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Dissimilar responses of larch stands in northern Siberia to increasing temperatures—a field and simulation based study

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Abstract. Arctic and alpine treelines worldwide differ in their reactions to climate change. A northward advance of or densification within the treeline ecotone will likely influence climate–vegetation feedback mechanisms. In our study, which was conducted in the Taimyr Depression in the North Siberian Lowlands, we present a combined field- and model-based approach helping us to better understand the population processes involved in the responses of the whole treeline ecotone, spanning from closed forest to single-tree tundra, to climate warming. Using information on stand structure, tree age, and seed quality and quantity from seven sites, we investigate effects of intra-specific competition and seed availability on the specific impact of recent climate warming on larch stands. Field data show that tree density is highest in the forest-tundra, and average tree size decreases from closed forest to single-tree tundra. Age-structure analyses indicate that the trees in the closed forest and forest-tundra have been present for at least ~240 yr. At all sites except the most southerly ones, past establishment is positively correlated with regional temperature increase. In the single-tree tundra, however, a change in growth form from krummholz to erect trees, beginning ~130 yr ago, rather than establishment date has been recorded. Seed mass decreases from south to north, while seed quantity increases. Simulations with LAVESI (Larix Vegetation Simulator) further suggest that relative density changes strongly in response to a warming signal in the forest-tundra while intra-specific competition limits densification in the closed forest and seed limitation hinders densification in the single-tree tundra. We find striking differences in strength and timing of responses to recent climate warming. While forest-tundra stands recently densified, recruitment is almost non-existent at the southern and northern end of the ecotone due to autecological processes. Palaeo-treelines may therefore be inappropriate to infer past temperature changes at a fine scale. Moreover, a lagged treeline response to past warming will, via feedback mechanisms, influence climate change in the future.

Key words: climate change; closed forest; dendroecology; forest change; latitude; recruitment; tundra; vegetation model.

INTRODUCTION

The high-northern latitudes are among the regions with maximum projected temperature changes (IPCC 2014), which, as a consequence, might lead to a northward advance of the treeline ecotone, i.e., the transition zone between boreal forests and open tundra, or to its densification. Climate is an important driver for treeline position (Holtmeier and Broll 2005), but globally, reactions of Arctic and alpine treelines are diverse (Harsch

et al. 2009). Depending on the precipitation regime, increasing temperatures may both positively or negatively influence tree growth (Wilmking et al. 2012). Through vegetation–climate feedbacks, these changes might further alter global climate (Bonan 2008) and lead to changes in biodiversity (Dirnböck et al. 2011). A detailed understanding of temporal and spatial processes involved in treeline responses to a warming signal is thus necessary.

Treeline advance or encroachment within the treeline ecotone depends on successful recruitment, which in turn depends on favorable climatic conditions for a certain period of time (Szeicz and Macdonald 1995). However, increasing temperatures did not positively influence cone production and seed viability in the Mackenzie

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Delta (Walker et al. 2012). A variety of abiotic and biotic factors have been proposed to affect recruitment (Holtmeier and Broll 2007) on smaller spatial scales. Successful recruitment, for example, depends on microsite conditions (Maher and Germino 2006). Intraspecific competition with larger trees (Wang et al. 2016) or interspecific competition with ground vegetation (Hangs et al. 2004) may hinder establishment of tree seedlings. Recruitment success in the upper parts of the ecotone has been found to be further hampered by seed availability and quality (Roland et al. 2014), while others have found highest recruitment rates in these areas (He et al. 2013b). Generally, population drivers and species interactions can change along stress gradients (Coll et al. 2013, He et al. 2013a) and black spruces showed differential growth reaction to climate warming along a Canadian forest-tundra gradient (Gamache and Payette 2004). Studies detecting infilling or advancing treelines do not report stand changes (i.e., increasing recruitment success) in the lower parts of their study regions (Mazepa 2005, Kirilyanov et al. 2012). These findings indicate a dissimilar impact of climate change along the gradient.

The Siberian Arctic treeline is known to display climate change (MacDonald et al. 2000, Herzsuh et al. 2013), by advancing farther north in warmer, and retreating southwards in colder times. The current position, however, is farther south than in previous times with similar climatic conditions (MacDonald et al. 2008), indicating that climate and vegetation are not in an equilibrium state (Herzsuh et al. 2016). After some early work (e.g., von Middendorf 1864), field-based studies of the Siberian treeline have become more numerous only since the end of the 20th century (e.g., Bondarev 1997, Esper and Schweingruber 2004, Kirilyanov et al. 2012). One reason for this lack of studies might be the remoteness and difficult accessibility of many parts of northern Siberia.

While the impact of climate change on ecosystems can be studied with the help of long-term studies and replicated measurements over several decades on permanent plots (Groffman et al. 2012, Lutz 2015), tree-rings allow the inference of past growth conditions (Wimmer 2002) or establishment history (Kirilyanov et al. 2012, Trant and Hermanutz 2014). But replicated studies are infeasible in such remote regions and tree-rings give only information on the past. To analyze future scenarios or to test the importance of population drivers, models are widely used. The recently developed individual-based and spatially explicit model LAVESI (Kruse et al. 2016) is able to capture species- and site-specific forest dynamics of *Larix gmelinii* trees growing in the Siberian treeline ecotone. Such an approach helps to identify population drivers across a large range of forest types from closed forest to single-tree tundra. The combination of field-data and simulation studies could help to extrapolate knowledge, especially in remote and hard to access areas, in space and time, but has to be conducted

carefully due to small-scale effects, which might not be captured when sampling sites across large gradients.

The Taimyr Depression is home to the northernmost tree population worldwide, and the treeline is formed by only one tree species, namely *Larix gmelinii* (Rupr.) Rupr., a deciduous, needle-leaved tree. While most studies in this region focus on the forest enclave at Ary-Mas or on elevational treelines (Kharuk et al. 2006, 2013, Kirilyanov et al. 2012), little is known about stand structure changes and their drivers along the broad latitudinal gradient. Our study investigates the influence of recent climate change across the whole treeline ecotone, using field data and simulation results of LAVESI to test the influence of seed availability, competition, and climate and their interplay. We hypothesize that climate warming will trigger the strongest responses in the forest-tundra, while autecological processes (e.g., interspecific competition) will limit the timing and strength of recruitment success in the closed forest and in the single-tree tundra.

