temperature but the exposure of trees to wind abrasion, snow and ice damage, and winter desiccation (Holtmeier, 2003). So far, winter stress has been mainly discussed as a potential growth constraint on a local scale and for individual trees (Lavoie & Payette, 1992; Weisberg & Baker, 1995; Holtmeier, 2003). Recently, although, Kullman & Öberg (2009) and Aune *et al.* (2011) observed that, at a landscape scale, treeline changes in the Scandes during the last century were greatest in regions with the highest winter precipitation and on wind-protected, concave slopes. In these locations, snow can accumulate and effectively remove winter stress by insulating plant tissues and the rooting zone, suggesting that snow conditions are at least an important codriver for treeline advances. In support of this 'snow hypothesis', a positive feedback between increases in snow fall and enhanced plant growth has been suggested as an important mechanism for the observed large-scale increases in shrub abundance in Northern Alaska and Siberia (e.g., Jia *et al.*, 2003; Sturm *et al.*, 2005; Frost & Epstein, 2014). In these regions, a larger snow pack leads to higher soil temperatures in winter, thereby increasing nutrient availability and plant growth, which in turn promotes the accumulation of more snow.

The fact that the rate of treeline advance differs strongly among regions as well as within a single area provides support for the idea that, although treeline formation is primarily caused by low temperature, other factors can determine the rates of change. While treelines in the Alps, interior Labrador, Alaska, and North-Western Canada have hardly advanced (Lloyd, 2005; Gehrig-Fasel *et al.*, 2007; Payette, 2007), treelines in the Scandes have risen by up to 200 m in altitude (Kullman & Öberg, 2009; Aune *et al.*, 2011). The reasons proposed for this large variation in the rate of change despite similar climatic warming include permafrost depth, topography, wind exposure, tree species, soil development, geomorphic processes, and snow cover (e.g., Holtmeier, 2003; Lloyd, 2005; Kullman & Öberg, 2009; Wilmking *et al.*, 2012; Macias-Fauria & Johnson, 2013). However, most of these assessments were single case studies and, when several sites were included, relatively few attempts were made to systematically assess *in situ* conditions such as topography, air and soil temperature, and snow height and distribution. In addition, climatic-driven treeline changes have been confounded with shifts due to land abandonment in many regions, especially in European mountain ranges, making it difficult to disentangle the drivers for treeline advances (Bolli *et al.*, 2007; Gehrig-Fasel *et al.*, 2007; Aune *et al.*, 2011).

Here, we synthesized regional surveys and new data from remote regions of the Ural mountains to quantify how and how fast the forest-tundra ecotone and its boundaries have changed during the last centuries and to identify the processes underlying these changes. Our approach was (i) to compare the current position of the forest-tundra ecotone with historical photographs and maps in four regions of the Urals along a 1500 km south-north gradient, (ii) to reconstruct the advances of the forest-tundra ecotone and the changes in tree growth form by determining sizes and ages of more than 10 000 trees on 16 altitudinal study plot series installed on slopes differing in topography and dominant tree species, (iii) to relate these changes to climate records from the last century collected at nearby weather stations, and (iv) to identify the effects of microclimatic conditions, such as air and soil temperatures but also the heights and distribution of snow within today's forest-tundra ecotone. Our hypothesis was that the forest-tundra ecotone has expanded upwards along the whole Ural mountain range and that snow cover has played a key role in these advances.

## Materials and methods

### *Study sites*

The treeline ecotone is a diffuse vegetation boundary between forest and alpine tundra (Körner, 2012) that is unique for each slope and therefore does not allow a strict definition of a forest line. Here, we distinguish between four upper limits (boundaries) according to Shiyatov *et al.* (2007) and Moiseev (2011): (i) '*species line*', with trees growing in creeping and shrubby forms (multi- or single-stemmed) with heights reaching the average snow surface; (ii) '*treeline*', with individuals or tree islands of multi- and single-stemmed trees with heights of more than 2 m, distances between trees from 20 to 60 m and a total crown cover of 5–10%; (iii) '*open forest' line*, with distances between trees from 7 to 30 m and total crown cover of 20–30%; and (iv) '*closed forest' line*, continuous forest with distances between trees below 7–10 m and a total crown cover above 40–50%.

Our treeline study was conducted along a 1500 km latitudinal gradient in the Ural mountains, spanning the South Urals (massif Iremel'), North Urals (Konzhakovsky Kamen'), Sub-Polar Urals (massif Neroika), and Polar Urals (massif Rai-Iz, Tchernaya, Slancevaya) (see Fig. 1, Table 1). The altitude of the forest-tundra ecotone increases from about 170–320 m a.s.l. at the Polar Circle to 1225–1375 m a.s.l. in the


**Fig. 1** The Ural mountains span about 1500 km, from 54° to 66°N. The four study regions are 'Iremel' in the South Urals, 'Konzhakovsky Kamen' in the North Urals, 'Maly Chender' and 'Neroika' in the Sub-Polar Urals, and 'Rai-Iz' and 'Chernaya' in the Polar Urals.

South Urals. Dominant tree species are Siberian spruce [(*Picea obovata* (Ledeb.))] and white birch (*Betula pubescens* Ehrh. *ssp. tortuosa* (Ledeb.) Nyman) in the Southern Urals; spruce, birch, Siberian larch (*Larix sibirica* Ledeb.), and Siberian stone pine [*Pinus cembra ssp. sibirica* (Du Tour) E. Murray] in the North Urals; and larch and birch in the Sub-Polar and Polar Urals. More details on the altitudinal ranges and climatic conditions are given in Table 1.

### *Comparisons with historical photographs and mapping of treeline shifts*

Changes in the forest-tundra ecotone of the Ural mountains were assessed by comparing present-day photographs with historical photographs and maps, as well as by analyzing stand age structure. Historical photographs were taken by A.A. Mitenkov in 1900–1905 (South Urals), L.N. Tyulina in 1929–1930 (South), K.N. Igoshina in 1955–1962 (South, Polar), L.D. Dolgushin in 1938–1956 (Sub-Polar), P.L. Gorchakovsky in 1951–1961 (South, North, Sub-Polar), and by S.G. Shiyatov in 1956–1983 (South, North, Sub-Polar, Polar). At the same locations, we made more than 1000 photographs between 1999 and 2011 (Table S1). The locations of the original photographs were identified in the field by seeking and matching the most noticeable landmarks (rocks, hills, summits) on multiple horizon lines (Moiseev & Shiyatov, 2003). On both the historical and recent photographs, we marked the treeline and the boundaries of the closed and open forest and estimated their changes in altitudinal and horizontal distance using Adobe Photoshop v8.0 software. Historical topographic and field-derived thematic maps showing the distribution of different types of forest-tundra vegetation communities were available for the 1910s (Polar Urals), 1950s (Sub-Polar and North Urals), 1960–1970s (South Urals) and 2000s (all parts of Urals) (Shiyatov *et al.*, 2005, 2007; Kapralov *et al.*, 2006, 2007; Fomin *et al.*, 2007). On Russian topographic maps (1:25′000, 1:50′000),

