WILEY

RESEARCH PAPER

Latitudinal decline in stand biomass and productivity at the elevational treeline in the Ural mountains despite a common thermal growth limit

Frank Hagedorn[1] | Melissa A. Dawes[1] | Maxim O. Bubnov[2] | Nadezhda M. Devi[2] | Andrey A. Grigoriev[2] | Valeriy S. Mazepa[2] | Zufar Y. Nagimov[3] | Stepan G. Shiyatov[2] | Pavel A. Moiseev[2]

[1]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

[2]Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, Russia

[3]Ural State Forest Engineering University, Yekaterinburg, Russia

Correspondance
Frank Hagedorn, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, CH-8903, Birmensdorf, Switzerland.
Email: frank.hagedorn@wsl.ch

Funding information
ERA.Net RUS, Grant/Award Number: STProject-207 ; Russian Scientific Foundation, Grant/Award Number: RSF-17-14-01112 ; Russian Ministry of Science and High Education, Grant/Award Number: RFBR-19-05-00756

Handling Editor: Sebastien Lavergne

Abstract

Aim: To quantify tree biomass and stand productivity of treeline ecotones and identify driving factors.

Location: treeline ecotones of seven regions from the South to Polar Urals, spanning a latitudinal gradient of 1,500 km.

Taxa: *Picea obovata*, *Betula pubescens*, *Larix sibirica*.

Methods: Stand biomass and productivity were estimated across 18 elevational transects from the tree species line to the closed forest line based on allometric measurements of 326 trees (including roots for 53 trees), stand structure assessments and demographic patterns of 20,600 trees. Stand growth data were linked to (a) temperatures monitored in situ for five years in the South and Polar Urals, (b) climate variables extrapolated from nearby climate stations and (c) measures of nutrient availability in soils and tree foliage.

Results: treeline position along the latitudinal gradient occurred at a similar mean growing season temperature. Despite the common cold limitation of tree distribution along the Ural mountain range, stand biomass and productivity within the treeline ecotone decreased by a factor of three and five from the South to the Polar Urals, mainly due to a declining stand density. Among climatic variables, growing season length decreased by 20% and winter temperatures declined by 4°C towards the Polar Urals, whereas growing degree days > 5°C remained similar, averaging 554 ± 9°C. Soil development was poorer in the Polar than in the South Urals, and plant-available N and P in the soil were 20 and 30 times lower, respectively, probably due to lower winter temperatures.

Main conclusions: Our results suggest that once the thermal limitation for tree growth is relieved, soil fertility—restricted by permafrost and low soil temperatures during winter—plays a key and yet underexplored role for stand productivity in

treeline ecotones. The observed latitudinal decline in stand productivity is important for above- and belowground diversity and functioning.

KEYWORDS

allometry, climate, growing season length, nitrogen, permafrost, phosphorus, soil, treeline

1 | INTRODUCTION

Climate warming during the past century has repeatedly been shown to have profound effects on the productivity, distribution and diversity of vegetation throughout the world (Walther et al., 2002). The most pronounced temperature increases have occurred at high elevations and high latitudes (Pepin et al., 2015; Stocker et al., 2013), and ecosystems in these cold regions have experienced particularly striking changes (e.g. Devi et al., 2008; Steinbauer et al., 2018). Responses of vegetation to changes in climate are expected to be rapid and extreme in ecotones, boundary ecosystems where plant life-forms and soil conditions change rapidly over relatively short distances (e.g. Allen & Breshears, 1998).

The treeline ecotone, where closed forest transitions to alpine or arctic tundra, is both a boundary and a cold ecosystem and is thus particularly valuable as a bio-indicator of climate change (Holtmeier, 2003). Indeed, treelines in many regions of the world have shifted to higher elevations or higher latitudes over the last century (Hagedorn et al., 2014; Harsch, Hulme, McGlone, & Duncan, 2009; Kullman & Öberg, 2009; Lloyd, 2005; Shiyatov, Terent'ev, Fomin, & Zimmermann, 2007). The expansion of forests into alpine and arctic tundra can impact plant productivity and diversity (Gazol, Moiseev, & Camarero, 2017) and has important implications for carbon and nutrient cycling (Hagedorn, Gavazov, & Alexander, 2019; Kammer et al., 2009; Speed et al., 2015), as well as snow accumulation and albedo (de Wit et al., 2014; Schwaab et al., 2015), which can in turn affect ecosystem functioning and result in further vegetation change. It is therefore highly relevant to understand how environmental conditions influence current treeline ecosystems and contribute to future shifts in treeline position and characteristics.

The positions of high elevational treelines throughout the world follow an isotherm of a mean growing season temperature of 6–8°C (Körner, 1998; Körner & Paulsen, 2004; Müller et al., 2016), strongly suggesting that the high-elevation limit of tree growth at the global scale is primarily driven by low-temperature constraints on growth processes (Holtmeier, 2003; Körner, 2012). The importance of temperature in treeline formation has been supported by studies documenting treeline shifts in association with rising regional temperatures, although warmer winter conditions with more snow seem to have contributed to treeline changes as well (Hagedorn et al., 2014; Harsch et al., 2009). Other factors have also been found to determine treeline position and characteristics at the local level and may drive tree growth rates once a low-temperature limitation is released. For example, low nutrient availability has been linked to low rates of photosynthesis and growth of

trees at the alpine treeline in Alaska (Sullivan, Ellison, McNown, Brownlee, & Sveinbjörnsson, 2015), and increased growth of trees with nutrient addition has been observed in treeline ecotones in the subarctic (Susiluoto, Hilasvuori, & Berninger, 2010; Sveinbjornsson, Nordell & Kauhanen, 1992) and in the Swiss Alps (Möhl et al., 2019). Soil moisture, permafrost depth, wind exposure and snow cover have also been found to be important drivers of tree growth and survival in treeline ecosystems (Barbeito, Dawes, Rixen, Senn, & Bebi, 2012; Lloyd, 2005; Müller et al., 2016).

Most treeline studies have focused on understanding drivers and limitations of tree aboveground growth. In comparison, knowledge of tree biomass and productivity, especially regarding the belowground compartment, and the environmental factors influencing biomass production is severely limited, probably because of the enormous field effort and logistical challenges involved in measuring biomass at remote treeline locations. Investigations including estimates of biomass pools and productivity have mainly come from a single or small number of sites (Bernoulli & Körner, 1999; Liu, Nie, Kong, & Luo, 2016; Moiseev, Bubnov, Devi, & Nagimov, 2016) and/or have been confounded with experimental manipulation (Dawes et al., 2015; Speed et al., 2015). At larger scales, tree biomass and vegetation productivity have increasingly been estimated by remote sensing techniques (e.g. Park et al., 2016). The resolution provided by satellite images is, however, too coarse to assess treeline dynamics, and the use of aerial photographs or Light Detection and Ranging (LiDAR) requires ground truthing (Coops, Mörsdorf, Schaepman, & Zimmermann, 2013) through labour-intense tree allometry determination. Therefore, larger-scale investigations including detailed measurements of stand structures, tree biomass and productivity within natural treeline ecotones are valuable for improving our understanding of C dynamics and the overall climate balance including albedo effects through vegetation changes in current treeline ecosystems, as well as for predicting how these systems will be altered by global change (De Wit et al., 2014; Schwaab et al., 2015).

In this study, we investigated treeline patterns along a north–south gradient in the Ural mountains of Russia. The 13.3° latitudinal range of the study sites comprises treelines with different tree species and varying aspects, climatic conditions and soil properties, making it possible to differentiate between local and larger-scale factors shaping treelines. In contrast to other European mountain ranges, the Urals have never been disturbed by extended human activities or exposed to considerable regional air pollution (Hagedorn et al., 2014). Comparisons of historical and recent photographs coupled with detailed analyses of tree demography have demonstrated a clear upward shift in treeline, by 4 to 8 m per decade, across

the north–south extent of the Urals (Devi et al., 2008; Hagedorn et al., 2014; Moiseev et al., 2016; Shiyatov & Mazepa, 2015). Here, we combine demographic information with detailed biomass measurements of three key treeline tree species to estimate stand-level biomass and productivity within the treeline ecotone across the entire Ural latitudinal gradient. Our objectives were: (a) to quantify the biomass and productivity of trees along elevational gradients spanning the treeline ecotone, across the north–south extent of the Ural mountains; and (b) to identify the key factors influencing treeline position and productivity of treeline trees along the latitudinal gradient by relating tree data to regional climate records and site properties, including multi-year data on temperature and soil conditions. We hypothesized that treeline position is primarily related to growing season temperature, whereas tree productivity is driven by other factors, such as soil fertility, whose importance increases with increasing distance downward from the treeline.

## 2 | MATERIALS AND METHODS

2.1 | Study sites

Our treeline study was conducted at 18 sites across a 1500-km latitudinal gradient in the Ural mountains (54.5 to 67.9°N), spanning the South Urals (massif Iremel', with peaks Mali Iremel' and Bolschoi Iremel'), North Urals (Konzhakovskii Kamen', Serebryankii Kamen', Tylaiskii Kamen', Molebnii Kamen', Yaruta), Sub-Polar Urals (Hus-Oika, Neroika) and Polar Urals (Tchernaya, Malikpe) (Figure 1, Table S1). The elevation of the treeline ecotone decreases from 1225–1375 m a.s.l. in the South Urals to 150–300 m a.s.l. in the Polar Urals (Figure 1, Table S1). The dominant tree species are as follows: Siberian spruce (*Picea obovata* Ledeb.) and white birch (*Betula pubescens* Ehrh. ssp. *tortuosa* (Ledeb.) Nyman) in the South Urals; spruce, birch and Siberian larch (*Larix sibirica* Ledeb.) in the North Urals; and larch and birch in the Sub-Polar and Polar Urals (Figure 1). Although

tree species co-exist in each region, each transect was clearly dominated by one species. In the South Urals, the tundra is dominated by dwarf shrubs (*Vaccinium uliginosum* L., *Vaccinium vitis-idaea* L.), grasses (e.g. *Festuca igoschiniae* Tzvelev) and sedges (e.g. *Carex vaginata* Tausch). Below 1,300 m a.s.l., *Picea obovata* trees alternate with open areas where herbaceous species (*Polygonum bistorta* L., *Polygonum alpinum* All.) grow to a height of 1.5 m. From the North to Polar Urals, the vegetation forming the tundra and dominating the open areas between groups of trees consists of various shrubs and dwarf shrubs (*Betula nana* L., *Salix* spp., *Vaccinium* spp., *Empetrum* spp., *Arctous alpina* L., *Dryas* spp.) and herbs (e.g. *Polygonum bistorta* L., *Anemone narcissifolia* L. subsp. *biarmiensis* (Juz.) Jalas, *Carex bigelowii* Torr. ex Schwein. subsp. *ensifolia* (Turcz. ex Gorodkov) Holub, *Festuca ovina* L., *Thalictrum alpinum* L., *Solidago lapponica* With.).