METHODS

Study area

The study area is located in the Taimyr Depression, bordered by the Putorana Plateau in the south and the Taimyr Peninsula in the north (Fig. 1, Table 1), where a narrow forest belt trends southwest to northeast. It extends ~220 km from south to north (70.7° to 72.4° N) and ~300 km from west to east (97.7° to 105.4° E) and follows the southwest-northeast trend of the forest belt, encompassing a vegetation gradient of closed forest (site CF), forest-tundra (sites FTa–FTe) and single-tree tundra (site STT). The region is characterized by a continental climate with long, cold winters (mean January temperature –32°C [Khatanga meteorological station, 1929–2010, number 20891, 71.98° N, 102.47° E]) and short summers (mean July temperature 13°C). Annual mean temperature is –12°C and mean annual precipitation is ~250 mm, about half of it falling between June and August. Average temperatures of the warmest six months (May–October) and the coldest six months (November–April) increased slightly during the last ~20 yr (see Appendix S1: Fig. S1), especially for May and June (see Appendix S1: Fig. S2). In contrast, precipitation of the coldest six months strongly increased, while it remained stable for the warmest six months (see Appendix S1: Fig. S1).

The whole region is underlain by continuous permafrost up to 500 m thick (Brown 1960). Mean active-layer depths range between 22 and 75 cm (Table 1). Understorey vegetation includes shrubs (e.g., *Salix* spp., *Alnus viridis*, *Betula nana*), dwarf shrubs (e.g., *Vaccinium uliginosum*, *V. vitis-idaea*, *Ledum palustre*), grasses and a moss-lichen ground cover. Anthropogenic influence in this remote area, with only 0.03 inhabitants per km² (<http://www.krskstate.ru/msu/terdel/0/doc/58>, in russian, accessed 31.05.2017), is restricted to the direct vicinity of Khatanga.

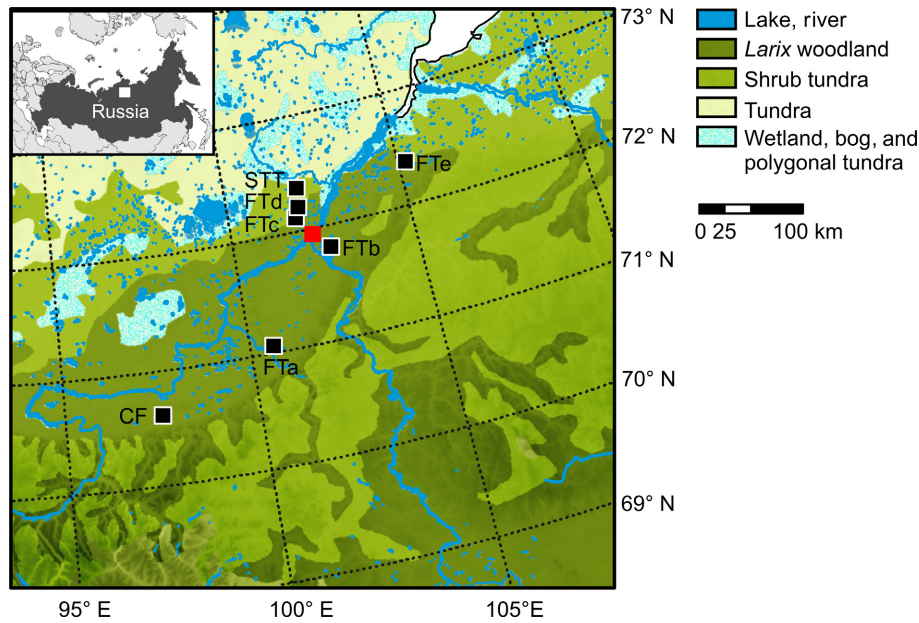


FIG. 1. Map of the study region. Study sites are indicated by black squares and the town Khatanga by a red square. Vegetation types follow Stone and Schlesinger (2003), shading represents the relief. Site codes are CF, closed forest; FTa–e, forest tundra; STT, single-tree tundra. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1. Regional setting and site characteristics and stand structure of the seven study sites.

Parameter	CF	FTa	FTb	FTc	FTd	FTe	STT
Latitude (°N)	70.66	71.10	71.84	72.15	72.24	72.40	72.40
Longitude (°E)	97.71	100.82	102.88	102.09	102.23	105.44	102.30
Plot area, sum (m ²)	800	976	800	1152	880	800	12700
Elevation (m)	117	97	40	41	57	52	67
Active-layer depth (cm)	75	26	47	40	55	22	60

Note: Site codes are CF, closed forest; FTa–e, forest tundra; STT, single-tree tundra.

Field-based approach

Data on *L. gmelinii* stand structures were collected in 2011 (sites CF, FTb, FTd, STT) and 2013 (sites FTa, FTc, FTe; Table 1, see Appendix S2: Table S1, Fig. S1). Sites were reached by means of helicopter because of their remote location with respect to rivers or roads. Regions were chosen a priori from aerial photographs such that the typical vegetation types of the forest belt would be covered. Final location depended on suitable helicopter-landing and camping conditions. Two plots (between ~300 and 1,500 m apart) were set up at each site to account for spatial heterogeneity, covering at least 400 m² each. We aimed to record at least 30 trees (size-class definitions: seedling <40 cm, sapling 40–200 cm, tree ≥200 cm), or 50 trees and saplings. In the single-tree tundra (STT), larch was sparse and growing in delimited groups (Appendix S2: Fig. S2). In this region, we walked from group to group until 30 groups per plot were recorded.

All individuals in the 14 plots were measured for height, basal diameter, and, for individuals >130 cm,

diameter at breast height (DBH). Tree crown cover was estimated by measuring the longest crown axis and calculating the resultant circle area. Vitality (alive, dead) was noted and the number of cones estimated in four categories (0, ≤10, 11–50, >50). Seedlings were recorded and measured in at least 124 m² of each plot. Most individuals in the study region were single-stemmed and upright growing trees. In the single-tree tundra, larch grows in krummholz growth-form with creeping trees as well as erect tree clusters, which are most probably the upright branches of one individual, as confirmed by digging around a few individuals. A group comprised up to 125 upright stems, making it impossible to measure all stems due to time limitations. Instead, we fully recorded at least three stems of each size class in every group. For those stems not fully recorded, we recorded the size class, presence/absence of cones, and the vitality, resulting in 262 fully and 647 partially recorded stems. Seedlings in the single-tree tundra were searched for in the nearby surroundings of each group and additionally in 30 randomly placed 4-m² tree-free sub-plots.