**Table 1** Characteristics of the four study areas in the Ural mountains

| | Study area in the Urals | | | |
|---|---|---|---|---|
| | South | North | Sub-Polar | Polar |
| Local name of mountain | Iremel′ | Konzhakovsky Kamen′ | Neroika | Rai-Iz |
| Geographical coordinates | | | | |
| N | 54°30′–54°34′ | 59°30′–59°40′ | 64°30′–64°35′ | 66°47′–66°51′ |
| E | 58°49′–58°54′ | 59°00′–59°20′ | 59°30′–59°35′ | 65°26′–65°38′ |
| Max. altitude, m a.s.l. | 1586 | 1569 | 1608 | 1236 |
| Altitudinal range, treeline ecotone m a.s.l. | 1225–1375 | 875–1025 | 575–725 | 200–300 |
| Geology | Quartzite, carbon-clay shale | Pyroxenit, gabbroid | Metamorphized shale, granite | Ultramafic rock |
| Mean June air temperature | 16–19°C | 15–18°C | 14–16°C | 12–14°C |
| Mean January air temperature | −15 to −17°C | −17 to −19°C | −19 to −23°C | −21 to −24°C |
| Annual precipitation*, mm | 600–900 | 800 | 400–900 | 450–820 |
| Maximal snow depth, cm | 80–150 | 100–200 | 150–300 | 150–250 |
| Dominant tree species† | Po, Bp | Ls, Po, Bp, Ps | Ls, Bp | Ls, Bp |

*measured at nearest metero stations with altitudes of 457 and 1102 m a.s.l. in the South, 464 m in the North, 29 and 432 m in the Sub-Polar, and 16 and 890 m in the Polar Urals.
†Po - *Picea abies ssp. obovata*, Bp - *Betula pubescens ssp. tortuosa*., Ls–*Larix sibirica*; Ps–*Pinus sibirica*.

forests are defined as areas with a crown cover above 20% and average tree heights above 4 m. Historical maps were compared with online-available satellite images with a spatial resolution of less than 1 m (www.maps.yandex.ru; www.google.ru/maps; www.bing.com/maps). Based on the historical photographs, old topographic maps and old geo-botanical maps, we assessed the altitudinal shifts of the upper boundaries of open (20–30% tree cover) and closed forests (>40–50% tree cover) quantitatively using the ARC/INFO geographic information system (GIS; ESRI Inc., USA) with the AML language. The boundary lines reflecting the positions of trees stands with different cover values in former decades and in the 2000s were converted into a raster format (each line was represented by a set of cells 10 × 10 m in size) and superimposed on a 10-m digital elevation model of the study region in the GIS. Thus, information on altitudinal position was obtained for each raster cell. On this basis, we plotted histograms showing the distributions of upper altitudinal boundaries of open and closed forests at the beginning and end of the study period.

### *Stand structure analysis*

In 2002–2008, we established 16 altitudinal study plot series (transects) along different slopes of the forest-tundra ecotones in all four regions of the Ural mountains (Table S1). Each altitudinal transect consisted of three altitudinal levels: the treeline, the open forest line and the closed forest line. At each altitudinal level, we established 3–6 plots of 20 × 20 m. In each of these plots, all saplings taller than 20 cm and all trunks of single- or multi-stemmed trees were recorded (total $n$ = 20 600). We mapped the location of each stem and measured its height, diameter at the base and breast height, and the area covered by the crown. The age structure of all plots was determined by dendrochronological methods as follows. From trees with diameters exceeding 3–5 cm at their base, we took a tree core at heights from 0 to 30 cm from every second single-stemmed living tree and from every fourth stem of multi-stemmed trees. From every second tree taller than 0.2 m but less than 3–5 cm in diameter, we sampled stem disks at the root collar.

All cores were mounted on wooden strips. Cores and stem disks were both cleaned with a paper knife and a shaving blade. After enhancing ring boundary contrasts with white powder, samples with narrow annual rings were measured on the linear table LINTAB-V (F. Rinn S.A., Heidelberg) to a precision of 0.01 mm and were cross-dated using the computer program TSAP-3.0 (Rinn, 1998) and Cofecha (Holmes, 1995). Samples with wide rings were visually cross-dated, paying special attention to frost and light rings. The dates of tree germination (single-stemmed trees) or the starting of upright growth of individual trunks of multistemmed trees were estimated by correcting for the number of years required to grow to the height of sampling and for the number of years to the pith when the core missed the inner ring. For cores hitting the pith, the distance to the center of the tree was estimated by fitting a circular template to the innermost curved ring (Braeker, 1981). The number of years it took for a stem to grow to the core height was determined from a regression of tree age with height established for all seedlings and saplings at each study site. Age and height were significantly related to each other with an exponential relationship at all sites ($R^2 > 0.6$, $P < 0.001$). In total, we determined the ages of 11 100 trees. The differences among slope types (concave, uniform, convex) were tested by fitting mixed-effects models using maximum likelihood [lme function from the nlme package, R 2.10.1, R Development Core Team (2010)]. The model included effects of region ($n$ = 4), altitude (treeline, open, and closed forest) and slope type sequentially, and we separated our data set into 50-year intervals (e.g., 1801–1850, 1851–1900).

### *Microclimatic measurements*

Temperatures at 2 m height and at 10 cm soil depth were recorded hourly with StowAway TidbiT TBI32-20 + 50 temperature data loggers (Onset Computer Corp., Bourne, MA, USA) from September 2003 until August 2005 at treeline and at open and closed forest lines in the South, North, and Polar Urals (total $n$ = 146). Loggers for measuring air temperature were installed in tree crowns at 2 m height and shielded with tree bark and branches to prevent direct exposure to sun; soil temperature loggers were buried at 10 cm depth both under and outside of tree crowns. To study winter conditions in greater detail, we buried additional temperature loggers at 10 cm soil depth across the forest-tundra ecotone in the South and North Urals for 5 days during additional measurement campaigns in March. These soil temperatures represent minimum values, as soil temperatures continuously decrease throughout the cold season and reach their minimum in March. Snow heights were measured during sampling campaigns in March from 2006 until 2008 in all plots used for stand structure analyses in the four study regions.