In 2002–2013, we established 18 elevational transects along the forest–tundra transition in the four regions of the Ural mountains (3 in South Urals, 9 in North Urals, 2 in Sub-Polar Urals, 4 in Polar Urals; Table S1). The transects were located on shallow, evenly inclined slopes (4–15°) with different aspects (Table S1). Each transect consisted of three elevation levels: the tree species line (tree individuals or 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%); the open forest line (distances between trees from 7 to 30 m and a total crown cover of 20%–30%); and the closed forest line (continuous forest with distances between trees < 7 m and a total crown cover greater than 50% (as defined by Shiyatov et al. (2007) and Hagedorn et al. (2014)). At each elevation level, we established 3–6 plots, each 20 × 20 m in area, covering a horizontal distance of approximately 200–1900 m.

2.2 | Climate data

Climate data were obtained from a combination of direct monitoring in or near the transects and external sources. On three
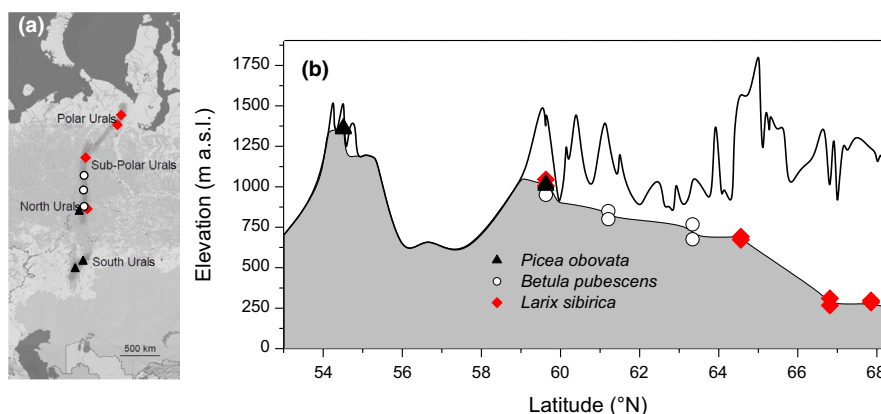
FIGURE 1 (a) The Ural mountains span a latitudinal gradient of 1,500 km, from 53 to 68 °N. (b) The elevation of treeline (grey shading) decreases from approximately 1,350 m a.s.l. in the South Urals to 270 m a.s.l. in the Polar Urals. The treeline almost reaches the mountain tops (black line) in the South Urals, whereas it remains about 1,000 m below the highest mountains in the Sub-Polar and Polar Urals. Forest stand characteristics were studied in seven regions along 18 elevational gradients, with each of them reaching from the tree species line down to the closed forest line [Colour figure can be viewed at wileyonlinelibrary.com]

mountains along the Ural mountain range, soil temperatures were monitored at treeline from 2010 to 2016 (Mali Iremel' and Bolschoi Iremel' in the South Urals, Molebnii in the North Urals and Tchernaya in the Polar Urals) using data loggers (StowAway Tidbit v2, Onset Corporation, Bourne, MA, USA or Mlog-5W, GeoPrecision, Ettlington, Germany) or Maxim iButtons (model DS1921G; San Jose). Soil temperature loggers were installed at 10-cm depth in the open terrain near tree clusters, but outside of their canopy. However, due to logger failure, temperature data were only available for five complete years in the South Urals and four years in the Polar Urals. Using these data, we calculated the mean growing season soil temperature and growing season length for each site, adopting the 3.2°C soil temperature threshold for defining the beginning and the end of the growing season established by Körner and Paulsen (2004). Air temperatures at 2 m height were monitored using a HOBO micro station (Onset Corporation) on Bolschoi Iremel' in the South Urals and Tchernaya in the Polar Urals.

Long-term air temperature data were additionally available from two climate stations near the treeline (Taganai in the South Urals, Neroika in the Sub-Polar Urals). Temperatures for the three other mountains were reconstructed using monitored temperatures during individual years and long-term records from the closest climate station (Zlatoust for Iremel', Ivdel for Molebnii, Elestkaya for Tchernaya) using linear regressions with recorded in situ temperatures. For each climate station, the mean temperature for each day of the year was averaged over the years 1970–2006. Using these average values, the days of the year when the air temperature first rose above (in spring) and fell below (in autumn) 5°C for more than three consecutive days were identified to determine the growing season. The duration (days) and mean air temperature were determined for this period. We additionally calculated the mean growing degree days (GDD) for the period 1970–2006 using the formula

$$\sum_i^a \left(T_{average} - T_{critical} \right) \tag{1}$$

where $T_{average}$ represents the daily average temperature.

Solar radiation was estimated from satellite data (NASA; data.nasa.gov) near each of the six mountain peaks. From daily radiation values for each day of the year, averaged over 2000–2010, we summed radiation for the growing season at treeline using start and end dates as defined above.

Precipitation data were only available for weather stations near the Taganai treeline in the South Urals and Neroika in the Sub-Polar Urals. In addition, we estimated latitudinal trends in precipitation using data from weather stations at lower elevations on the eastern and western sides of the Ural mountain range: Ufa, Zlatoust, Kazan', Krasnoufimsk, Ekaterinburg, Perm, Biser, Karpinsk, Cherdyn', Njaksimvol', Troiztko-Pecherskoe, Ust'-Schugor, Saran-Paul', Pechora, Petrun' and Salekhard. All precipitation data were adjusted according to KNMI Climate Explorer http://climexp.knmi.nl and www.meteo.ru. For each weather station, we determined total precipitation in summer (June, July, August) and winter (November to March) of each year from 1970 to 2006 and calculated the mean values for this period.

2.3 | Stand characteristics

In each plot, all saplings taller than 20 cm and all trunks of single- or multi-stemmed trees were recorded (N = 20,600). We mapped the location of each stem and measured its height, diameter at the base and breast height, and projected ground area covered by the crown. The age structure of all plots was determined by dendrochronological methods, following protocols used by Hagedorn et al. (2014) and Moiseev et al. (2016). From trees with a diameter ≥ 3 cm at the stem base, we took a single tree core at a height between 0 and 30 cm from every second single-stemmed living tree and from every fourth stem of every multi-stemmed tree. From every second tree taller than 0.2 m, but < 3 cm in basal diameter, we sampled stem discs at the root collar.

All cores were mounted on wooden strips. Cores and stem discs were cleaned with both 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, Germany) to a precision of 0.01 mm and were cross-dated using the computer programs 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 (for single-stemmed trees) or the start of upright growth of individual trunks (for multi-stemmed 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 centre 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. At all sites, tree age and height were significantly related to each other with an exponential relationship ($R^2 > 0.6$, $P < 0.001$).

2.4 | Tree and stand biomass

In 2002–2012, trees of each dominant species present (spruce, birch and/or larch) were sampled from the immediate vicinity of study plots at each elevation level (tree species line, open and closed forest lines) to estimate the allometric parameters and biomass of tree stands. These model trees were selected to cover the range of diameters, heights and crown sizes occurring along a given elevational transect (326 trees in total; 10–30 individuals per site for *P. obovata* and B. *pubescens* at Mali Iremel, *B. pubescens* at Konzhakovskii Kamen, *L. sibirica* at Serebryankii Kamen,

TABLE 1 Parameters of exponential equations ($y = ax^b$) modelling the dependence of (a) total aboveground biomass (kg tree^{-1}) and (b) belowground biomass (coarse roots > 5 cm) on stem basal diameter for Siberian spruce (*Picea obovata*, PO), mountain birch (*Betula pubescens* ssp. *tortuosa*, BP) and Siberian larch trees (*Larix sibirica*, LS) growing in the treeline ecotone in different regions of the Ural mountains.

a) Aboveground

Region	Species	Growth form	Elevation level	a	b	*n*	R^2
South	PO	single	Tree species line	0.074	1.85	14	0.69
			Open forest	0.083	2.15	28	0.93
			Closed forest	0.028	2.51	34	0.93
		multi	Tree species line	0.047	2.11	32	0.88
			Open forest	0.089	2.1	35	0.87
			Closed forest	0.053	2.26	31	0.97
	BP	single	Tree species line & Open	0.033	2.39	20	0.92
North	PO	single	Tree species line	0.039	2.21	8	0.97
		single	Open forest	0.017	2.48	15	0.96
		single	Closed forest	0.018	2.57	18	0.94
	BP	single	Open & Closed	0.007	3.03	20	0.95
		single	Tree species line	0.008	2.93	7	0.98
		single	Open & Closed	0.017	2.6	12	0.98
Sub-Polar	LS	single	Tree species line	0.016	2.63	7	0.98
		single	Open forest	0.014	2.75	14	0.96
		single	Closed forest	0.013	2.75	10	0.99
Polar	LS	single	Open forest	0.016	2.51	11	0.98
		single	Closed forest	0.016	2.58	10	0.99

b) Belowground

Region	Species	Growth form	Elevation level	a	b	*n*	R^2
South	PO	single	All	0.033	2.29	5	0.93
		multi[a]	All	0.137	1.25	5	0.91
North	PO	single	All	0.045	2.08	9	0.89
	BP	single	All	0.0078	2.8	4	0.98
	LS	single	All	0.0065	2.69	12	0.96
Polar	LS	single	All	0.0041	2.82	18	0.98

Note.: Parameters were determined for different tree species, for trees with a single-stemmed (single) or multi-stemmed (multi) growth form (South Urals only), and for different elevation levels within the treeline ecotone. The number of model trees used to establish the relationship (n) and the coefficient of determination (R^2) for the relationship based on these model trees are given.
[a]Square of cross section of stem base used instead of stem basal diameter.