Age analyses.—We collected tree discs at ground level (as close to the ground as possible) or complete specimens of at least 19 individuals across all size classes from at least one plot at each site, giving a total of 220 individuals for the seven sites. Discs were polished and ring width measured along one radius with a mechanical measuring table (Lintab, F. Rinn SA, Heidelberg, Germany) and WinDendro software (Regent Instruments Inc., Québec, Canada). Samples were first crossdated visually and then checked with the help of Cofecha (Holmes 1983). Missing rings were carefully inserted, as high proportions of compression wood hampered ring width analysis. Thin sections of small individuals (saplings and seedling with <5 cm basal circumference) were dyed with astra blue and safranin, and rings were counted under a Zeiss light microscope (Carl Zeiss Microscopy GmbH). With the help of site-specific regressions between the tree height or basal circumference and age (see Appendix S3), the ages of all recorded living larches at each site were calculated (see Table 2 for *F* statistics). Discs with heart rot were removed from the analyses. In 2011, basal circumference was not measured for seedlings. Basal circumference was thus used for age estimations of all individuals with a basal circumference >2 cm; ages of smaller larches were calculated by height–age regressions. In 2013, basal circumference was gained for all larches, except the very smallest ones, and as only as an explanatory variable. At site STT, no seedlings were sampled for age analyses.

Stand structure analyses.—Statistical analyses were conducted in R (R Core Team 2015). Sampling data from the two plots at each site were pooled. For better comparability between different plot sizes, stand values were normalized to 1 ha. As the density of seedlings differed highly between sites and years, we only included seedlings

>2 cm tall at all sites from 2013 in our analyses to exclude differences of probable mass establishments between the two sampling years. Age analyses of some very small seedlings from 2011 sites suggested that, for such small seedlings, height (in cm) is a good estimator of age (in years). Unless noted otherwise, only living individuals were used for statistical analyses. To gain information on tree size (height and DBH) and age differences across the transect, Kruskal-Wallis test with post hoc pairwise Wilcoxon test and Benjamini and Yekutieli (2001) correction for multiple testing were applied. We furthermore assessed differences in the amount of all size classes, crown cover and basal area between all sites. These categorical variables were assessed with a χ^2 test.

Seed analyses.—If available, we collected at least 10 cones of all cut individuals. Cones from three sites (CF, FTd, and STT) were carefully opened and all seeds inside counted. Seed quality was not visible and randomly chosen seeds were opened under a Zeiss stereo microscope, inspected, and quality level (empty, damaged/shriveled, full) recorded, until a total of 100 full seeds were found. At site STT, we stopped with 50 full seeds, due to low seed quality. Seeds were dried and weighed to obtain the mass of 100 (50) full seeds. To provide a conservative estimate of seeds density, independent of seed quality, we multiplied the mean number of seeds per cone at each site by 1 for trees with ≤ 10 cones, by 11 for trees with 11–50 cones, and by 51 for trees with >50 cones.

Establishment history.—Because long climate time-series are not available from northern Siberia, we used $\delta^{18}\text{O}$ values originating from an ice core ~800 km north of the study area that is claimed to be a good proxy for temperature change in the region (Opel et al. 2013) and

TABLE 2. Regression formula including *F* statistics for age estimations of larches.

Site	Regression	Adjusted R^2	df	<i>F</i>	<i>P</i>
CF					
log <i>A</i>	$0.5642 \times \log C + 3.25537$	0.7635	1,22	75.25	<0.001
<i>A</i>	$1.0219 \times H - 1.4448$	0.9042	1,8	85.95	<0.001
FTa					
log <i>A</i>	$0.68606 \times \log C + 2.85403$	0.9241	1,19	244.3	<0.001
FTb					
log <i>A</i>	$0.79048 \times \log C + 2.65195$	0.8789	1,17	131.6	<0.001
log <i>A</i>	$0.6460 \times \log H + 0.6698$	0.4891	1,7	8.658	<0.05
FTc					
log <i>A</i>	$0.51559 \times \log C + 3.08518$	0.8716	1,21	150.3	<0.001
FTd					
log <i>A</i>	$0.5888 \times \log C + 2.8972$	0.9249	1,47	591.9	<0.001
<i>A</i>	$0.67370 \times H + 4.47387$	0.7786	1,20	74.87	<0.001
FTe					
log <i>A</i>	$0.52623 \times \log C + 2.62290$	0.7812	1,17	65.26	<0.001
STT					
log <i>A</i>	$0.4947 \times \log C + 2.9169$	0.2755	1,28	12.03	<0.01

Note: Variables are *A*, age; *C*, basal circumference; *H*, height.

positively correlated with spring and early summer temperatures (May and June) of the Khatanga weather station (see Appendix S3: Fig. S2). Data are available until the year 1998. To assess the influence of temperature on tree establishment for each site, $\delta^{18}\text{O}$ and establishment data gained from tree-ring analyses were pooled into 10-yr bins, starting with 1995, and compared using Spearman's rank correlation coefficient. We furthermore fitted linear regressions, helping to better identify establishment trends over time. Furthermore, Mann-Kendall trend tests for monotonic increase were performed on the data, to statistically substantiate the occurrence or absence of trends. To remove the influence of some very old trees on all tests, we only accounted for larches established after 1700, as *L. gmelinii* commonly dies at an age of 250–300 yr (Praciak et al. 2013).

Modelling approach

For this part of our study we applied LAVESI, an individual-based, spatially explicit model developed by Kruse et al. (2016), to simulate three larch stands in the closed forest, the forest-tundra and the single-tree tundra. The model was developed to understand population dynamics of *L. gmelinii* at the Siberian treeline under changing climatic conditions. It simulates the whole life cycle of individual larches and the biotic and abiotic environment they are growing in. Simulated trees establish, grow, die, produce, and disperse seeds in yearly time steps. All individual-based processes, beside dispersal, depend on temperature, annual precipitation, and population density. Model parameters were based on field investigations (namely baseline diameter growth rates, height-diameter relationships, minimum height for maturity, background mortality, and youth mortality), literature and, in cases where robust estimations were lacking, tuned in a parameterization procedure (see Kruse et al. 2016 and Appendix S4 for further details).