### *Climate records*

Historical climatic data for the Ural mountains were taken from weather stations on the eastern and western side along the Ural mountain range: Ufa (54°N45′, 56°E00′; since 1888), Zlatoust (55°N11′, 59°E41′, since 1837), Kazan′ (55°N47′, 49°E11′; since 1812), Krasnoufimsk (56°N37′, 57°E45′; since 1926), Ekaterinburg (56°N48′, 60°E38′; since 1832), Perm (57°N57′, 56°E12′; since 1883), Biser (58°N31′, 58°51′; since 1889), Karpinsk (59°N45′, 60°E01′; since 1838), Cerdyn (60°N24′, 56°E31′; since 1890), Njaksimvol (62°N26′, 60°E52′; since 1888), Troicko–Pecerskoe (62°N42′, 56°E12′; since 1888), Ust′-Sugor (64°N16′, 57°E37′; since 1896), Saran–Paul (64°N17′, 60°E53′; since 1888), Pecora (65°N07′, 57°E06′; since 1888), Petrun′ (66°N28′, 60°E45′; since 1888), and Salekhard (66°N32′, 66°E32′; since 1883). All precipitation data were adjusted according to KNMI Climate Explorer http://climexp.knmi.nl and www.meteo.ru. Temporal changes in summer (June–August) and winter (November–March) temperatures and precipitation were estimated by linear regression for the period 1930–2008 where climate data were available from all weather stations. For longer periods, we used data from the weather station at Zlatoust (457 m a.s.l.; 90 km north-east of Iremel) for the South Urals. For the North

Urals, historical climatic data were taken from the weather station Karpinsk, 45 km east of Konzhakovsky Kamen' at 228 m a.s.l.. Monthly average temperatures were available for 1838–2008 and monthly precipitation for 1837–2004. For the Polar Urals, we took climatic data from the weather station Salekhard, 55 km east of the study sites at 16 m a.s.l., where monthly average temperatures were recorded from 1881–2008 and monthly precipitation from 1899–2000.

## Results

### *Reconstructing treeline advances using historical photographs and maps*

The comparisons of historical with recent landscape photographs, of old topographic maps with modern satellite photos, and of historical with recent tree stand surveys clearly documented advances of the forest-tundra ecotone along the Urals in the second half of the 20th century (Figs. 2, 3; Table 2). The woody vegetation has expanded upwards in all of the four regions and on all slopes, with formerly open areas becoming significantly more forested. Table 2 represents a synthesis of all data, showing upward shifts of the upper treeline, open and closed forest lines by 4.3–8.4 m per decade during the last 33–57 years. The historical photographs demonstrate that the forest advances depended upon substrate and relief. For instance, on the south-west facing gentle and concave slope of Maly Iremel in the South Ural (Fig. 2), the closed forest line (40–50% canopy cover) shifted by 80 m in altitude and by 600 m in horizontal distance during the last 80 years. The cover of the formerly open forest increased from 20% to 60–70%. By comparison, on the southern stony slope of Maly Iremel (Fig. 2; on the right hand side in the background), the boundaries of the open and closed forest only moved upwards by 20–40 m and horizontally by 100–300 m. In the North Urals on the south-western slope of the Serebryansky Kamen', the upper limits of closed and open larch forests moved by 30–40 m in altitude and horizontally by up to 200–300 m over last 50 years on the slopes with developed soil (Fig. 2). However, on the steep boulder fields, the forest expansion was only 10–20 m in altitude and 50–150 m in horizontal distance. Similar changes occurred in the Sub-Polar Urals (Maly Chender; 750 m a.s.l.), where the canopy cover of the forest-tundra ecotone in the valley became more dense between 1939 and 2008 (Fig. 3). In the Polar Urals, on the south-eastern slope of the Rai-Iz Massif at about 300 m a.s.l., the canopy cover increased from 20–30% in 1962 to 50–70% in 2004 (Fig. 3), but the positions of the uppermost tree individuals on paired photos hardly changed. During the same period, the average tree height increased from 8 to 12 m. This pair of photos also documents that not only the trees but also the cover and height of the alder layer has increased significantly in the Polar Urals; young individuals and patches of *Alnaster fruticosus* are now growing on many formerly grass-covered open sites.

### *Tree age structure*

The age structure analysis based on 11 100 trees was carried out on the same slopes where the historical photographs documented an upward shift of the forest-tundra ecotone. Therefore, the age distributions of the living trees reaching 300 years back reflect the development of forest-tundra ecotone since the Little Ice Age (Fig. 4; Figures. S1, S2, and S3). The analysis

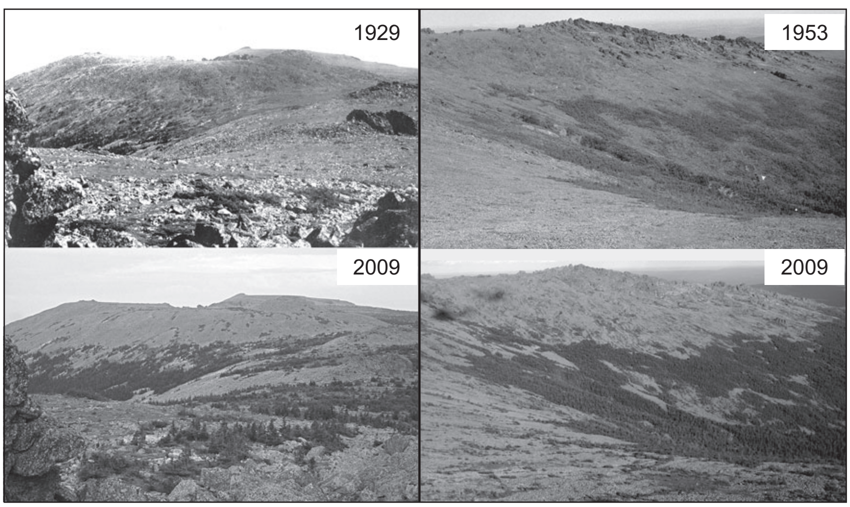


**Fig. 2** Treeline advances in the South Urals ('Maly Iremel', left) and North Urals ('Konzhakovsky Kamen', right) documented by the comparison between historical and recent photographs.

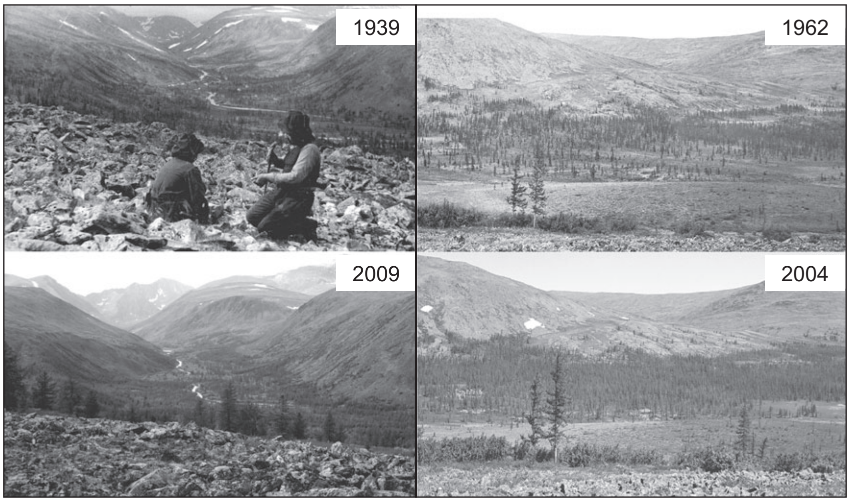


**Fig. 3** Treeline advances in the Sub-Polar Urals ('Maly Chender') and Polar Urals ('Rai-Iz') documented by the comparison between historical and recent photographs.