P. obovata at Tylaiskii Kamen' and *L. sibirica* at Hus-Oika and Tchernaya; Table 1).

The aboveground biomass of model trees was determined by separating felled trees into stem wood and bark, branch wood and bark, needles or leaves, and dead branches, as described by Moiseev et al. (2016). The fresh mass of stems, including bark, was determined in the field by cutting them into 1-m sections and weighing them to a precision of 50 g. The percentage of dry matter in this wood and the bark biomass fraction was determined for cross-cut samples from the butt end of the sections. These sections were weighed in the field to a precision of 0.1 g and then transported to the laboratory to measure dry weight. To determine the biomass of the tree crown and its structural components, all branches (including leaves) were cut off and divided into three groups with respect to their location in the upper, middle or lower section of the crown. The total fresh mass of each group was measured in the field, and then the crown was divided into foliage-bearing and foliage-less parts and weighed separately. For a sample from the foliage-bearing part (20%–30% of total crown fresh mass), the foliage was removed from the branches and weighed. A sample from the foliage-less part (5%–10% of total crown fresh mass) was used to determine the proportions of wood and bark in the branches. The fraction of dry matter in foliage was determined for 20-g samples from each section of the crown.

In the South, North and Polar Urals, we estimated belowground biomass by excavating the coarse root system (threshold > 5-cm root diameter) for a subset of the model trees, covering the full elevation range of the transects (53 trees total; Table 1). The weight of excavated roots was estimated directly in the field to a precision of 50 g, and roots were then transported to the laboratory for dry weight

measurements. The percentage of dry matter in this wood and bark biomass fraction was determined for 10 cross-cut samples of roots with different diameters (covering the whole range from minimum to maximum values). The fraction of dry matter in root wood and bark was determined for 20-g samples. All biomass samples were dried by keeping them in an oven at 106°C until the mass remained stable. The ratios between the masses of samples measured before and after drying were used to calculate the dry mass of different fractions of the model trees.

Allometric relationships were estimated for the model trees of each growth form (single-stemmed and multi-stemmed) by applying regression equations relating the amounts of aboveground and belowground biomass (i.e. coarse roots) to the diameter at the stem base. The exponential equation $y = ax^b$ provided the best fit for these allometric relationships. Statistical parameters of these equations, calculated separately for each region, tree species and growth form are shown in Table 1. These equations were combined with data on stem basal diameter and height of all trees in the plots (20 × 20 m in area) to estimate the aboveground and belowground (coarse root) stand biomass on an area basis along the elevational transects. For transects where biomass was not measured, we applied species-specific allometric functions from the closest transect.

As forest stands of the treeline ecotone represent the first tree generation established after the Little Ice Age in 1850, we can estimate the 'apparent' stand productivity by dividing tree biomass by tree age. Aboveground stand productivity was calculated by dividing stand biomass by the average age of the stand. In addition, the change in stand aboveground biomass and in aboveground stand productivity per metre of elevation change were calculated by dividing the difference in biomass or productivity between the tree species line and the closed forest line by the total elevation difference in the transect (37–126 m).

2.5 | Soil measurements

In the South Urals (Mali Iremel' and Bolschoi Iremel', 2 transects), North Urals (Konzhakovskii Kamen', 1 transect) and Polar Urals (Tchernaya, 2 transects), soil properties were measured at the tree species line in mid growing season (July–August). In three plots from each transect, we collected the L- and F-layer from a 20 × 20 cm area using a frame at locations under the tree canopy and in open areas. In the South Urals, samples from the deeper soil were taken using a corer with an inner diameter of 2 cm. Specifically, eight soil cores were taken from 0- to 5-cm depth, six cores from 5- to 10-cm depth, and four cores from 10- to 20-cm depth and from 20-cm depth down to the bedrock, which occurred at an average soil depth of 29 cm. In the stone-rich North and Polar Urals, we sampled soils using two quantitative soil pits per sub-plot, where soils were excavated down to the bedrock (usually less than 20-cm depth) from an area of approximately 20 × 20 cm. The exact soil and stone volume for each depth layer was determined by measuring the pit's dimensions with a ruler or by filling the pit with a known volume of sand. At the field

station, we carefully removed root biomass and gravel/stones from the soil samples using a 4 and a 2 mm sieve. An aliquot of the soil was transported to the laboratory, where a portion of the soil was freeze-dried for the determination of water content and texture and for chemical analysis. Clay, silt and sand contents were measured by the sedimentation method according to Gee and Bauder (1986).

Inorganic nitrogen (N) concentrations were extracted with 1 M KCl, using a 1:10 ratio for 1 hr for soil from 0- to 5-cm depth and 1:5 for 1 hr for soil from 5- to 10-cm depth and 10- to 20-cm depth. In the extracts, NH_4^+ concentration was measured by automatic flow injection analysis (PE FIAS-300, Perkin-Elmer, Waltham, MA, USA) and NO_3^- concentration by ion chromatography (DX-120, Dionex, Sunnyvale, CA, USA). Soil pH was measured potentiometrically in the same KCl extracts. Extractable phosphorus was determined using the P(Bray I) method, extracting soils with NH_4F for 1 min (Irving & McLaughlin, 1990). For soil C analysis, subsamples were dried at 40°C for 24 hr and ground with a ball mill. Carbon concentrations were measured using a CN-analyser (Euro EA 3,000, HEKAtech GmbH, Wegberg, Germany) interfaced with a continuous flow isotope ratio mass spectrometer (Delta-V Advanced IRMS, Thermo GmbH, Bremen, Germany). Carbon and nutrient pools were estimated by multiplying the element concentration by the mass of fine earth per area and depth increment.

2.6 | Foliar nutrient concentrations of Larix sibirica

Larch needles were collected for measurements of nitrogen (N), phosphorus (P) and potassium (K) concentrations at mid growing season in plots at the tree species line and closed forest line in the South Urals (Mali Iremel'; n = 2 trees) and the Polar Urals (Tchernaya; n = 6 trees). For each tree, 100–200 needles were collected from mid-canopy height from all four directions. Samples were dried at 60°C until a stable dry mass was achieved, weighed and ground to a fine powder. N concentration was measured using the same CN-analyser as for soils. Contents of leaf P and K were determined by first digesting ground plant material in 40% HNO_3 with 1.2% HF in a microwave digestion unit (MW ultraCLAV MLS, Milestone Inc., Shelton, CT, USA) and then measuring total P and K concentrations using ICP-OES (Optima 7300 DV, Perkin Elmer).

2.7 | Statistical analysis

We assessed the effect of latitude on tree variables at the stand level (aboveground, belowground and total biomass, belowground to aboveground biomass ratio, aboveground productivity, stand density, projected crown area) and individual tree level (mean age, aboveground biomass, height, basal diameter) with linear mixed-effects models fitted with the restricted maximum likelihood method (Pinheiro et al., 2016). The random effects structure of the statistical models reflected the experimental design, with the three elevational levels (tree species line, open forest line, closed forest line)

nested within the 18 transects and the transects nested within the four regions of the Urals (South, North, Sub-Polar, Polar). As fixed effects, we included latitude, elevation level and the interaction between these variables. We additionally considered the cosine of the slope aspect, thought to be roughly representative of exposure to radiation, and its interactions with latitude and elevation level as potential fixed effects. To analyse the effect of latitude on changes in stand biomass and productivity with elevation, we used mean values of tree variables for each transect, averaged over the three elevation levels within the treeline ecotone. Data on soil properties and larch foliar nutrient concentrations were available for a limited number of transects and regions. For these variables, we tested differences between regions (and elevation levels in the case of larch nutrient data) instead of including site latitude as a fixed effect. To assess how climate variables were related and varied with latitude, we used Pearson's correlations.

Response variables were square-root transformed (stand aboveground and belowground biomass and productivity, stand density) or log transformed (projected crown area, tree age, tree aboveground biomass, tree height, tree basal diameter, larch foliar nutrient concentrations, soil properties) when necessary to meet assumptions of normality and homoscedasticity of the residuals. We considered fixed effects significant at $P < 0.05$. All analyses were performed using the nlme package of R version 3.3.3 (R Development Core Team, 2017).

3 | RESULTS

3.1 | Climate conditions

In the South and Polar Urals, data from loggers placed at 10-cm soil depth at treeline in open terrain near tree clusters from 2010 to 2016 indicated that mean soil temperatures for the growing season, defined using spring and autumn threshold soil temperatures of 3.2°C, were between 6.6 and 10.9°C (Figure 2). They averaged 7.6 ± 0.7°C in the South Urals (Mali Iremel') and 7.6 ± 1.7°C in the Polar Urals (Tchernaya) and thus did not differ significantly between these two extremes of the 1500-km latitudinal gradient. Soil temperatures in the winter were lower in the Polar Urals except for the winter 2012/2013 (Figure 2). Growing season length (GSL$_5$) varied strongly among years, particularly in the Polar Urals, where the period of air temperatures exceeding 5°C ranged from 85 to 135 days. On average, the growing season was 16 days longer in the South than in the Polar Urals. In contrast, measured summer air temperatures (JJA) were slightly higher in the Polar than in the South Urals (12.4 ± 1.9°C versus 11.6 ± 2.3°C).