Climate data as model input were gained by using weather station data from Khatanga (1929–2011). To gain site-specific curves, the difference in mean temperature of the weather station series and the mean of the CRUTS2.1 data set (1929–1998; Mitchell and Jones 2005) was calculated and the weather station series adapted to that value. This procedure gave us site-specific climate data for the closed forest (CF, weather data increased by 1.18°C), forest-tundra (FTd, weather data decreased by 0.07°C), and single-tree tundra (STT, weather data decreased by 0.65°C). 200-yr long climate series were then created by sampling with replacement out of these site-specific data from the years 1951–2011.

For each site, simulations with a spin-up phase of 5001 yr were conducted and the final stand structure then operated as starting point for 200-yr-long experimental runs, which were conducted to separate the effects of temperature, competition, and seed availability on the structure of *L. gmelinii* stands. The model parameter “influencing zone of trees” was reduced from 10.0

to 5.0 (e.g., from 100 to 25 m² for trees with basal diameter of 50 cm) to test the influence of competition on stand density and recruitment. The influence of seed input on stand structure was examined by an additional seed input of 10,000 seeds per year. To test for the influence of temperature, we ran the model with an increase of 2°C, first keeping all other parameters constant, and then adding either reduced competition or high seed input. All scenarios were run with 30 repetitions on a 100 × 100 m grid. To account for edge effects, only the innermost 20 × 20 m were analysed.

RESULTS

Field data

Stand structure.—In total, 773 trees, 944 saplings, and 2,520 seedlings were recorded across all sites. Tree density across the treeline ecotone followed a hump-shaped curve with highest values in the forest-tundra at FTa, FTb, and FTc (Fig. 2a). Crown cover decreased from south to north, with similar cover in the forest-tundra sites (Fig. 2d). Tree basal area (m²/ha) decreased from south to north, too (Fig. 2e). While tree height and stem diameter were highest in the closed forest (CF) and lowest in the single-tree tundra (STT, Fig. 3), both parameters were rather similar in the forest-tundra (FTc to FTe). Sapling density increased from CF to FTc, with a steep decrease to STT (Fig. 2b). Seedling density showed a parabola between CF and FTe, with the lowest number of seedlings at FTb (Fig. 2c). A very low density of only ~200 seedlings/ha were found in the single-tree tundra (STT). Of the recorded offspring, only six saplings and four seedlings established from seed.

Larix establishment and temperature change.—Tree age decreased slightly from CF to FTe (Fig. 3). Maximum measured tree age at FTd (295 yr) was only a little younger than at CF (325 yr). In the southern part of the forest-tundra (FTb), we found two trees with heart rot in their basal discs, but their breast height age was 341 and 497 yr. While maximum tree age at FTe was only 172 yr, trees with 225 and 237 yr were found in the surroundings of the study sites. About 140 yr ago, the first larches in the single-tree tundra (STT) started to change from creeping to upright growth form. Establishment date of the creeping trees, however, could not be derived.

In the closed forest (CF), most larches established during the 18th century, while recent establishment was virtually lacking (Fig. 4). Establishment is best depicted by linear decrease and also the Mann-Kendall test shows a significant negative trend. In the southern part of the forest-tundra (FTa), establishment was constant over time, showing no trend at all despite a peak in the last decade (1985–1995). While establishment only slightly increased at FTb with a linear trend, farther north in the forest-tundra (FTc to FTe), establishment increased stronger since the end of the 19th century and is best