of tree ages shows a decreasing mean tree age from the closed forest line to the treeline. In the South, North, Sub-Polar, and Polar Urals, mean tree ages decreased by 50, 100, 50, and 100 years, respectively, across 100 m in altitude. Moreover, tree ages changed from mostly even-aged structures in the lower parts of the forest-tundra ecotone to left-skewed age distributions dominated by trees younger than 70 years in the upper part of the ecotone. Nine of 11 sites at the treeline had a predominance of younger trees, and only one snow-rich convex site in the South Urals had an even age structure. The age structures show three main recruitment phases, the first starting around 1840 and peaking in 1900, the second peaking in the 1940s, and the third peaking in the 1970s (Fig. 4). However, the advances of the forest-tundra ecotone differed strongly among the various altitudinal transects, with slope topography playing a significant role in the rate of advance ($P < 0.01$; Fig. 4, Figures. S1, S2, and S3). On wind-sheltered concave slopes with thick snow covers, treeline reached higher altitudes and tree establishment started earliest, followed by transects with uniform slopes, and the more wind-exposed slopes with a shallow snow cover showed the smallest and latest advances. This pattern occurred in all four regions (see Figures. 4, S1, S2, and S3).

In the North Urals, slope topography also determined tree species composition (Fig. 4): *Larix sibirica* grew primarily on convex and uniform slopes, *Picea obovata* on concave slopes, and *Betula pubescens* on very concave slopes. Our tree age analysis indicated that these patterns changed during the last century: young *Picea obovata* trees started to appear on uniform slopes, and *Betula pubescens* trees started to appear on uniform as well as on concave slopes. In the Sub-Polar Urals, *Betula pubescens* additionally started to grow on uniform and concave slopes during the last century (Figure. S2). Our analysis of tree ages showed that the appearance of the two tree species indeed resulted from the establishment of 'new' tree species and did not simply reflect shorter regeneration cycles, as both *Betula* and *Picea* can reach much greater ages (at least 200 years) under favorable growing conditions on other transects.

### *Changes in growth forms*

Trees in the forest-tundra ecotone have two main growth forms: single-stemmed trees with one upright stem and multistemmed trees with several upright stems per tree individual (Fig. 5). The contribution of these two growth forms changed across the forest-tundra ecotone, with higher contributions of multistemmed trees at the treeline than in the closed forest (data not shown; for Polar Urals see Devi *et al.*, 2008). In addition, the contribution of multistemmed trees was smaller on transects with a concave slope and thick snow cover than on transects with uniform or convex slopes (15% vs. 60%; data not shown). Our analysis of tree ages showed a changing contribution of multi- vs. single-stemmed trees during the last centuries (Fig. 5). The multistemmed trees are substantially older than the single-stemmed ones: 87%, 31%, and 93% of the stems appearing before 1950 were from multistemmed trees in the South, North, and Polar Urals respectively. Thereafter, more than 95% of the stems were from single-stemmed trees.

**Table 2** Altitudinal shifts of treeline, open and closed forest lines on slopes of the Ural mountains in the second half of the 20th century (Means ± SD). The boundary shifts were estimated by comparisons of historical with recent landscape photographs (regular font), old topographic maps with modern satellite photos (*italic font*) and data of historical and recent tree stand surveys (**bold font**). More details on measured parameters can be found in Table S1

| | Study region | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | South (massif Iremel') | | | North (Konzhakovsky Kamen') | | | Sub-Polar (massif Neroika) | | | Polar (surroundings Mnt. Chernaya) | | |
| | | Altitude shift (m) | | | Altitude shift (m) | | | Altitude shift (m) | | | Altitude shift (m) | |
| Upper boundary | Span year | Absolute | Per decade | Span year | Absolute | Per decade | Span year | Absolute | Per decade | Span year | absolute | per decade |
| Treeline | **1973–2006*** | **14.1 ± 13.5** | **4.6 ± 4.1** | – | – | – | – | – | – | 1962–2004 | 28 ± 9.3 | 6.4 ± 2.2 |
| Open forests line | *1952–2009* | *47.9 ± 25.7* | *8.4 ± 4.5* | **1956–2005‡** | **42 ± 25.5** | **8.4 ± 4.9** | 1970–2009 | 31 ± 19.5 | 7.9 ± 3.8 | 1962–2004§ | 31 ± 12.5 | 7.1 ± 2.9 |
| Closed forests line | *1955–1985†* | *24.6 ± 24.3* | *8.1 ± 8.1* | *1956–2009* | *41 ± 25.0* | *7.7 ± 4.7* | *1956–2009* | *41 ± 22.9* | *7.7 ± 4.4* | 1962–2004§ | 29 ± 11.6 | 6.7 ± 2.7 |

*Kapralov *et al.* (2007), stand survey.
†Fomin *et al.* (2007), historic maps vs. satellite photos.
‡Kapralov *et al.* (2006) stand survey.
§Shiyatov *et al.* (2005, 2007), historical vs. recent photographs combined with mapping.
others, this study.

### *Microclimate in the forest-tundra ecotone*

Microclimatic conditions varied strongly across the forest-tundra ecotone during winter but only slightly in summer. Mean annual air temperatures differed by less than 1 °C between the three altitudinal levels within the forest-tundra ecotone. At 10 cm soil depth, mean temperatures during the growing season were between 8.0 and 11.7 °C at the treeline in the South and Polar Urals (Table 1). Across forest-tundra ecotones, growing season temperatures in soils hardly changed, with less than 1 °C higher temperatures in the closed forest than at treeline. In contrast with the summer, soil temperatures during winter were less uniformly distributed within the forest-tundra ecotone. They were around −1 °C in the closed forest of all regions but −2 °C to −12 °C at the treeline (Fig. 6). The strong decrease in soil temperature from the closed forest to the treeline was related to the strong decline in snow heights in all transects (Fig. 6), which additionally depended upon the canopy cover and wind exposure of the transects. Averaged across all transects and all measurement campaigns in the South and North Urals, the mean snow height increased slightly from 77 ± 2 cm in the closed forest to 91 ± 3 cm at the upper boundary of the open forest but decreased strongly to 30 ± 2 cm toward the treeline. At treeline, the snow height was spatially highly heterogeneous. Snow accumulation was often more than 100 cm on the leeward side of tree clusters but was less than 25 cm on the windward side and in open areas. Snow height also differed among slope types. At treeline, snow heights were less than 30 cm on convex slopes but above 100 cm on concave slopes (data not shown).