Temperatures extrapolated from climate stations (1976–2006) corresponded closely to those measured in situ at the two extremes of the latitudinal transect (2010–2016). For instance, extrapolated GSL$_5$ was 120 and 102 days in the South and Polar Urals (Figure 3), respectively, whereas GSL$_5$ measured in situ had a duration of 123 and 107 days. The latter values also agreed with GSL based on measured soil temperatures (>3.2°), which averaged 128 and 114 days in the South and Polar Urals, respectively. Latitudinal patterns of
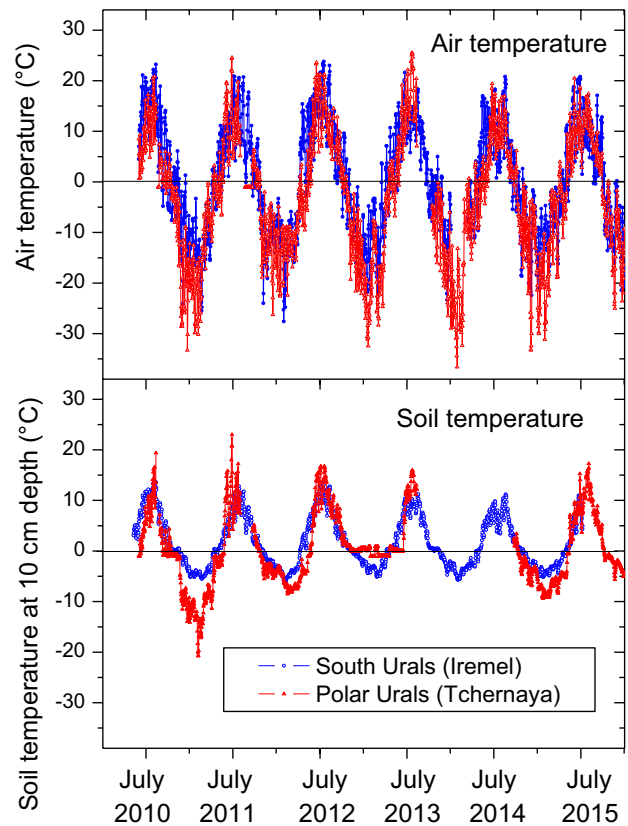

FIGURE 2 Air and soil temperature monitored from 2010 to 2015 at treeline in the South and Polar Urals. Soil temperature sensors were installed at 10-cm soil depth in open terrain near tree clusters, but outside of their canopy. Temperatures were logged hourly and averaged on a daily basis [Colour figure can be viewed at wileyonlinelibrary.com]

extrapolated temperatures from climate stations showed similar mean summer air temperatures at the treeline in all regions, but a decline in winter temperature with increasing latitude (Figure 3). In contrast to the decreasing length of the growing season, growing degree days (GDD$_5$) at treeline did not show a latitudinal trend and averaged 554 ± 9°C. Satellite-based solar radiation summed for the growing season and winter air temperatures (November to March) declined considerably towards more northern latitudes (Figure 3). Precipitation measured at regional weather stations averaged 216 mm in summer (June, July, August) and showed the highest precipitation in the North Urals (286 mm), but similar amounts occurred in the South and Polar Urals; in winter (November through March), precipitation ranged from 94 to 233 mm (mean 154 mm) and showed no consistent latitudinal pattern (precipitation data not shown). All pairwise correlations between latitude and growing season length, growing season radiation and winter air temperature were significant (Pearson correlation $r > 0.9$, $P < 0.05$; Table S2).

3.2 | Stand biomass and productivity at treeline

Based on biomass measurements from 326 trees, tree mapping data on 20,600 trees, and the application of allometric functions
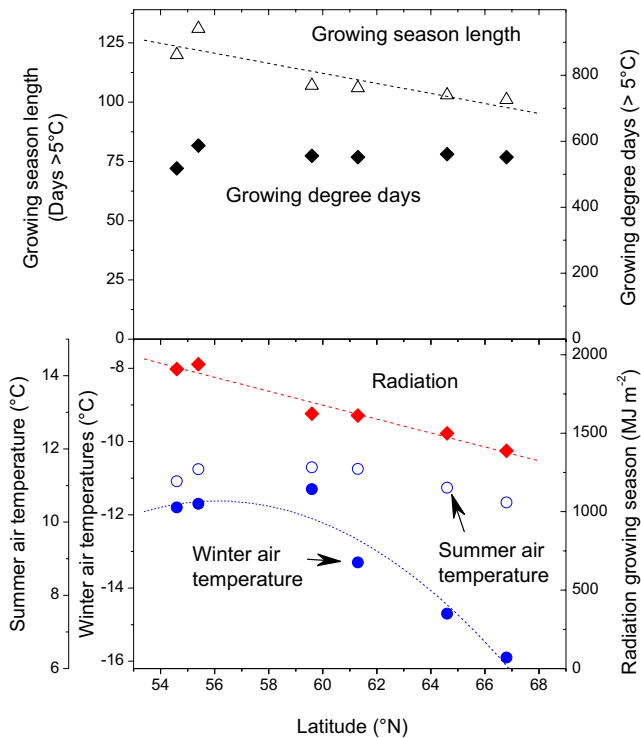
FIGURE 3 Latitudinal patterns of climatic data (1970–2006) reconstructed from meteorological stations along the Ural mountain range using in situ data. Top panel: growing season length and growing degree days (>5°C). Bottom panel: air temperatures in winter (November–March) and in summer (June–August), and satellite-based solar radiation during the growing season. Relationships between latitude and climate variables are shown when significant at $P < 0.05$ [Colour figure can be viewed at wileyonlinelibrary.com]

(Table 1), we calculated that stand aboveground biomass averaged across all 18 transects in the Urals was 27 ± 3 t/ha (mean ± 1 SE, averaged across the three elevation levels). Estimates of long-term annual stand aboveground productivity averaged 0.32 ± 0.04 ha^{-1}y^{-1} (Figure 4). Averaged across the three elevation levels and across the 12 transects where data were available, stand belowground (coarse root) biomass was 13 ± 1 t/ha, yielding a total stand biomass of 43 ± 4 t/ha and an average belowground to aboveground biomass ratio of 0.42 ± 0.03 (Table 2). On average, there were 1,075 ± 103 tree stems per hectare and total projected crown area was 4,621 ± 362 m^{2}ha^{-1} (Figure 4). Analysis with linear mixed-effects models indicated that, with the exception of the ratio of belowground to aboveground biomass, there was a highly significant increase in all variables (stand level and individual tree level) with decreasing elevation, that is from the tree species line to open forest line to closed forest line (Figure 4, Table 3). Averaged across all transects, the average tree height increased significantly from 2.5 ± 0.2 m at the species line to 4.2 ± 0.4 at the open forest line and 6.5 ± 0.4 m at the closed forest line ($P < 0.001$). Tree heights did not change systematically with latitude (Table 3). Stand aboveground biomass averaged across all transects increased from 2.7 ± 0.5 t/ha at the tree species line to 46.8 ± 5.5 t/ha at the closed forest line. Including slope aspect and associated interactions did not

improve the model fit for any of the measured variables, and these explanatory variables were therefore excluded from final models. With increasing latitude, there was a significant decrease by a factor 2.5–3.3 in stand total biomass (modelled slope with latitude, averaged across the three elevation levels = −2.5 t/ha°N^{-1}) and aboveground biomass (−2.3 t/ha°N^{-1}), as well as in stem density (−73 stems/ha°N^{-1}; Figure 4, Table 3). Long-term aboveground net stand productivity, estimated by dividing biomass by mean tree age, exhibited the same latitudinal pattern as stand biomass, showing a decline by a factor of 5.2 along the latitudinal gradient (Figure 4, Table 3). This finding demonstrates that the latitudinal pattern in stand aboveground biomass was not caused by differences in tree age among regions and transects. Nonetheless, the mean age of trees at the tree species line decreased slightly with increasing latitude, whereas the opposite pattern occurred at the closed forest line and no latitudinal pattern was apparent for tree age at the open forest line (n.s. trend of latitude x elevation level interaction; Table 3, Figure S1). Overall, mean tree age was 78 ± 5 years. The estimates of mean tree ages were not biased by systematic differences in forest age structures with latitude (Figure S1; for tree species-specific patterns see Hagedorn et al., 2014). Distributions of tree ages were left- skewed at the species line and open forest line, but rather normally distributed in the closed forest, which reflects the establishment of a new tree generation at a higher elevation.

For stand total biomass, aboveground biomass and productivity, there was a significant interactive effect between latitude and elevation level, indicating that the latitudinal effect was greatest at the closed forest line, followed by the open forest line and finally the tree species line (Figure 4, Table 3). This result was supported by a significantly smaller change in stand productivity (but not biomass) per height metre, by a factor of three, along the latitudinal gradient towards the Polar Urals (Figure 4). Results regarding stand productivity did not differ qualitatively if values were calculated using stand total biomass (aboveground compartment plus coarse roots; data not shown). Stand coarse root biomass and, to a lesser extent, projected crown area also tended to become smaller at higher latitudes, but this effect was not significant (Table 3). A larger reduction in aboveground biomass than in belowground (coarse root) biomass with increasing latitude meant that the ratio of belowground to aboveground biomass at the stand level increased significantly moving north along the latitudinal gradient (Table 2).

In contrast to stand-level variables, at the individual tree level there was no detectable change with latitude in mean aboveground biomass (mean across all transects and the three elevation levels ± 1 SE = 25 ± 3 kg), height (4.4 ± 0.3 m) or basal diameter (9.8 ± 0.7 cm; Table 3). These results demonstrate that the latitudinal pattern observed for stand-level biomass and productivity was primarily driven by a change in stem density.