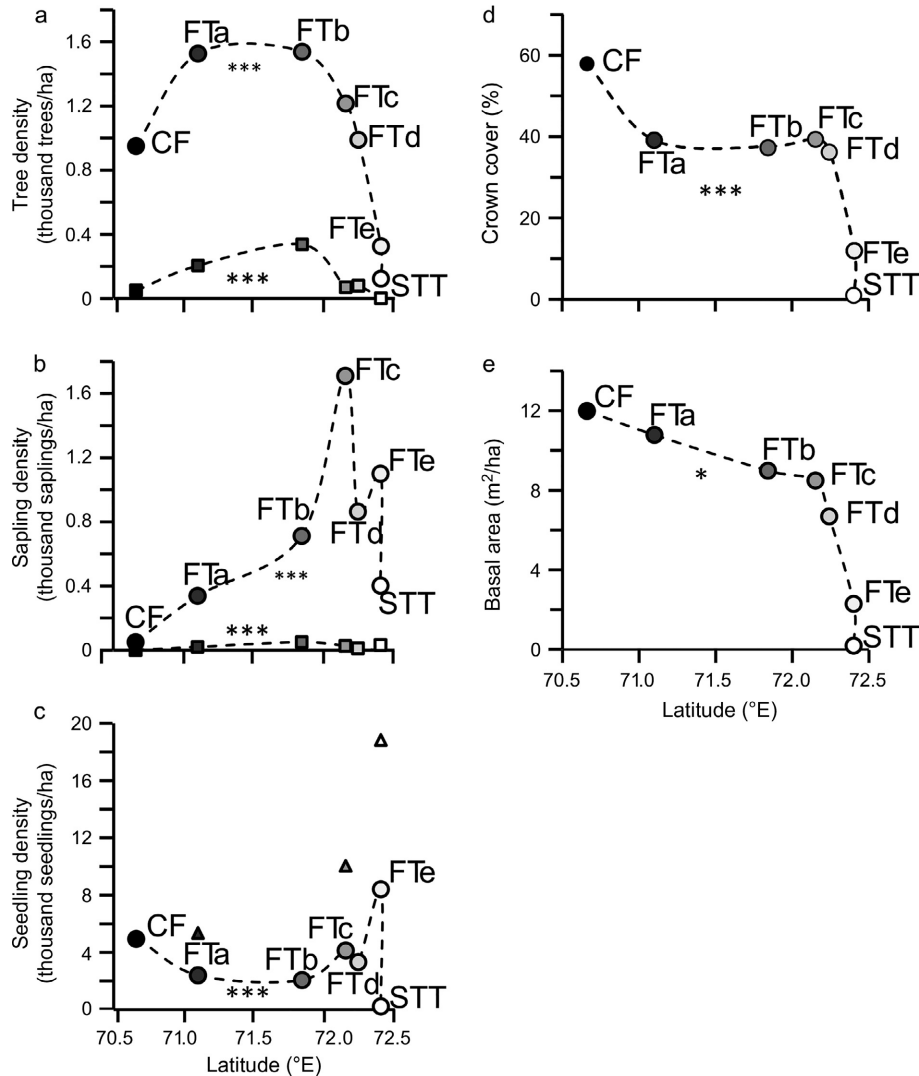


FIG. 2. Density of (a) trees (height ≥ 200 cm), (b) saplings (height 40–200 cm), and (c) seedlings (height < 40 cm). Circles are all individuals, squares dead individuals. As the density of seedlings differed highly between sites and years, we only included seedlings > 2 cm tall at all sites from 2013 in our analyses (shown as circles). Triangles depict the number of all seedlings recorded in 2013. Crown cover and basal area of living trees are shown in panels d and e, respectively. Site codes as in Fig. 1. * $P < 0.05$; *** $P < 0.001$ according to the χ^2 test.

described by exponential functions. All forest-tundra sites show a significant positive trend according to the Mann-Kendall test. A distinct peak, best described by a quadratic function, was found in the single-tree tundra (STT) and likely represented a change in growth form. Establishment in the forest-tundra (FTb to FTe, $P < 0.05$) and change to upright growth in the single-tree tundra (STT, $P < 0.1$) was positively correlated with our temperature proxy (Fig. 4), but no positive correlation was found for the closed forest (CF) and the southernmost forest-tundra (FTa).

Reproduction.—At most sites, the majority of adult trees bore cones (Fig. 5a). Few saplings were cone bearing and their quantity increased with increasing latitude. Of the

cone-bearing individuals, a majority had > 50 cones (Fig. 5a), except for forest-tundra sites FTa and FTc. However, variability for all three classes (i.e., < 10 , 10–50, and > 50 cones) was high and showed no latitudinal trend. In contrast, the number of seeds per cone increased markedly from south to north (Fig. 5b), while seed quality (estimated from the fraction of full seeds and seed mass) was lowest in the north (Fig. 5c). We found the lowest seed density in the single-tree tundra (STT) and highest at the northern forest-tundra site FTd (Fig. 5c).

Simulation study

Simulations using LAVESI were conducted to separate the temperature effects on population density from

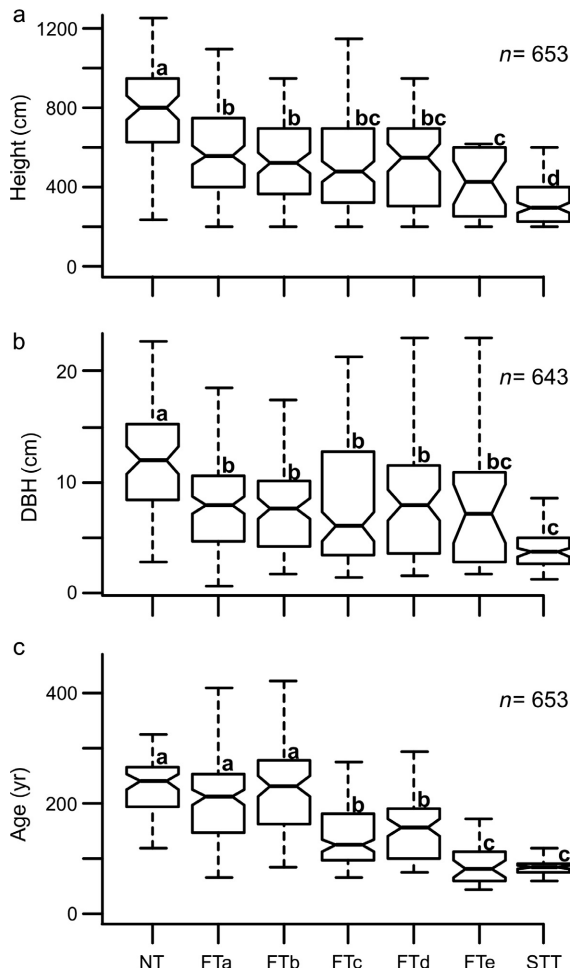


FIG. 3. Notched boxplots of (a) height, (b) diameter at breast height (DBH) and (c) age of trees (height ≥ 200 cm), showing decreasing tree size and age from closed forest to single-tree tundra. Notches denote the confidence interval for the median, given by $\pm 1.58 \times \text{IQR}/\sqrt{n}$ (IQR, interquartile range); box edges denote the 0.25 and 0.75 quartiles; whiskers denote the minimum and maximum. Sites that differ significantly ($P < 0.05$) according to the pairwise Wilcoxon test are labelled with different letters above the boxes. Box plots for age include those values gained by site-specific age–diameter regression analyses. Site codes are as in Fig. 1. Note that STT age data rather depict change from creeping to upright growth form than establishment.

those of competition and seed-limitation across the tree-line ecotone (Fig. 6). While tree density was captured well by the model, sapling density was strongly overestimated in the closed forest and the single-tree tundra.

Reducing competitive strength increases stand density (“Comp-,” Fig. 6), particularly in the closed forest. After 200 yr with reduced competitive strength, stand density more than doubled in both size classes (trees and saplings). Competition was of minor importance in the single-tree tundra. Instead, additional seed input had the strongest effect in this region, increasing tree and sapling density 26 and 34 times, respectively. Though additional seed input increased density at all sites (“Seed+,” Fig. 6),

the effect is strongest in the simulated single-tree tundra. The effect of a 2°C increase was strongest in the forest-tundra, increasing tree density by 668 individuals per hectare, compared to an additional 194 and 176 in the closed forest and single-tree tundra, respectively. Interestingly, sapling density in the closed forest slightly decreased in such a scenario. A combination of reduced competition and increasing temperature lead to the highest stand density increases in the closed forest and forest-tundra. In the closed forest, the value only slightly exceeded the sum of results for the single factors, whereas the combination of both parameters boosted the effects of each in the forest-tundra. A combination of increasing temperature with high additional seed input boosted the effects of each factor in the single-tree tundra, but not for the other two vegetation types.