### *Climate records at weather stations*

Climate records at weather stations along the Ural mountains documented a particularly strong change in winter conditions during the 20th century (Fig. 7). For the period 1930–2009, there were no significant increases in summer temperature at any of the 16 weather stations. Winter temperatures, however, increased at eight of the stations, and all of these stations were located south of 59°N (linear regression; $P < 0.05$; Figure. S4). Precipitation increased significantly at 14 of the 16 stations during winter but at only five stations during summer. The increase in winter precipitation was greater on the western side than on the eastern side of the Urals (10 vs. 4 mm decade$^{-1}$; Fig. 7). In relative terms, this increase in winter precipitation corresponded on average to 50 ± 8% higher values compared to the period from 1930–1940.

 

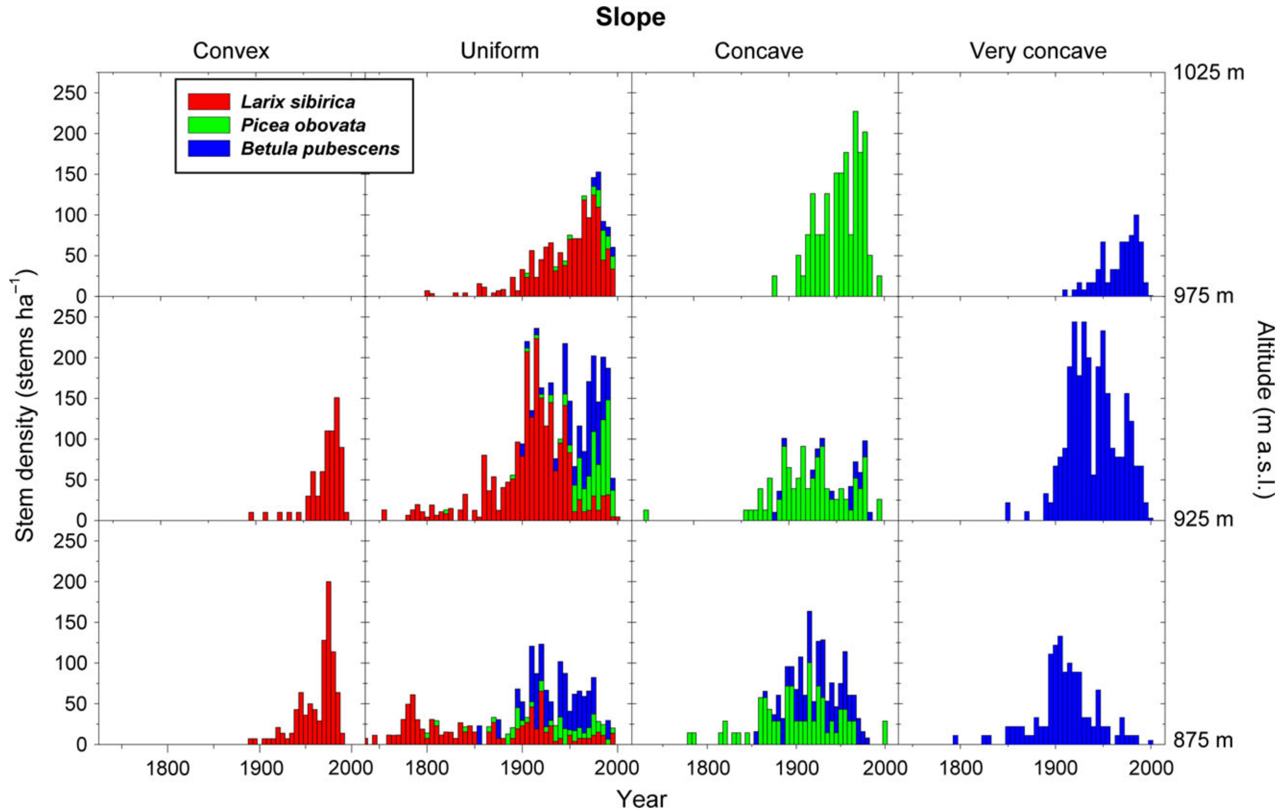


**Fig. 4** Tree age structure within the treeline ecotone on slopes with different topographies in the Northern Urals ('Konzhakovsky Kamen'). Columns represent the number of living trees established in a specific 5 years interval (e.g., 1901–1905).

Tree establishment showed a closer relationship with winter precipitation than with summer temperatures. During the first recruitment phase from 1840 until 1925, mean summer temperatures did not change significantly (Fig. 8). Winter precipitation, however, increased between 70% and 100% from 1840 until 1925 ($P < 0.05$) and correlated significantly with tree establishment ($r = 0.76$; $P < 0.001$ for the North Urals; $r = 0.62$, $P < 0.01$ for the South Urals). In the Polar Urals, the precipitation record of Salekhard started in 1895 and, hence, did not allow such an analysis. After the first recruitment wave, there was no direct relationship between climatic parameters and tree establishment. However, the greatest winter precipitation occurred in years after 1960.

## Discussion

### *Large scale treeline advances*

Our results show that the forest-tundra ecotones along the whole Ural mountain range have changed substantially during the last century. The comparisons of historical and recent photographs, old topographic maps, and the tree-age analysis along 16 transects all indicate upward shifts of the upper treeline as well as the open and closed forest lines in the four different regions of the Ural mountains. Areas that had a sparse tree cover of less than 20% at the beginning of the 20th century are now covered by a dense forest, and thus, the forested areas have advanced upwards. Koshkina *et al.* (2008) observed high numbers of seedlings and sapling within the open-forest areas of the South and Polar Urals, which implies that the forest expansion is ongoing and that further changes can be expected in the near future. The photographic comparisons, however, show that tree species lines have hardly shifted upwards; the establishment of trees without shelter in the open tundra is apparently much slower than in areas where existing trees provide protection against extreme climatic conditions. We therefore conclude that the major changes in the forest-tundra ecotone have been a densification of formerly open forests and an increase in biomass of existing trees.

In the Polar Urals, there are thousands of 1500 year old subfossil trees, both standing upright and lying horizontally, at and above the current treeline (Mazepa, 2005). These trees all died between the 7th and the 19th century and their wood decomposes extremely slowly in the dry climate with extremely cold winters. The tree