Stand aboveground biomass and productivity correlated significantly with growing season length, growing season radiation and winter air temperature, which all correlated with latitude (Pearson correlation r > 0.9, $P < 0.05$; Table S2). In contrast, stand biomass and productivity did not correlate with summer temperatures or GDD$_5$.
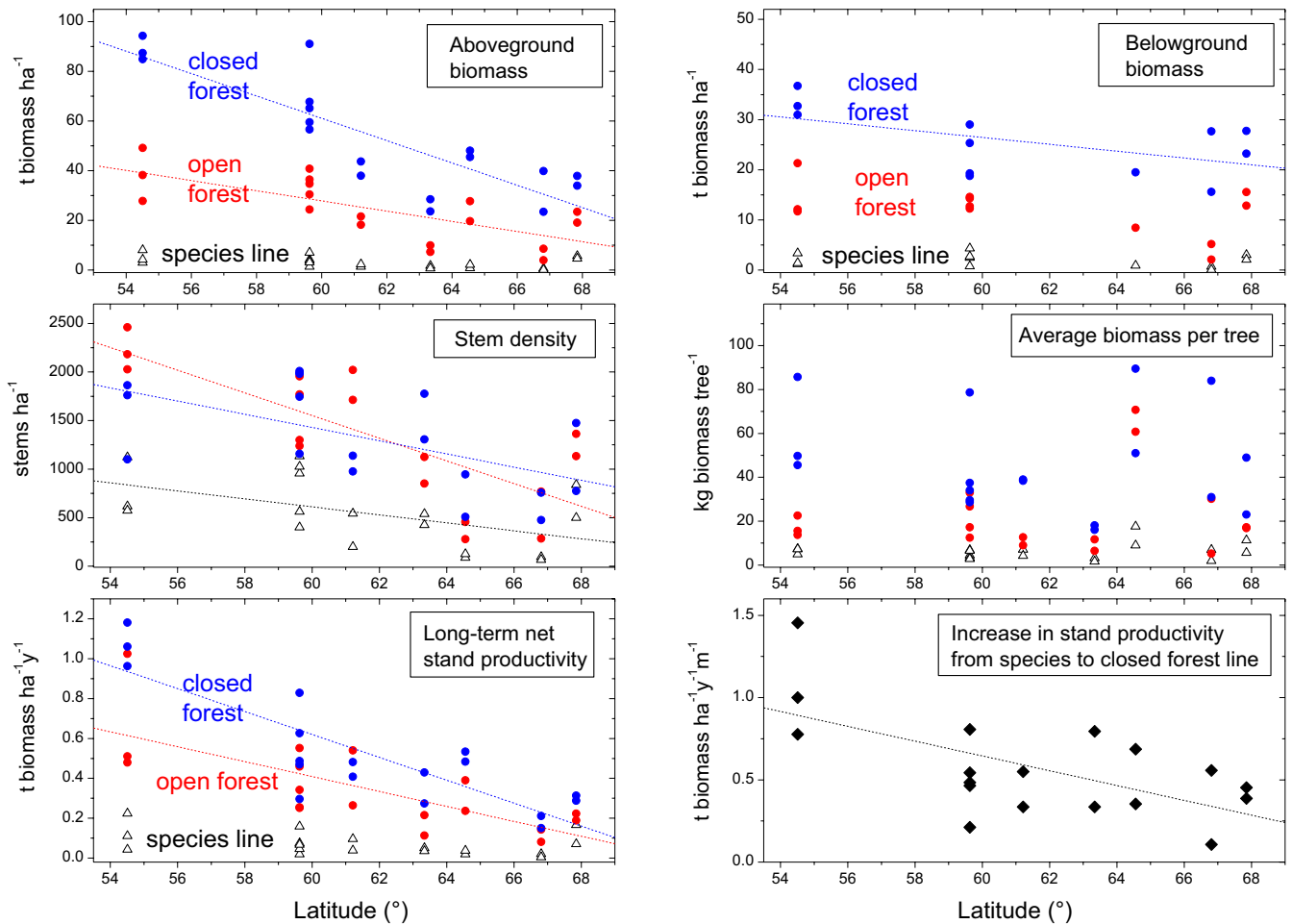
FIGURE 4 Stand above- and belowground biomass, stem density, long-term aboveground stand productivity, average biomass of individual trees, and increase in stand productivity with elevation from species to closed forest line. Linear relationships of stand characteristics with latitude of the Ural mountain range are shown when significant at $P < 0.05$. Stem density includes all stems, with multi-stemmed trees having several stems. Stand productivity was calculated by dividing tree biomass by mean tree age and represents the long-term net production in biomass. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Ratios of belowground to aboveground tree biomass.

Region	Tree species	Tree species line	Open forest line	Closed forest line
South Urals	*Picea obovata*	0.380 ± 0.024	0.390 ± 0.037	0.376 ± 0.007
North Urals	*Betula pubescens*	0.676 ± 0.058	0.384 ± 0.035	0.307 ± 0.011
North Urals	*Larix sibirica*	0.581 ± 0.001	0.460 ± 0.042	0.353 ± 0.021
Polar Urals	*Larix sibirica*	0.622 ± 0.152	0.615 ± 0.035	0.693 ± 0.014

Note.: Means and standard errors are shown of three elevational transects in the South Urals, two transects per tree species in the North Urals and four transects in the Polar Urals. Values were calculated by applying allometric relationships based on 10 (South Urals), 25 (North Urals) or 18 (Polar Urals) excavated individual trees.

3.3 | Soil properties and nutrient pools

Soil properties showed significant differences among the three regions where data were collected and indicated less developed soil in the northern regions (Table 4). In the Polar Urals, the surface was patterned and soils showed signs of cryoturbation, indicating that soils were affected by permafrost. Active layer depth was greater than 20 cm. No signs of permafrost were visible in the South or North Urals, and soil depth decreased from the South to the Polar Urals. Consistent with these results, stone and sand contents were higher in the Polar and North Urals than in the South Urals (Table 4). In addition, total soil organic C stocks (soil surface down to bedrock) declined from the South to the North and Polar Urals, and extractable N and P pools (0- to 20-cm soil depth) were approximately 20

TABLE 3 Results of the linear mixed-effects model testing the effect of latitude on response variables at the stand and individual tree levels (for data see Figure 4)

Response variable	Fixed effect	DF	F	P
Stand aboveground (AG) biomass	Latitude	1,13	24.33	<0.001
(t/ha)	Elevation level	2,32	389.22	<0.001
	Latitude x Elevation	2,32	12.52	<0.001
Stand belowground (BG) biomass	Latitude	1,7	5.53	0.051
(t/ha)	Elevation level	2,20	143.57	<0.001
	Latitude x Elevation	2,20	0.73	0.493
Stand total biomass	Latitude	1,7	18.06	0.004
(t/ha)	Elevation level	2,20	264.81	<0.001
	Latitude x Elevation	2,20	6.56	0.006
Stand BG:AG biomass	Latitude	1,7	18.16	0.004
(–)	Elevation level	2,20	1.65	0.217
	Latitude x Elevation	2,20	1.54	0.240
Stand aboveground productivity	Latitude	1,13	25.02	<0.001
(t/hay^{-1})	Elevation level	2,32	148.27	<0.001
	Latitude x Elevation	2,32	11.03	<0.001
Stand density	Latitude	1,13	5.84	0.031
(stems/ha)	Elevation level	2,32	44.69	<0.001
	Latitude x Elevation	2,32	2	0.152
Stand projected crown area	Latitude	1,13	0.56	0.466
(m^2)	Elevation level	2,32	213.15	<0.001
	Latitude x Elevation	2,32	0.68	0.514
Tree aboveground biomass	Latitude	1,13	2.59	0.132
(kg)	Elevation level	2,32	110.28	<0.001
	Latitude x Elevation	2,32	0.42	0.662
Tree height	Latitude	1,13	0.3	0.594
(m)	Elevation level	2,32	153.5	<0.001
	Latitude x Elevation	2,32	1.77	0.187
Tree basal diameter	Latitude	1,13	2.49	0.139
(cm)	Elevation level	2,32	3.76	0.034
	Latitude x Elevation	2,32	1.73	0.194
Mean tree age	Latitude	1,13	0.03	0.875
(years)	Elevation level	2,32	63.63	<0.001
	Latitude x Elevation	2,32	3.08	0.060

and 30 times smaller, respectively, in the Polar than in the South Urals (Table 4).

3.4 | Larch foliar nutrient concentrations

Larch foliar concentrations of N, P and K were higher at the closed forest line than at the tree species line (Table 5; all $P < 0.02$) and higher on Mali Iremel' in the South Urals than on Tchernaya in the Polar Urals (all $P < 0.02$). The difference between regions occurred at both elevation levels for N and K, but was greater at the closed forest line than at the tree species line for P (significant region x elevation level interaction; $F_{1,12} = 11.07$, $P = 0.02$).

4 | DISCUSSION

4.1 | Consistent growing season temperatures at treeline along the Urals

Our study along a 1500-km north–south transect in the Ural mountains shows that the elevational position of the treeline ecotone

TABLE 4 Soil properties at the tree species line in the South, North and Polar Urals (mean values ± 1 *SE*).

	Stone content	Texture		SOC stock	Mineral *N*	P_Bray
	volume-%	% sand	pH	kg C m^{-2}	mg *N*/m^2 0.2 m^{-1}	mg P m^{-2} 0.2 m^{-1}
South Urals	2.9 ± 0.8	25 ± 3	3.5 ± 0.02	9.96 ± 0.54	2,460 ± 340	992 ± 134
North Urals	21.7 ± 8.1	57 ± 2	4.3 ± 0.12	8.75 ± 1.96	*n.d.*	*n.d.*
Polar Urals	61.9 ± 1.6	44 ± 3	4.3 ± 0.06	1.33 ± 0.17	122 ± 23	31 ± 5
DF	2,2	2,2	2,2	2,2	1,2	1,2
F	31.21	260.28	127.69	26.49	136.07	135.84
P	0.010	0.004	0.008	0.036	0.007	0.007

Note.: Mineral N and P_Bray are representative of plant-available N and P, respectively. Results of linear mixed-effects models testing for differences between the regions are displayed below the estimates. Values are given down to 20-cm soil depth, except for soil organic carbon (SOC) stock, which was estimated down to the bedrock.

TABLE 5 Nutrient concentrations of needles from Siberian larch, *Larix sibirica* (mean values ± 1 SE).

	Elevation	Needle N	Needle P	Needle K
	Level	mg N g^{-1}	mg P g^{-1}	mg K g^{-1}
South Urals	Tree species line	29.8 ± 0.70	1.81 ± 0.23	5.92 ± 0.43
	Closed forest	33.8 ± 0.78	3.14 ± 0.06	11.41 ± 3.41
Polar Urals	Tree species line	21.9 ± 0.61	1.77 ± 0.11	3.29 ± 0.21
	Closed forest	27.2 ± 0.71	2.07 ± 0.03	4.52 ± 0.26
Region		<0.001	0.013	0.0013
Elevation level		<0.001	0.0023	0.014
Region x Elevation		0.15	0.02	*n.s.* (0.30)

Note.: Results of linear mixed-effects models testing for differences between the regions and elevation levels are displayed below the estimates.

occurs at similar mean and cumulated temperatures during the growing season. At sites located at the two extremes of the transect, in the South and Polar Urals, mean growing season temperatures in the soil averaged 7.6°C (Figure 2), which is in the upper range of values reported in the global survey by Körner and Paulsen (2004). High interannual variability and high spatial variability may obscure an exact determination of soil temperatures at treeline (Müller et al., 2016). Moreover, current climate conditions are only partly representative of the thermal growth limitation at treeline: trees growing at the current treeline established under colder conditions several decades ago and temperature limitation of growth has declined with climatic changes over the last decades (Jochner, Bugmann, Nötzli, & Bigler, 2018; Kurkashki et al., 2018). Inter- and intraspecific competition and plant–soil interactions may additionally contribute to the lag between climatic changes and treeline advances and thus to uncertainty in estimates of critical temperatures at treelines (Hagedorn et al., 2019; Wieczorek et al., 2017).