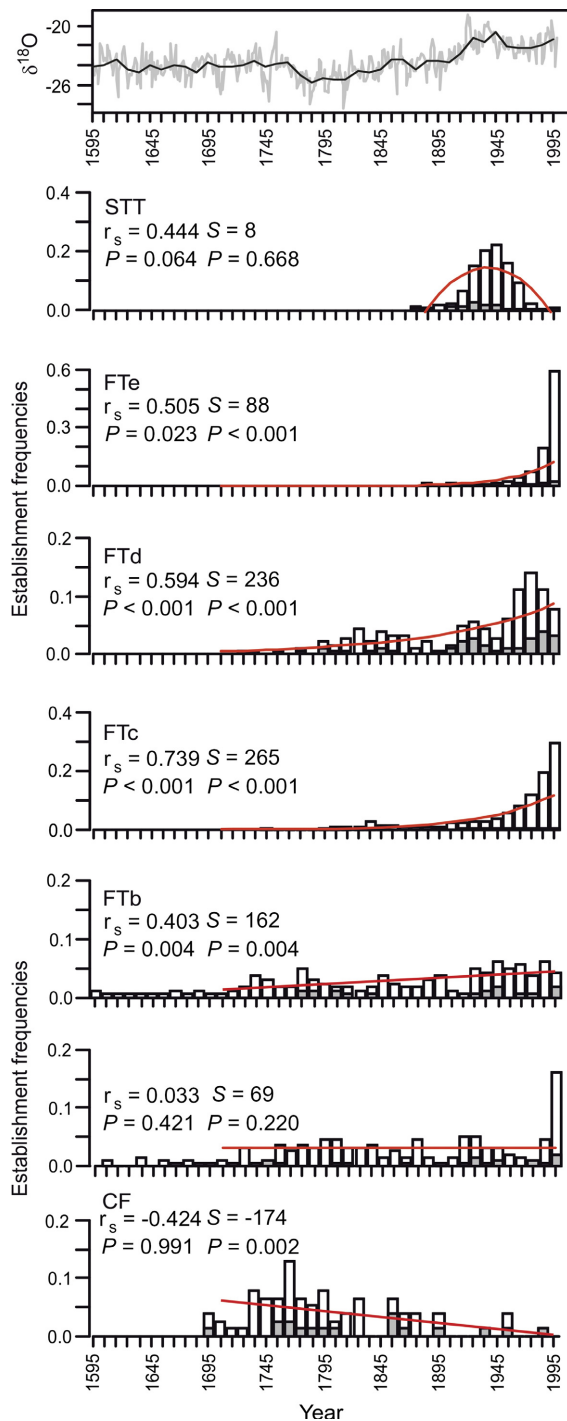
In summary, within the model, competition was the main limiting factor in the closed forest, a combination of competition and temperature mainly limited recruitment in the forest-tundra and a combination of temperature and seed availability was the main limitation in the single-tree tundra.

DISCUSSION

Data acquisition

The aim of our study was to analyze a broad gradient with different larch stand patterns from the southern closed forest up to the northern single-tree tundra. For this purpose, larch stands on 14 plots at 7 sites have been recorded during two expeditions, including a thorough search for the very small seedlings. While such studies can be conducted on complete transects from closed forest to the treeline (Camarero and Gutiérrez 2002, Elliott 2011, Kharuk et al. 2013), also plot-wise analyses are possible (Caccianiga and Payette 2006, Kharuk et al. 2011, Kirilyanov et al. 2012). Complete transect studies can provide a good picture of the ecotone structure and changes within the ecotone, however, this approach is not possible on lowland treelines, where the ecotone spans over more than 100 km (Timoney et al. 1992). Furthermore, the snow-free period, in which field work and (expensive) helicopter flights are possible, is rather short. This results in a trade-off between time, money, and data acquisition.

Some care is needed when using regression analysis for the inference of establishment history, as growth rates even within one site can be highly variable and small larches can survive under the canopy for many years (Osawa et al. 2010). While these differences are important when using trees for dendroclimatological analyses (e.g., Babushkina et al. 2015), growth differences clearly influence age–size relationships, too. Nonetheless, most of our regressions fit well, having adjusted $R^2 > 0.75$ and giving us confidence in capturing the right trends. Outliers in this context are small larches at FTb, where regression for young trees (in that case up to 30 yr) does



not fit well. The worst fit is found in the single-tree tundra, where many larches grow as krummholz, leading to an adjusted R^2 of only 0.28. While the exact timing of growth change might thus not have been captured by our data, the 30 dated trees to a majority also erected in the first half of the 20th century, which is further in consistency with results from the Ural Mountains wide

FIG. 4. Establishment history of larch along the latitudinal gradient from closed forest (CF) to single-tree-tundra (STT), showing a lack of recent recruitment in the closed forest and the single-tree tundra, while recruitment increases across the forest-tundra. Gray sections in each barplot represent dated tree discs, while white sections represent age data gained by regression analysis. The $\delta^{18}\text{O}$ values originating from Severnaya Zemlya are shown with yearly values (gray) and a 10-yr running mean (black). Site codes are as in Fig. 1. Spearman's rho and S value of Mann-Kendall trend test and their P values are given. Red lines depict linear regressions, calculated as follows: CF, $y = \text{year} \times -0.000205712 + 0.4126018$, adjusted $r^2 = 0.28$; FTa, $y = 0.03127$; FTb, $y = \text{year} \times 0.0001068 - 0.1671362$, adjusted $r^2 = 0.31$; FTc, $\log(y) = \text{year} \times 0.01664 - 35.31427$, adjusted $r^2 = 0.83$; FTd, $\log(y) = \text{year} \times 0.009457 - 21.314323$, adjusted $r^2 = 0.59$; FTe, $\log(y) = \text{year} \times 0.02797 - 57.85806$, adjusted $r^2 = 0.66$; STT, $y = \text{year}^2 \times -4.958 \times 10^{-5} + \text{year} \times 0.1921 - 1.860 \times 10^2$, adjusted $r^2 = 0.56$. [Color figure can be viewed at wileyonlinelibrary.com]

(Devi et al. 2008) and proves our results to give a good estimation on stand history.