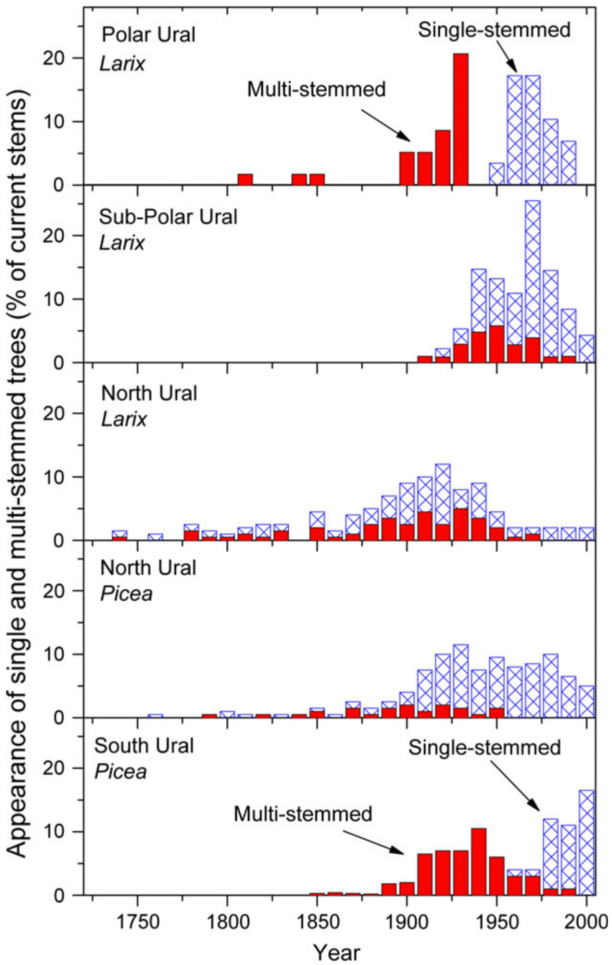


**Fig. 5** Appearance of living multistemmed and single-stemmed trees in the treeline ecotone of the Ural mountains.

remnants show that past climatic changes caused upward and downward shifts of the forest-tundra ecotone (Mazepa, 2005; MacDonald *et al*., 2007). In addition, the subfossil wood indicate that the current tree generation has not reached its former growth limit and that it lags behind ongoing climatic changes. Moreover, the presence of subfossil trees implies that the ages and the spatial distribution of the current living tree generation mostly reflect the expansion of a 'new' forest in space and time. For the other more southern regions such as the South and North Urals, where tree remnants do not occur, the historical photographs provide evidence of a spreading of trees into formerly open areas.

Our analysis of historical photos and tree-age structures reveal that the rates of forest expansion have been very site dependent, with the highest upward shifts occurring on gentle concave slopes with well-developed soils. The measured mean elevational shifts of the treeline ecotone of 4.6–8.4 m per decade are similar to shifts reported in Siberian mountains further east. For the Putorana Mountains in Northern Siberia, a tree-age analysis along an altitudinal gradient indicated an upward shift of the forest-tundra ecotone by 30–50 m during the last century (Kirdyanov *et al*., 2012). In Southern Siberia, Kharuk *et al.* (2010) used archived maps and satellite images from the Senigelen Ridge to estimate that the treeline advanced by about 60 m in altitude between 1960 and 2000. Comparable treeline advances have also been reported for the Scandes, where Kullman & Öberg (2009) observed mean treeline advances of 70–90 m in altitude over the past century, but only on 'protected' concave slopes and not under wind-exposed topoclimatic conditions. Compared to the rapid forest expansion, the historical photographs of the Urals did not indicate substantial shifts of the positions of the uppermost trees and thus, of the species line (Figs. 2,3). Also, Koshkina *et al.* (2008) did not find tree seedlings beyond the current species line in the South and Polar Urals, strongly suggesting that the uppermost trees will not move upwards in the near future. Greater amounts of viable seeds and facilitated growth of trees emerging in the shelter of already established trees are likely reasons for the faster upward spread of the forested zones than of the species lines. Trees in forested zones are less exposed to wind, are covered under more snow, and grow in warmer soils than the uppermost tree individuals that have to survive in open terrain. At the Alaskan treeline, for instance, Lloyd (2005) estimated that the timespan for an open forest to develop from the first tree seedling is 150 years, i.e. the time period since the Little Ice Age.

### *Snow cover may drive forest expansion*

What drives the large scale upward expansion of the forest-tundra ecotone? Although treeline sites in the Urals are in rather remote areas, changing pressure by browsers might have contributed to this change, as reported for the Subarctic Scandes and the European Alps (Gehrig-Fasel *et al*., 2007; Aune *et al*., 2011; Van Bogaert *et al*., 2011). In the Urals, however, hunting pressure had been consistently intense for centuries: for fur trading until the 19th century and in organized hunting during the Soviet time. Hunting has decreased slightly only in recent years after the breakdown of the Soviet Union (Korytin, 2011). In the Polar Urals, the intensity of reindeer herding by nomadic Nentsy people has also been continuous for centuries, with a slight increase during the last decades (Stammler, 2005). Given that treeline advances occurred along the whole Ural mountain range, we presume that pressure by browsers did not change substantially during the last

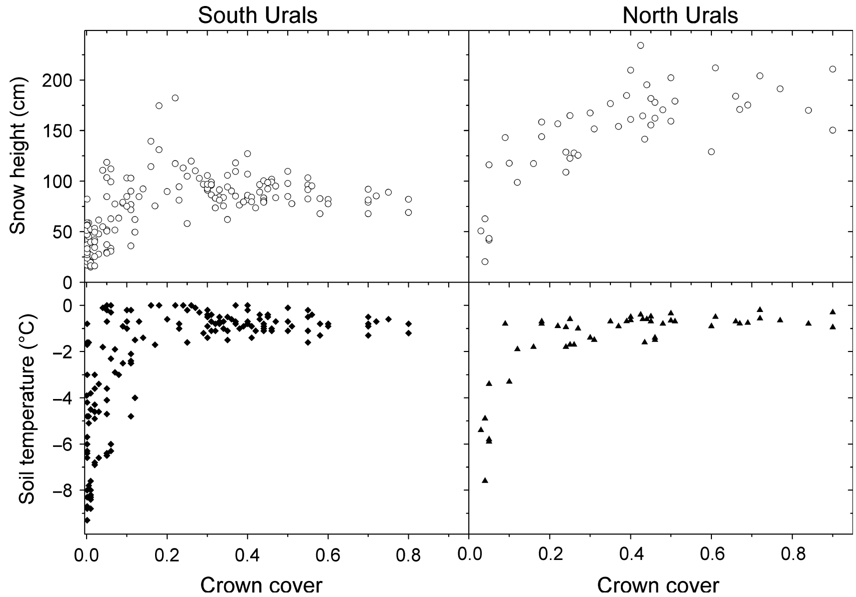


**Fig. 6** Relationship between crown cover and snow height, as well as soil temperatures at 10 cm depth. Measurements of snow heights and soil temperatures were carried out in March 2006–2008.