In our study, in situ measurements were supported by the extrapolation of temperature regimes from longer time series of climate stations, which indicated similar growing season temperatures along the whole Ural mountain range (Figure 3). The South and Polar Ural treeline ecotones encompass different soil properties, with the pools of plant-available N and P a magnitude smaller in the Polar than

in the South Urals, demonstrating that nutrient availability is unlikely to determine the treeline position. Our results are in contrast to those from an Alaskan treeline on permafrost soil, where diminishing soil N availability, rather than low-temperature constraints, was proposed to be primarily responsible for reduced aboveground growth of white spruce towards the elevational treeline. Instead, our findings lend strong support to the concept that the elevational position of treelines is primarily linked to growing season temperatures (Hoch, 2013; Körner & Paulsen, 2004), most likely through thermal constraints on xylogenesis and the metabolization of assimilates in the roots, where temperatures are generally lower than in the canopy (Ferrari, Hagedorn, & Niklaus, 2016; Hoch, 2013; Hoch & Körner, 2012; Rossi, Deslauriers, Anfodillo, & Carraro, 2007).

4.2 | Tree biomass and productivity in the treeline ecotone

In agreement with the few other existing biomass estimates for treeline ecotones, calculated for sites in the Alps, the Scandes and Tibet (Leuzinger, Manusch, Bugmann, & Wolf, 2013; Liu et al., 2016; Speed et al., 2015), stand biomass and productivity in the Urals increases dramatically, by a factor of three to nine, as one moves downward

approximately 100 m in elevation from the tree species line, corresponding to a 0.5–0.65°C increase in air temperature. Hence, stand productivity clearly follows a threshold function, with an abrupt increase occurring once the thermal limitation of tree growth is released below the tree species line. In addition to the expected elevational pattern, our study revealed a clear decrease in total biomass and stand productivity with increasing latitude along the Urals (Figure 4). At first glance, this pattern seems to follow the general decline in forest growth with increasing latitude observed at low elevation, primarily related to declining growing season length and growing degree days (e.g. Jung et al., 2011; Salminen & Jalkanen, 2007). However, treeline trees grow near their thermal growth limit along the whole north–south gradient in the Ural mountains and hence at a very similar temperature regime during the growing season, indicating that factors other than growing season temperature must have been responsible for the decline in productivity towards higher latitudes. One reason could be different tree species growing at treeline, with spruce dominating in the South Urals and larch becoming increasingly dominant from the North to the Polar Urals, which impedes a clear differentiation between species differences and latitudinal effects. However, in the southern part of the North Urals, where spruce and larch coexist on slopes with different aspects, north-exposed 'colder' treeline stands dominated by larch had only a 20% smaller stand biomass than south-exposed slopes dominated by spruce. In a 30-year-long afforestation experiment in central Siberia, *Larix sibirica* grew larger than *Picea obovata* and stand productivity did not differ significantly between the two tree species (Kuzmichev, Pshenichnikova, & Tretyakova, 2004). Likewise, in mixed forest stands in the forest–tundra ecotone of central Siberia, tree-ring widths were about 60% greater for *L. sibirica* than for *P. obovata* (Knorre, Kirdyanov, & Vaganov, 2005). All these results indicate that the fivefold decrease in stand productivity in the treeline ecotone from the South to Polar Urals is clearly too large to be explained by an inherent difference in biomass productivity among tree species, which actually tends to be greater for larch than for spruce. This conclusion is supported by the latitudinal decline in biomass from the North to the Sub-Polar and Polar Urals when larch-dominated stands were considered separately (Figure 4). The lower production and biomass may partly result from a lower reproduction and recruitment at higher latitudes (Koshkina, Moiseev & Goryacheva, 2008; Wieczorek et al., 2017), but we regard this as an integral part of treeline stand dynamics.

The latitudinal decline in tree stand biomass and productivity could be counterbalanced by an increasing contribution of understorey vegetation. Indeed, the understorey biomass is greater in the closed forest of the Polar Urals, with a dense mat of *Betula nana* shrubs, compared to in the South Urals, where herbaceous plants (e.g. *Polygonum alpinum*) dominate (Solly et al., 2017). However, understorey plants do not differ in productivity along the latitudinal gradient, as the shorter longevity—and thus higher productivity—of annual herbs in the South Urals than of perennial shrubs in the Polar Urals compensates for the smaller biomass of herbaceous species. Thus, we consider the observed latitudinal gradient in productivity to apply not only to trees but also to the entire ecosystem.

What drives the latitudinal decline in stand biomass and productivity at treeline? The climatic factors correlating significantly with stand biomass and productivity were growing season length, radiation summed over the growing season and winter temperature. These variables are all correlated with each other, however, making it difficult to disentangle their individual impacts (Table S2).

Growing season length (GSL) has been observed to correlate more closely with tree growth than average growing season temperatures at treelines in the Alps and in Tibet (Jochner et al., 2018; Li et al., 2017), very likely through its effect on the timespan above critical temperatures when xylogenesis can take place. In our study, the length of the growing season decreased slightly towards the north, with 20% shorter summers, but longer days during summer in the Polar Urals (Figure 3). This finding is consistent with the declining GSL at treeline on the global scale reported by Körner and Paulsen (2004). However, this decrease did not translate to fewer growing degree days (GDD) above 5°C in the Polar Urals, which is generally considered an important control for tree growth at high latitudes and elevations because it quantifies the total energy available for trees to grow (Jochner et al., 2018; Leuzinger et al., 2013; Salminen & Jalkanen, 2007). The decreasing length of the growing season towards the north in our study was also linked to a decline in incoming short-wave radiation per growing season (Figure 3). Moreover, the low sun angle at high latitudes leads to stronger absorption of UV-B light in the atmosphere than at locations further south (Olsen & Lee, 2011). Both growth models and experimental work, predominantly focusing on agricultural crops, indicate that radiation and growth are linearly coupled (Russel, Jarvis, & Monteith, 1989). However, given that radiation and biomass production scale linearly, it seems unlikely that diminishing radiation is the primary driver of the latitudinal decline in productivity, as growing season radiation decreases by only 40% along the latitudinal gradient (Figure 3), whereas the observed decline in stand productivity was manifold (Figure 4). Moreover, tree canopies adapt to lower sun angles through the formation of vertically extending crowns (Kuuluvainen, 1992). There is also growing evidence that tree growth is predominantly limited by C sink strength, that is the metabolization of assimilated C, rather than by C uptake, in particular for trees growing at high elevations (e.g. Hoch & Körner, 2012; Li et al., 2018). Nonetheless, C metabolization might be indirectly related to sun angle, as a lower solar angle at higher latitudes leads to greater shading by trees and associated cooling of the rooting zone (Aakala, Shimatani, Abe, Kubota, & Kuuluvainen, 2016; Bonan & Shugart, 1989). In our study, the occurrence of such a shading effect was supported by the decline in stand density, corresponding to larger spacing among trees, at higher latitudes. The latitudinal increase in the shading effect might be counterbalanced by the change in tree species from spruce, with a dense canopy, in the South Urals to larch, with a transparent canopy, in the Polar Urals. Systematic assessments of the spatial structures involved in microclimatic conditions would help quantify the importance of this potential mechanism.

Latitude may also influence tree growth through its effects on the circadian rhythm of tree growth, as cell expansion and structural

growth occur mainly during nighttime, in concert with improved water status and thus more favourable turgor (see review by Steppe, Sterck, & Deslauriers, 2015). Consequently, shorter nights towards the north during the growing season may impair growth processes. However, in quantitative terms the importance of these ecophysiological processes are still poorly understood. For the latitudinal gradient along the Urals, we consider the effect of diel growth dynamics rather limited because growth at the individual tree level was independent from latitude.

4.3 | Winter temperatures and their link to soil nutrient availability

Among all estimated climatic variables, winter air temperature showed the strongest change with latitude, decreasing by about 4°C along the 1500-km gradient (Figure 3). Although winter temperatures do not directly impact tree growth because trees adapt to very low temperatures in the dormant season (Holtmeier, 2003; Körner, 2012), concentrations of non-structural carbohydrates in treeline trees have been found to decrease during the winter season (Li et al., 2018). However, a complete depletion of carbon reserves over winter has not been reported, indicating that the C balance of trees seems rather to be driven by the extent to which C stores in trees are replenished during the growing season.

In comparison to the limited direct effects on tree physiology, winter temperature and conditions may exert a considerable indirect influence on forest growth through impacts on nutrient mineralization (Sturm et al., 2005) and the depth and duration of permafrost. Permafrost has been identified as one of the key determinants of tree growth and treeline advances in Alaska and northern Canada, as permafrost restricts rooting depth and nutrient availability (Lloyd, 2005; Sullivan et al., 2015). In the Urals, permafrost has been reported to reach as far south as the North Urals (Westermann, Østby, Gisnås, Schuler, & Etzelmüller, 2015), but the active layer depth exceeds the rooting zone in these mountain soils. However, periglacial processes associated with permafrost in the deeper soil (e.g. stone sorting) impede weathering and soil development (Dymov, Zhangurov, & Hagedorn, 2015), which in turn results in reduced soil fertility. In support of these indirect effects of winter conditions, our soil survey indicated a strong decrease in soil development and fertility at treeline with increasing latitude. Stone contents tripled towards the Polar Urals and soil organic matter stocks were almost seven times smaller in the Polar than in the South Urals (Table 4). Furthermore, mineral N and available P in the soil were 20 and 30 times smaller, respectively, in the Polar than in the South Urals (Table 4), a pattern that was also reflected in foliar nutrient concentrations (Table 5). Fertilization experiments in treeline ecosystems have demonstrated a positive growth response to nutrient additions (Möhl et al., 2019; Sveinbjornsson, Nordell, & Kauhanen, 1992), strongly suggesting that once thermal growth limitation is relieved, nutrient availability may become a key determinant of stand productivity (Hoch, 2013). Along elevation gradients, nitrogen availability has been found to increase from

the tundra to the closed forest, due to enhanced N mineralization in more favourable microclimates (Kammer et al., 2009; Thébault et al., 2014), which potentially contributes to growth release below the tree species line.

The decreasing nutrient availability towards the Polar Urals might also be mirrored in the latitudinal increase in the ratio of belowground to aboveground biomass (Table 2), which is generally regarded as a tree's adaptation to resource limitation in the soil (e.g. Solly et al., 2017). However, more systematic soil studies at treeline in other mountain ranges are needed to elucidate how winter climate, soil development and nutrient availability are interlinked and influence stand productivity (Hagedorn et al., 2019).