Larch-stand patterns across the Siberian treeline ecotone

Our field-based investigation in north-central Siberia found dissimilar *L. gmelinii* stand structures on sites located on a vegetation gradient from closed forest to single-tree tundra. The observation of decreasing tree cover and basal area index across the vegetation types was expected and is in agreement with results from comparable transect studies crossing diffuse and krummholz treelines worldwide (Šrůtek et al. 2002, Devi et al. 2008, Batllori et al. 2009). A general latitudinal decline has further been documented on the broad scale across the entire northern circumpolar region by analysis of satellite images (Lorantý et al. 2014). However, interpreting latitudinal trends from single plots has to be done with some care. In a study on northeastern Siberian larch stands, for example (Alexander et al. 2012), documented highly variable stand densities, ranging from 800 to 37,000 trees/ha in mid- and late-successional stands. These differences were mainly a result of different pathways after fires. While wildfires are common in southern boreal forest, their frequency decreases with latitude (Goldammer and Furyaev 1996). Furthermore, they seem to be more common in northeastern than in north-central Siberia (Sukhinin et al. 2004, Hantson et al. 2015), having return intervals of around 350 yr in the Taimyr region (Kharuk et al. 2008).

Our study documents differences in establishment histories across the entire latitudinal treeline ecotone of the Taimyr Depression. In the closed forest and southern forest-tundra, tree density appears to be rather stable, showing no marked recruitment phases in recent times. In contrast, we find a clear densification of larch stands in the northern forest-tundra during the last 50–100 yr, which is in consistency with Frost and Epstein (2014) who found a 5% increase of tree cover by analyzing satellite images of that region, but do not detect enhanced recruitment in the single-tree tundra. However, the forested area

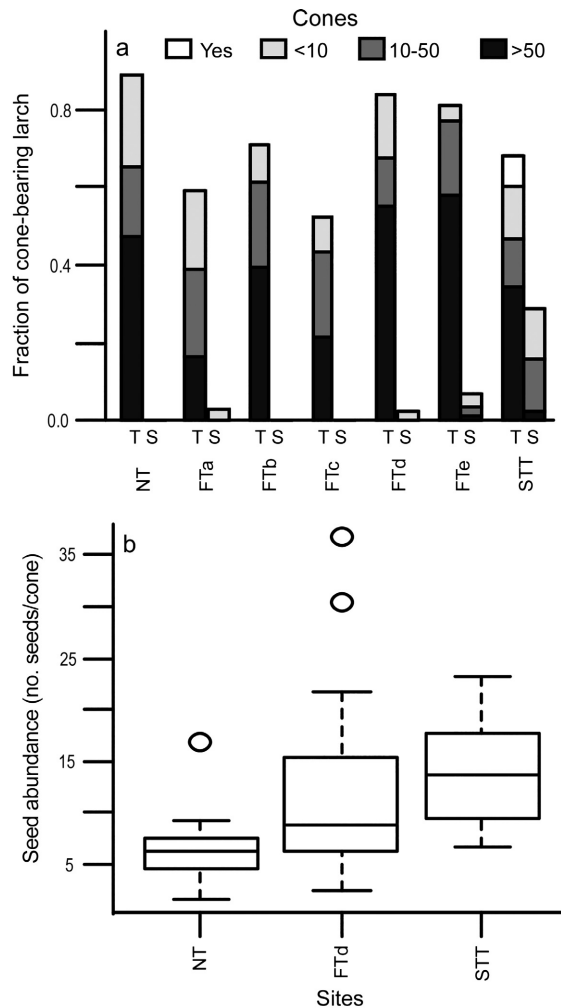


FIG. 5. (a) Fraction of cone-bearing *Larix gmelinii* individuals per site by size class (tree and sapling). Bars are divided into classes of number of cones. (b) Number of seeds per cone. Box plots mid line is the median; box edges, 0.25 and 0.75 quartiles; whiskers, extent up to 1.5 times of the interquartile range (IQR); circles, depict outliers with values >1.5*IQR. (c) Table with fraction of full seeds, dry mass of 100 full seeds, and extrapolated number of seeds of all qualities per hectare. While seed quantity within the cones increases, quality given by seed mass decreases along the vegetation gradient from closed forest (CF) to single-tree-tundra (STT). Site codes are as in Fig. 1.

of the single-tree tundra increased in the last ~120 yr due to the transformation of formerly creeping trees into upright growth forms. Population patterns revealed by

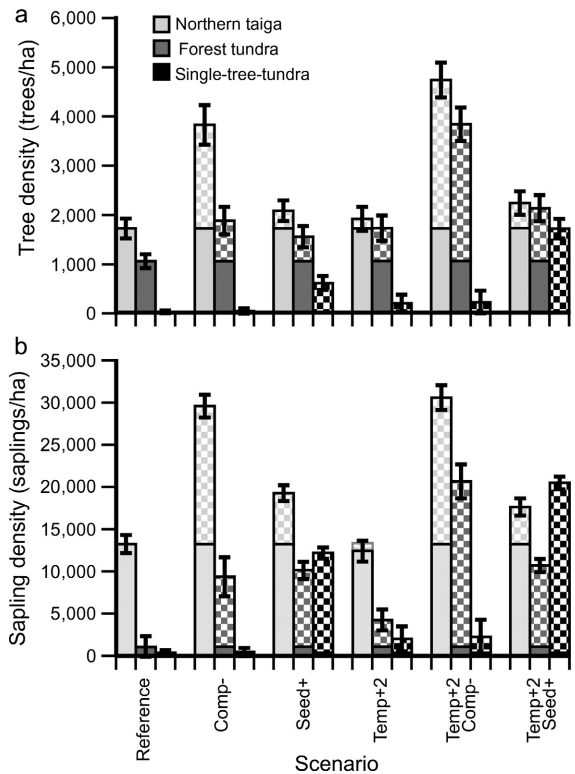


FIG. 6. Stand density resulting from simulation runs for (a) trees and (b) saplings. “Reference” is the number of individuals in a run without changes, and is given in solid bars for each scenario. Scenario runs increase stand density, shown as patterned bars. “Comp-” are runs with reduced competition, “Seed+” are runs with additional seed input and “Temp+2” is a temperature increase of 2°C. Note that sapling density in the closed forest decreases in the “Temp+2” scenario. Error bars are based on 30 repetitions for each scenario.

our study, showing marked density increases especially in the forest-tundra, but not in the closed forest, share some similarities with those at alpine treelines, e.g., in the Ural Mountains (Mazepa 2005) and the Putorana Mountains (Kirilyanov et al. 2012).