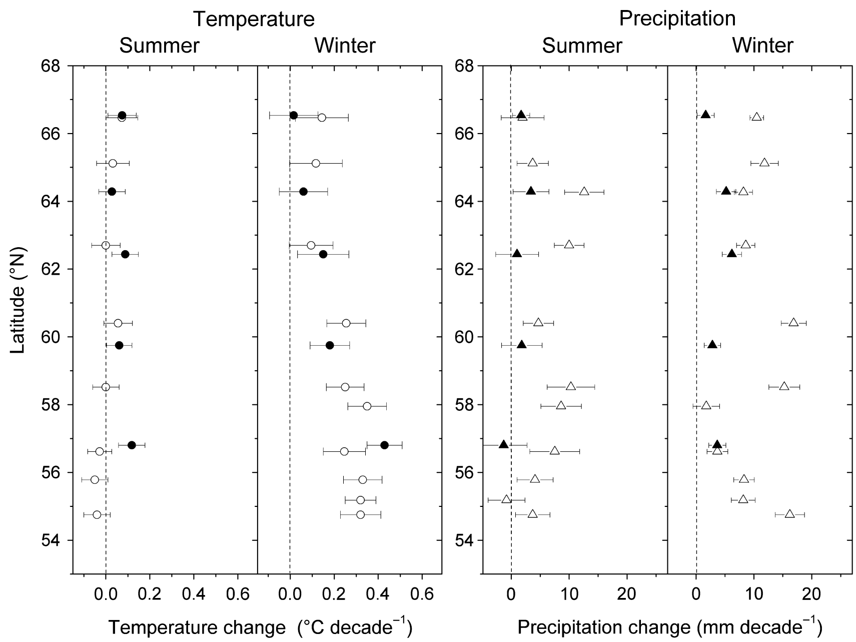


**Fig. 7** Decadal changes in summer and winter temperature and precipitation from 1930–2000 at weather stations along the Ural mountain range. Open symbols represent climate records from weather stations on the western side of the Urals and filled symbols indicate stations on the eastern side of the mountain range.

century and that treeline advances were rather driven by climatic change.

Treeline advances have often been attributed to climatic warming, particularly summer warming because temperatures during the vegetation period are thought to be the main factor controlling treeline formation (Holtmeier & Broll, 2005; Kharuk *et al.*, 2010). In the Urals, however, climate records show only very small increases in summer temperatures, i.e. less than 0.05 °C per decade (Fig. 7). Our study rather suggests that changes in winter conditions, particularly increases in snow fall, might have been the primary cause of the

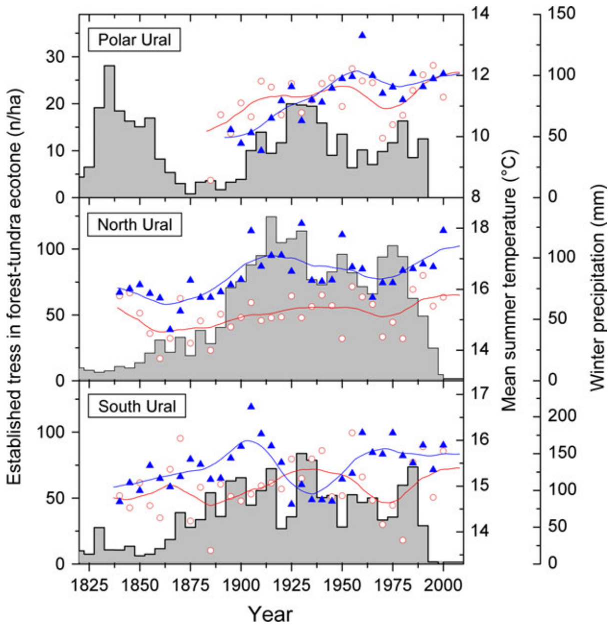


**Fig. 8** Age distribution of established trees in the forest-tundra ecotone (grey bars) and climate records in the Urals. Summer temperatures are indicated by the red line, which shows the moving average over 20 years, and by the red circles, which represent 5 year averages. Winter precipitation is indicated by the blue line and blue triangles. Climate records are taken from nearby weather stations: Salekhard in the Polar Urals, Karpinsk in the North Urals and Zlatoust in the South Urals.

forest advances in the Urals: (i) Warming observed during winter was double that observed during summer, but winter precipitation showed the largest changes (Fig. 7). In the Ural mountains, winter precipitation has increased on average by 7 mm per decade. This change corresponded almost to a doubling of winter precipitation during the 20th century in the Polar Urals. (ii) Snow cover played an important role in the spatio-temporal dynamics of treeline advances in the Urals. First, forest-tundra ecotones reached higher altitudes on concave slopes covered with a thick snow pack during winter (80–200 cm) than on wind-exposed ridges with a shallow snow cover of less than 30 cm (Fig. 4). Second, forest-tundra ecotones experiencing a thick snow cover mainly started to shift upwards around 1900 AD while forests on slopes with medium and shallow snow covers started to expand in the 1950s and 1970s (Fig. 4).

Our conclusion that increasing winter precipitation is an important driver for the observed shift of the forest tundra-ecotone is in agreement with a recent satellite image based survey from the lowlands of Northern Siberia by Frost & Epstein (2014), which showed that canopy expansion rates of tall shrubs and trees during the last decades correlate more closely with winter precipitation than with summer temperature. A thick snow cover protects young trees from frost, wind damage, and abrasion (Holtmeier, 2003). Moreover, snow insulates soils effectively. Our *in situ* measurements show higher winter soil temperatures under thick snow packs, either on wind-protected slopes, in the closed forests, or on the leeward side of tree clusters than under shallow snow cover (Fig. 6). Warmer soils are associated with less damage of the fine root system (Sveinbjörnsson *et al.*, 1996; Groffman *et al.*, 2001) and can lead to higher nitrogen availability (Sturm *et al.*, 2005). In the South Urals, Kammer *et al.* (2009) showed that much more nitrogen is mineralized in soils in snow-protected forests than in soils in tundra above the treeline. As trees affect snow accumulation, the increase in snow fall, especially in the late 19th and early 20th centuries, might have induced a positive feedback. More snow allowed trees to grow better and larger trees promoted the accumulation of additional snow, thereby providing more favorable conditions for the establishment of a new tree generation (Fig. 9). Our measurement campaigns within the forest-tundra ecotone in late winter support such a feedback: when crown covers were below 20%, snow heights in between trees were low and soil temperatures reached as low as −10 °C. However, when tree crowns covered more than 20% of the area, then snow heights exceeded 50–70 cm and soil temperatures in winter remained above −2 °C. This snow feedback might be accentuated further when higher summer temperatures (e.g., between 1920 and 1940 and during the last two decades) stimulate the growth of trees thereby enhancing their role as barriers for drifting snow. The decoupling of tree establishment with climate after the first recruitment phase might also be due to a feedback between snow and tree growth (Fig. 8). While the establishment of the first tree generation correlated positively with

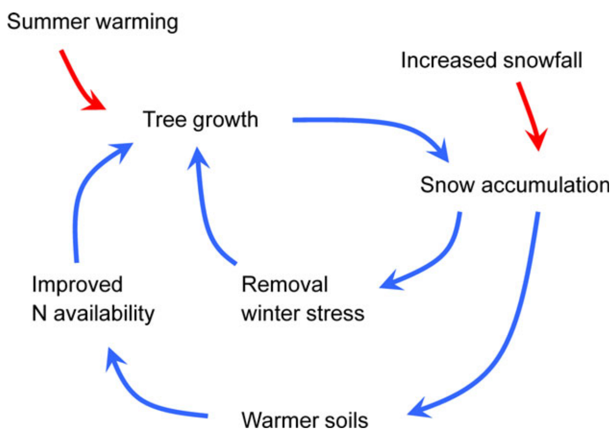


**Fig. 9** Feedback between climatic changes and forest expansion.

winter precipitation (1840–1925), the establishment of the following tree generation was less directly dependent on the amount of snow fall, probably because snow accumulating between existing trees facilitated the survival of seedlings and trees.