4.4 | Consequences for C sequestration

The latitudinal decline in treeline stand productivity and biomass observed here implies that the amount of C stored in treeline ecosystems and sequestered during upward forest expansion into former tundra decreases with increasing latitude. As a tree age structure analysis indicated that all treeline stands in our study represent the first tree generation established since the Little Ice Age around 1850 (Hagedorn et al., 2014), we can roughly estimate the amount of carbon sequestered in these Ural treeline ecotones during the past century. The apparent stand productivity in aboveground and belowground biomass combined corresponds to a net C uptake of approximately 0.37 ± 0.06 t C ha^{-1} y^{-1} and 0.09 ± 0.05 t C ha^{-1} y^{-1} (averaged for all three elevation levels) in the South and Polar Urals, respectively, and thus a reduction by a factor of four along the latitudinal gradient. Although one may expect a strong C sink associated with the striking forest expansion into former treeless tundra, these sequestration rates are rather small compared with those of temperate forests. Despite the continuous biomass removal with harvest in low-elevation forests, net C uptake rates for European forests have been estimated at approximately 0.5 t C ha^{-1} y^{-1} (Janssens et al., 2003).

5 | CONCLUSIONS

Our study is one of the first assessments of stand biomass and productivity at multiple treeline sites, variables that serve as the basis for estimating and modelling various ecosystem functions. In combination with novel remote sensing techniques, the allometric functions for treeline trees provided here could facilitate large-scale estimations of stand biomass in treeline ecotones. Our results demonstrate that treeline positions are located at similar temperature regimes during the growing season along the entire 1500-km latitudinal gradient in the Ural mountains. Despite the consistent cold limitation of tree growth, stand biomass and productivity showed a manifold decrease from the South to the Polar Urals. Several potential explanatory factors—growing

season length and radiation, winter temperature, and soil nutrient availability—showed a corresponding change with latitude. As they correlated with each other, it was not possible to identify one key driver. We suggest that soil fertility, restricted by permafrost and low soil temperatures during winter, plays a key and yet underexplored role for stand productivity near treeline once the thermal limitation is relieved. The latitudinal patterns in stand biomass and productivity will impact a number of ecosystem functions, such as above- and belowground diversity and C sequestration, and how these are altered by a changing climate.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used in this publication are available at the WSL data portal: https://doi.org/10.16904/envidat.132.

ORCID

Frank Hagedorn https://orcid.org/0000-0001-5218-7776
Melissa A. Dawes https://orcid.org/0000-0003-4919-0151
Pavel A. Moiseev https://orcid.org/0000-0003-4808-295X

REFERENCES

Aakala, T., Shimatani, K., Abe, T., Kubota, Y., & Kuuluvainen, T. (2016). Crown asymmetry in high latitude forests: Disentangling the directional effects of tree competition and solar radiation. *Oikos*, *125*, 1035–1043. https://doi.org/10.1111/oik.02858

Allen, C. D., & Breshears, D. D. (1998). Drought-induced shift of a forest–woodland ecotone: Rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences*, *95*, 14839–14842. https://doi.org/10.1073/pnas.95.25.14839

Barbeito, I., Dawes, M. A., Rixen, C., Senn, J., & Bebi, P. (2012). Factors driving mortality and growth at treeline: A 30-year experiment of 92 000 conifers. *Ecology*, *93*, 389–401.

Bernoulli, M., & Körner, C. (1999). Dry matter allocation in treeline trees. *Phyton*, *39*, 7–12.

Bonan, G. B., & Shugart, H. H. (1989). Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics*, *20*, 1–28. https://doi.org/10.1146/annurev.es.20.110189.000245

Braeker, U. (1981). Der Alterstrend bei Jahrringdichten und Jahrringbreiten von Nadelhölzern und sein Ausgleich. *Mitteilungen Forstliche Bundes-Versuchsanstalt Wien*, *142*, 75–102.

Coops, N. C., Mörsdorf, F., Schaepman, M. E., & Zimmermann, N. E. (2013). Characterization of an alpine treeline using airborne LiDAR data and physiological modeling. *Global Change Biology*, *19*, 3808–3821. https://doi.org/10.1111/gcb.12319

Dawes, M. A., Philipson, C. D., Fonti, P., Bebi, P., Hättenschwiler, S., Hagedorn, F., & Rixen, C. (2015). Soil warming and CO_2 enrichment induce biomass shifts in alpine treeline vegetation. *Global Change Biology*, *21*, 2005–2021.

De Wit, H. A., Bryn, A., Hofgaard, A., Karstensen, J., Kvalevåg, M. M., & Peters, G. P. (2014). Climate warming feedback from mountain birch forest expansion: Reduced albedo dominates carbon uptake. *Global Change Biology*, *20*, 2344–2355. https://doi.org/10.1111/gcb.12483

Devi, N., Hagedorn, F., Moiseev, P., Bugmann, H., Shiyatov, S., Mazepa, V., & Rigling, A. (2008). Expanding forests and changing growth forms of Siberian larch at the Polar Urals treeline during the 20th century. *Global Change Biology*, *14*, 1581–1591. https://doi.org/10.1111/j.1365-2486.2008.01583.x

Dymov, A. A., Zhangurov, E. V., & Hagedorn, F. (2015). Soil organic matter composition along altitudinal gradients in permafrost affected soils of the Subpolar Ural Mountains. *Catena*, *131*, 140–148. https://doi.org/10.1016/j.catena.2015.03.020

Ferrari, A., Hagedorn, F., & Niklaus, P. A. (2016). Experimental soil warming and cooling alters the partitioning of recent assimilates: Evidence from a ^{14}C-labelling study at the alpine treeline. *Oecologia*, *181*, 25–37. https://doi.org/10.1007/s00442-015-3427-y

Gazol, A., Moiseev, P., & Camarero, J. J. (2017). Changes in plant taxonomic and functional diversity patterns following treeline advances in the South Urals. *Plant Ecology & Diversity*, *10*, 283–292. https://doi.org/10.1080/17550874.2017.1400126

Gee, G. W., & Bauder, J. W. (1986). Particle-size analysis. In: A. Klute, (Ed.). *Methods of soil analysis. Part I: physical and mineralogical methods* 2nd edn. (pp. 383-411). Madison, Wisconsin: ASA, SSSA. ASA Book Series No. 9.

Hagedorn, F., Gavazov, K., & Alexander, J. M. (2019). Above- and belowground linkages shape responses of mountain vegetation to climate change. *Science*, *365*, 1119–1123. https://doi.org/10.1126/science.aax4737

Hagedorn, F., Shiyatov, S. G., Mazepa, V. S., Devi, N. M., Grigor'ev, A., Bartish, A. A., ... Moiseev, P. A. (2014). Treeline advances along the Ural mountain range – driven by improved winter conditions? *Global Change Biology*, *20*, 3530–3543.

Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, *12*, 1040–1049. https://doi.org/10.1111/j.1461-0248.2009.01355.x

Hoch, G. (2013). Reciprocal root-shoot cooling and soil fertilization effects on the seasonal growth of two treeline conifer species. *Plant Ecology & Diversity*, *6*, 21–30. https://doi.org/10.1080/17550874.2011.643324

Hoch, G., & Körner, C. (2012). Global patterns of mobile carbon stores in trees at the high elevation treeline. *Global Ecology and Biogeography*, *21*, 861–871. https://doi.org/10.1111/j.1466-8238.2011.00731.x

Holmes, R. L. (1995). *Dendrochronological Program Library (computer program)*. The University of Arizona, Tucson, Arizona, USA.

Holtmeier, F.-K. (2003). *Mountain timberlines. Ecology. Patchiness, and dynamics* (p. 369). Dordrecht: Kluwer.

Irving, G. C. J., & McLaughlin, M. J. (1990). A rapid and simple field test for phosphorus in Olsen and Bray No. 1 extracts of soil. *Communications in Soil Science and Plant Analysis*, *21*, 2245–2255. https://doi.org/10.1080/00103629009368377

Janssens, I. A., Freibauer, A., Ciais, P., Smith, P., Nabuurs, G.-J., Folberth, G., ... Dolman, A. J. (2003). Europe's terrestrial biosphere absorbs 7 to 12% of European anthropogenic CO_2 emissions. *Science*, *300*, 1538–1542. https://doi.org/10.1126/science.1083592

Jochner, M., Bugmann, H., Nötzli, M., & Bigler, C. (2018). Tree growth responses to changing temperatures across space and time: A fine scale analysis at the treeline in the Swiss Alps. *Trees*, *32*, 645–660. https://doi.org/10.1007/s00468-017-1648-x

Jung, M., Reichstein, M., Margolis, H. A., Cescatti, A., Richardson, A. D., Arain, M. A., ... Williams, C. (2011). Global patterns of land-atmosphere fluxes of carbon dioxide, latent heat, and sensible heat derived from eddy covariance, satellite, and meteorological observations. *Journal of Geophysical Research*, *116*, G00j07. https://doi.org/10.1029/2010JG001566

Kammer, A., Hagedorn, F., Shevchenko, I., Leifeld, J., Guggenberger, G., Goryacheva, T., ... Moiseev, P. (2009). Treeline shifts in the Ural mountains affect soil organic matter dynamics. *Global Change Biology*, *15*, 1570–1583. https://doi.org/10.1111/j.1365-2486.2009.01856.x

Knorre, A. A., Kirdyanov, A. V., & Vaganov, E. A. (2005). Climatically induced interannual variability in aboveground production in forest tundra and northern taiga of central Siberia. *Oecologia*, *147*, 86–95. https://doi.org/10.1007/s00442-005-0248-4

Körner, C. (1998). A re-assessment of high elevation treeline position and their explanation. *Oecologia*, *115*, 445–459.

Körner, C. (2012). *Alpine treelines. Functional ecology of the global high elevation tree limits* (p. 220). Berlin: Springer.