Warming causes densification in the forest-tundra

We make the assumption that all discovered stand-structure changes mainly originate from climate change as the study was conducted in extremely remote areas. Reindeer are present for migration between summer and winter ranges (Kolpaschikov et al. 2015). Establishment events at all sites except CF and FTa are positively correlated with our proxy for regional temperature change and the most recent establishment phase coincides with a warm period across the entire Arctic (Opel et al. 2013). Rising CO₂ concentrations should not have any positive effect on tree growth (Körner 2003), but this effect might not apply to seedlings (Handa et al. 2005).

The most pronounced changes of age structure are found in the more northern forest-tundra (FTc-FTe),

although the methodological bias in estimating past establishment rates from the present stand structure rather than from monitoring, and with only a few data points per site needs to be kept in mind. Tree-ring studies in the Taimyr region have shown that tree growth is related to early summer temperature (Naurzbaev et al. 2002). However, seedling establishment is controlled by somewhat different climatic conditions than tree growth. Climate data from the Khatanga weather station show that early summer temperature and the number of days with a minimum temperature $>0^{\circ}\text{C}$ are increasing since the last 20–40 yr (see Appendix S1: Fig. S1), which probably enhances larch reproduction and establishment. Furthermore, winter precipitation has strongly increased, allowing a deeper snow cover to develop that can provide shelter from frost for small seedlings (Holtmeier 2009), as well as supplementing the water supply when it melts at the beginning of the growing season (Kirilyanov et al. 2003).

Our attribution of stand-density changes in the forest-tundra to climate change is supported by our simulation experiments. For the three modelled sites, a temperature

increase of 2°C leads to the greatest tree population increase in the forest-tundra. Still, reducing competition as well as increasing seed input likewise increased tree density, indicating that population dynamics in the forest-tundra are complex. However, the detected differences in stand structures across the ecotone do not necessarily result from changing temperatures: they might equally be caused by higher tree mortality in the north compared to the south, thus providing more light gaps for new recruits. But we do not find such a pattern in our data, as the highest quantity of dead trees is found in the southern forest-tundra.

*Intra-specific competition inhibits densification
in the closed forest*

In the closed forest, climate does not seem to have a strong influence on establishment rate, which was fairly constant throughout the last two centuries. Field-based data indicate that recruitment to sapling stage is rare in the closed forest despite a high fraction of full seeds,



FIG. 7. Concept of stand density drivers across the studied ecotone, showing recent stand structures (upper) and expected changes with reduced competition (middle) and additional seed input (lower). Combining field and simulation data, we find a recent densification only in the forest-tundra. A further temperature increase will increase stand density in the closed forest only when competition is reduced. Stand density in the single-tree tundra will only increase when seed availability is enhanced. [Color figure can be viewed at wileyonlinelibrary.com]

highest seed weight among all sites, and the presence of many seedlings. Seedlings, however, do not reach more than a mean height of 3 cm (data not shown), indicating that most die within their first years. Conditions are evidently good enough for investment in seed production, germination, and seedling establishment, but vegetation cover is probably too dense for the shade-intolerant larches (Osawa et al. 2010) to grow and mature. Observations of a high abundance of saplings in nearby old river beds and drained lake areas (without further sampling), further indicate that recruitment was generally possible in the area and a study on shade-intolerant western larch showed that under low light conditions, most seedlings died or were damaged within the first three years of their life (Chen and Klinka 1998). Thus, the lack of saplings inside the forest is most probably not attributable to climatic conditions but related to intra-specific competition.

This interpretation is further supported by the model's outcome. While closed forest's sapling density within the model is always higher than that found in the field, reducing competitive strength within the simulation model leads to an enormous density increase. Seed addition on the other hand has almost no effect on tree and only a light effect on sapling density within the closed forest. Additionally, higher temperatures and related drought stress might have reduced seedling performance in mature stands (Okano and Bret-Harte 2015).

Recruitment limitation decelerates densification and northward expansion of the single-tree tundra

In the single-tree tundra (STT), growth form rather than establishment rates are changes, starting earlier than the establishment phase in the nearby forest-tundra sites. Meristem temperatures in short vegetation can be up to 15°C above air temperature (Wilson et al. 1987). Under the cover of snow, layering trees should thus not suffer from extreme atmospheric winter temperatures as much as tall trees do and might be at an advantage compared to newly germinated and established seedlings, being able to react faster to changing temperature conditions.

Even though the trees at STT have the highest number of seeds per cone of all sites, the seed density is very low due to the low tree density. Furthermore, this site has the lowest seed quality. This finding is in accordance with results from germination experiments of *L. sibirica* by Wilmking et al. (2012), who find that the germination rate of seeds from the treeline ecotone is <1%, compared with 80% from more southerly forests. A study by Barchenkov (2011) finds that decreasing seed mass and germination capacity of *L. gmelinii* is correlated with elevation and the production of viable seeds is highly correlated with summer air temperature (Kullman 2007). Our model results likewise suggest that seed availability is a severe bottleneck for larch establishment in single-tree tundra sites.

CONCLUSIONS

Our combined model- and field-based investigations of *L. gmelinii* stands in north-central Siberia reveal dissimilar responses to a warming signal in populations located across the treeline ecotone (Fig. 7). The strongest and most direct response to temperature increase is found in plots of the forest-tundra zone, where enhanced recruitment led to infilling. In contrast, intra-specific competition for light or nutrients seems to hamper recruitment in the plots located in the closed forest. Seed limitation and/or low seed quality seem to hamper recruitment in the single-tree tundra sites, but nonetheless, tree cover there has increased due to the change from krummholz to erect growth form.

Our findings indicate that the treeline position is not a reliable proxy for temperature on short time scales because of the longevity of the species and slowness and variability of its response. Regarding treeline transitions in the course of ongoing high-latitude warming, our results suggest that densification in the northernmost treeline population is lagging climate change, with the implication that adaptation of the current treeline to present climate change might influence climate in the future via feedback mechanisms.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.1887/suppinfo>

DATA AVAILABILITY

Data sets are available at <https://doi.org/10.1594/pangaea.874615>.