Increased winter precipitation is also indirectly related to winter temperature and permafrost depth, two other factors discussed in the literature as potential drivers of treeline advances. In their global meta-analysis, Harsch *et al.* (2009) found, contrary with their expectations, that treeline advance was more strongly associated with winter rather than with summer warming. They explained this finding by the removal of winter stress. Winter precipitation was not included in their set of variables, but warmer winter temperatures usually occur at lower air pressures and are therefore generally associated with more precipitation. Findings from our study suggest that increases in snow cover will have a much larger impact on tree survival than increases in temperature by a few degrees under very cold conditions because a thick snow cover effectively removes winter stress (Holtmeier, 2003 and discussion above). Permafrost depth was identified as one of the key factors for the magnitude of treeline advances in Alaska and Northern Canada (Lloyd, 2005; Payette, 2007). For instance, Suarez *et al.* (1999) did not detect treeline advances in tundra soils with less than 0.5 m deep active layers. Similarly, at the latitudinal treeline in North-Western Siberia, Wilmking *et al.* (2012) observed a lack of tree establishment after the 1980s, which they attributed to a strong decrease in the active layer depth toward the treeless tundra. Snow cover is one of the key drivers of permafrost depth (Zhang, 2005). Hence, increases in winter precipitation and snow height will very likely promote permafrost melt, thereby improving conditions for tree establishment.

Reconstructions of climatic conditions indicate that the 20th century was the wettest period during the last millennium in Eurasia (Treydte *et al.*, 2006), and instrumental records show an increasing precipitation on land at mid and high latitudes in the Northern Hemisphere during the last century (New *et al.*, 2001). Moreover, climate change scenarios for Eurasia predict higher precipitation in the coming century, particularly in winter (Stocker *et al.*, 2013). We therefore suggest that that increases in snow fall have been and will continue to be at least as important for treeline advances as increasing winter temperatures in the Urals and probably also in other regions of Eurasia.

### *Changes in growth forms and tree species*

The growth form of treeline trees is a response to their harsh environment, in particular to winter stress (Lavoie & Payette, 1992; Pereg & Payette, 1998; Holtmeier, 2003; Harsch & Bader, 2011). At the upper limit of tree growth, trees often form clusters where several stems belong to one tree individual. These multistemmed trees result from winter stress such as wind abrasion, snow and ice damage, and winter desiccation (Pereg & Payette, 1998). For the Polar Urals, Devi *et al.* (2008) showed that these multistemmed trees grew in a creeping form for centuries but that vertical stems emerged when conditions improved at the beginning of the 20th century. In our large scale study, we found multistemmed trees at the treeline in three of four regions in the Urals. Moreover, the dominant growth form changed during the last century in the forest-tundra ecotone of the South, North, and Polar Urals (Fig. 5). While multistemmed trees were the predominant growth form 100 years ago, the majority of trees in the new generation in all regions were single stemmed. We consider these high contributions of multistemmed trees in the first phase of forest expansion and the recent establishment of single-stemmed trees as additional evidence that improving winter conditions has been an important driver for the observed treeline advances.

Another bio-indicator for increasing snow heights during the last century is the changing tree species composition in the North and Sub-Polar Urals (Fig. 4). *Betula pubescens*, characterized by flexible wood, primarily grows at sites that are protected by a thick snow cover (Kullman & Öberg, 2009), i.e. on concave slopes. However, in the mid 20th century *Betula* also started to appear on uniform slopes, very likely as a result of improving snow conditions.

The occurrence of multistemmed trees resulting from winter stress implies that treelines occur below the thermal growth limit of trees (Harsch & Bader, 2011). In our study, this assumption is supported by relatively high soil temperatures during the growing season. While the thermal limit for wood formation is approximately 6 °C (Rossi *et al.*, 2007) and 'typical' treelines occur at soil temperatures of 5.4–7.8 °C during the vegetation period (Körner & Paulsen, 2004), measured summer soil temperatures ranged between 8 and 11.7 °C at treeline in the Urals and hence above critical temperatures. The consequences of relatively high and hence nonlimiting summer temperatures are that the forest-tundra ecotone can advance rapidly when other restricting factors, such as winter conditions, improve. In addition, our findings suggest that the rate of forest expansion is particularly fast for treelines with multistemmed trees, where vertical stems develop from existing but so far creeping trees. In comparison, the establishment of 'new' trees will likely occur more slowly because these trees must successfully emerge from seeds and compete with other plants.

In summary, historical photographs and the analysis of tree-age structures in four regions throughout the 1500 km-long Ural mountain range show that the forest-tundra ecotone has moved upwards significantly during the last century. The closed and open forest lines have expanded by as much as 50 m in altitude during the second half of the 20th century and dominant growth forms of trees have changed from creeping, shrubby and multistemmed trees to trees with a single stem. The positions of the uppermost tree individuals, however, have hardly changed, presumably because tree establishment is hampered by the harsher environment and lack of viable seeds above the species line. Our results suggest that improving winter conditions, probably in combination with increasing summer temperatures and longer vegetation periods, contributed to the large changes observed in the forest-tundra ecotone. First, climate records indicate increases in winter precipitation during the last 150 years and second, the forest expansion started earlier on snow-rich and thus, protected sites. High seedling and sapling densities in the open forest indicate that the forest expansion is ongoing. The likely consequences of treeline advances are that the newly forested areas will absorb more solar radiation, particularly during winter (Loranty *et al.*, 2014; de Wit *et al.*, 2014), and C sequestration in plant and soils will be altered (Devi *et al.*, 2008; Kammer *et al.*, 2009). The ongoing forest expansion also indicates that alpine tundra vegetation will disappear from the South Urals and large parts of the North Ural, where the treeline is already close to the highest peaks.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Tree age structure of the forest-tundra ecotone in the South Urals ('Maly and Bolschoi Iremel').
**Figure S2.** Tree age structure of the forest-tundra ecotone in the Sub-Polar Urals ('Maly Chender').
**Figure S3.** Tree age structure of the forest-tundra ecotone in the Polar Urals ('Rai-Iz').
**Figure S4.** Summer and winter temperatures and precipitation in the South, North, and Polar Urals. Linear trends are indicated when significant ($P < 0.05$). Climate records are taken from nearby weather stations: Salekhard in the Polar Urals, Karpinsk in the North Urals and Zlatoust in the South Urals.
**Table S1.** Overview of measured parameters in this treeline study in the Ural mountains.