Körner, C., & Paulsen, J. (2004). A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, *31*, 713–732. https://doi.org/10.1111/j.1365-2699.2003.01043.x

Koshkina, N. B., Moiseev, P. A., & Goryaeva, A. V. (2008). Reproduction of the Siberian spruce in the timberline ecotone of the Iremel' Massif. *Russian Journal of Ecology*, *39*, 83–91. https://doi.org/10.1134/S1067413608020021

Kukarskih, V. V., Devi, N. M., Moiseev, P. A., Grigoriev, A. A., Bubnov, M. O. (2018). Latitudinal and temporal shifts in the radial growth-climate response of Siberian larch in the Polar Urals. *Journal of Mountain Science*, *15*, 722–729. https://doi.org/10.1007/s11629-017-4755-7

Kullman, L., & Öberg, L. (2009). Post-little ice age treeline rise and climatic warming in the Swedish Scandes: A landscape ecological perspective. *Journal of Ecology*, *97*, 415–429.

Kuuluvainen, T. (1992). Tree architectures adapted to efficient light utilization: Is a basis for latitudinal gradients? *Oikos*, *65*, 275–284.

Kuzmichev, V. V., Pshenichnikova, L. S., & Tretyakova, V. A. (2004). Productivity of six tree species plantations for three decades in the Siberian afforestation experiment. In D. Binkley, & O. Menyailo (Eds.), *Tree Species Effects on Soils: Implications for Global Change* (pp. 269–279). Berlin: Springer.

Leuzinger, S., Manusch, C., Bugmann, H., & Wolf, A. (2013). A sink-limited growth model improves biomass estimation along boreal and alpine treelines. *Global Ecology and Biogeography*, *22*, 924–932. https://doi.org/10.1111/geb.12047

Li, M.-H., Jiang, Y., Wang, A. O., Li, X., Zhu, W., Yan, C.-F., ... Wang, X. (2018). Active summer carbon storage for winter persistence in trees at the cold alpine treeline. *Tree Physiology*, *38*, 1345–1355. https://doi.org/10.1093/treephys/tpy020

Li, X., Liang, E., Gricar, J., Rossi, S., Cufar, K., & Ellison, A. M. (2017). Critical minimum temperature limits xylogenesis and maintain treelines on the southeastern Tibetan Plateau. *Science Bulletin*, *62*, 804–812.

Liu, X. S., Nie, Y. Q., Kong, G. Q., & Luo, T. X. (2016). Contrasting changes in above- and belowground biomass allocation across treeline ecotones in southeast Tibet. *Journal of Mountain Sciences*, *13*, 2036–2045. https://doi.org/10.1007/s11629-016-4003-6

Lloyd, A. H. (2005). Ecological histories from Alaskan treelines provide insight into future change. *Ecology*, *86*, 1687–1695. https://doi.org/10.1890/03-0786

Möhl, P., Mörsdorf, M. A., Dawes, M. A., Hagedorn, F., Bebi, P., Viglietti, D., ... Rixen, C. (2019). Twelve years of low nutrient input stimulates growth of trees and dwarf shrubs in the treeline ecotone. *Journal of Ecology*, *107*, 768–780. https://doi.org/10.1111/1365-2745.13073

Moiseev, P. A., Bubnov, M. O., Devi, N. M., & Nagimov, N. Z. (2016). Changes in the structure and phytomass of tree stands at the upper limit of their growth in the Southern Urals. *Russian Journal of Ecology*, *47*, 219–227. https://doi.org/10.1134/S1067413616030085

Müller, M., Schickhoff, U., Scholten, T., Drollinger, S., Böhner, J., & Chaudhary, R. P. (2016). How do soil properties affect alpine treelines? General principles in a global perspective and novel findings from Rolwaling Himal. *Nepal. Progress in Physical Geography*, *40*, 135–160. https://doi.org/10.1177/0309133315615802

Olsen, J. E., & Lee, Y. K. (2011). Trees and boreal forests. In K. B. Storey, & K. K. Tanino (Eds.), *Temperature Adaptation in a Changing Climate: Nature at Risk* (pp. 160–178). CAB International, Wallingford, UK.

Park, T., Ganguly, S., Tømmervik, H., Euskirchen, E. S., Høgda, K.-A., Karlsen, S. R., ... Myneni, R. B. (2016). Changes in growing season duration and productivity of northern vegetation inferred from long-term remote sensing data. *Environmental Research Letters*, *11*, 084001. https://doi.org/10.1088/1748-9326/11/8/084001

Pepin, N., Bradley, R. S., Diaz, H. F., Barar, M., Caceres, E. B., Forsythe, N., ... Yang, D. Q. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, *5*, https://doi.org/10.1038/NCLIMATE2563

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team (2016). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131.

R Development Core Team (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org. ISBN 3-900051-07-0.

Rinn, F. (1998). TSAP V 3.5: Computer program for tree-ring analysis and presentation. Frank Rinn Distribution, Heidelberg, Germany.

Rossi, S., Deslauriers, A., Anfodillo, T., & Carraro, V. (2007). Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. *Oecologia*, *152*, 1–12. https://doi.org/10.1007/s00442-006-0625-7

Russel, G., Jarvis, P. G., & Monteith, J. L. (1989). Adsorption of radiation by canopies and stand growth. In G. Russel, B. Marshall, & P. G. Jarvis (Eds.), *Plant Canopies: Their Growth, Form and Function* (pp. 21–39). Cambridge, UK: Cambridge University Press.

Salminen, H., & Jalkanen, R. (2007). Intra-annual height increment of *Pinus sylvestris* at high latitudes in Finland. *Tree Physiology*, *27*, 1347–1353. https://doi.org/10.1093/treephys/27.9.1347

Schwaab, J., Bavay, M., Davin, E., Hagedorn, F., Hüsler, F., Lehning, M., ... Bebi, P. (2015). Carbon storage versus albedo change: Radiative forcing of forest expansion in temperate mountainous regions of Switzerland. *Biogeosciences*, *12*, 467–487. https://doi.org/10.5194/bg-12-467-2015

Shiyatov, S. G., & Mazepa, V. S. (2015). Contemporary expansion of Siberian larch into the mountain tundra of the Polar Urals. *Russian Journal of Ecology*, *46*, 495–502. https://doi.org/10.1134/S1067413615060168

Shiyatov, S. G., Terent'ev, M. M., Fomin, V. V., & Zimmermann, N. E. (2007). Altitudinal and horizontal shifts of the upper boundaries of open and closed forests in the Polar Urals in the 20th Century. *Russian Journal of Ecology*, *38*, 243–248. https://doi.org/10.1134/S1067413607040017

Solly, E. F., Djukic, I., Devi, N., Andreyashkina, N. I., Göransson, M., Mazepa, V. S., ... Hagedorn, F. (2017). Treeline advances and associated shifts in the understory vegetation alter fine root dynamics and mycelia production in the South and Polar Urals. *Oecologia*, *183*, 571–586.

Speed, J. D. M., Martinsen, V., Hester, A. J., Holand, Ø., Mulder, J., Mysterud, A., & Austrheim, G. (2015). Continuous and discontinuous variation in ecosystem carbon stocks with elevation across a treeline ecotone. *Biogeosciences*, *12*, 1615–1627. https://doi.org/10.5194/bg-12-1615-2015

Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., ... Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, *556*, 231–234. https://doi.org/10.1038/s41586-018-0005-6

Steppe, K., Sterck, F., & Deslauriers, A. (2015). Diel growth dynamics in tree stems: Linking anatomy and ecophysiology. *Trends in Plant Science*, *20*, 335–343. https://doi.org/10.1016/j.tplants.2015.03.015

Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S. K., Boschung, J. ... Midgley, P. M. (2013). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom and New York, NY, USA.

Sturm, M., Schimel, J., Michaelson, G., Welker, J. M., Oberbauer, S. F., Liston, G. E., ... Romanovsky, V. E. (2005). Winter biological processes could help convert Arctic tundra to shrubland. *BioScience*, *55*, 17–26.

https://doi.org/10.1641/0006-3568(2005)055[0017:WBPCHC]2.0.CO;2

Sullivan, P. F., Ellison, S. B. Z., McNown, R. W., Brownlee, A. H., & Sveinbjörnsson, B. (2015). Evidence of soil nutrient availability as the proximate constraint on growth of treeline trees in northwest Alaska. *Ecology*, 96, 716–727. https://doi.org/10.1890/14-0626.1

Susiluoto, S., Hilasvuori, E., & Berninger, F. (2010). Testing the growth limitation hypothesis for subarctic Scots pine. *Journal of Ecology*, 98, 1186–1195. https://doi.org/10.1111/j.1365-2745.2010.01684.x

Sveinbjornsson, B., Nordell, O., & Kauhanen, H. (1992). Nutrient Relations of Mountain Birch Growth at and Below the Elevational Tree-Line in Swedish Lapland. *Functional Ecology*, 6, 213–220. https://doi.org/10.2307/2389757

Thébault, A., Clément, J.-C., Ibanez, S., Roy, J., Geremia, R. A., Pérez, C. A., … Lavorel, S. (2014). Nitrogen limitation and microbial diversity at the treeline. *Oikos*, 123, 729–740. https://doi.org/10.1111/j.1600-0706.2013.00860.x

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., … Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395. https://doi.org/10.1038/416389a

Westermann, S., Østby, T. I., Gisnås, K., Schuler, T. V., & Etzelmüller, B. (2015). A ground temperature map of the North Atlantic permafrost region based on remote sensing and reanalysis data. *The Cryosphere*, 9, 1303–1319. https://doi.org/10.5194/tc-9-1303-2015

Wieczorek, M., Kruse, S., Epp, L. S., Kolmogorov, A., Nikolaev, A. N., Heinrich, I., … Herzschuh, U. (2017). Dissimilar responses of larch stands in northern Siberia to increasing temperatures—a field and simulation based study. *Ecology*, 98, 2343–2355. https://doi.org/10.1002/ecy.1887

BIOSKETCH

Frank Hagedorn is a Biogeochemist at the Swiss Federal Institute for Forest, Snow and Landscape Research WSL. His research group assesses how changes in climate and land-use are affecting the dynamics of soil organic matter and nutrients, primarily in forest and alpine ecosystems. The approaches include ecosystem manipulation experiments—CO_2 enrichment, soil warming, drought and N deposition—and natural environmental gradients as surrogates for climatic changes

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Hagedorn F, Dawes MA, Bubnov MO, et al. Latitudinal decline in stand biomass and productivity at the elevational treeline in the Ural mountains despite a common thermal growth limit. *J Biogeogr*. 2020;47:1827–1842. https://doi.org/10.1111/jbi.13867