Regional opportunities for Siberian tundra conservation in the next 1000 years

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Abstract The biodiversity of tundra areas in northern high latitudes is threatened by invasion of forests under global warming. However, poorly understood nonlinear responses of the treeline ecotone mean the timing and extent of tundra losses are unclear but policymakers need such information to optimize conservation efforts. Our individual based model LAVESI, developed for the Siberian tundra-taiga ecotone, can help improve our understanding. Consequently, we simulated treeline migration trajectories until the end of the millennium, causing a loss of tundra area when advancing north. Our simulations reveal that the treeline follows climate warming with a severe, century-long time lag, which is overcompensated by infilling of stands in the long run even when temperatures cool again. Our simulations reveal that only under ambitious mitigation strategies (RCP 2.6) will ~30% of original tundra areas remain in the north but separated into two disjunct refugia.

Introduction

Arctic regions have experienced strong warming over recent decades as exemplified in Siberia (Box *et al.*, 2019). The warming is expected to continue drastically, based on future changes simulated with prescribed 'relative concentration pathway' (RCP) scenarios (Meinshausen *et al.*, 2011). Following climate simulations, mean July temperatures in the region could, by the end of the 21st century, be less than +2°C warmer with ambitious mitigation efforts (RCP 2.6), about +3.1°C (intermediate effort scenario RCP 4.5), or an extreme of +14°C warmer (high-emission high-warming RCP 8.5). In consequence, the treeline ecotone can expand and replace tundra (Hofgaard *et al.*, 2012; MacDonald *et al.*, 2008). This turnover threatens the existence of various types of sensitive tundra with differing vegetation structure along latitudinal and altitudinal bioclimatic gradients located between the treeline in the south and the Arctic Ocean in the north (Walker *et al.*, 2005; Pearson *et al.*, 2013; Yu *et al.*, 2009). The Siberian tundra areas are known for their alpine species biodiversity (Pauli *et al.*, 2012; Mod and Luoto, 2016; Arctic Climate Impact Assessment, 2004) and support special (indigenous) types of land use (e.g. reindeer herding, foraging). However, the expansion of forests in response to increasing temperature is not well understood and the uncertain timing of future tundra loss is challenging conservation efforts.

In Siberia, the modelled climate envelope for tundra migrates north by ~ 290 m yr⁻¹ (Loarie *et al.*, 2009). When assuming a direct relationship linking the modern position of the treeline to its main limiting factor of July temperature (MacDonald *et al.*, 2008), the treeline is expected to

reach its maximum expansion within the first centuries of the millennium. Regionally, where the shoreline of the Arctic Ocean is close to the treeline, the 100-200 km wide tundra corridor would be completely covered by forests. Moreover, even regions with wide tundra corridors in Siberia (~ 600 km; Taimyr Peninsula and Chukotka) could be forested in the warmest scenarios. However, the potential migration rates are likely constrained by other factors, partly acting on a small scale (Corlett and Westcott, 2013). This and the fact that in Siberia the treeline is formed solely by larch species growing on permafrost while in North America this niche is covered by a mix of species (Mamet et al., 2019; Herzsuh, 2020), make it impossible to transfer knowledge from any other treeline region to inform Siberian tundra responses.

Equilibrium-based estimations are not backed by empirical studies which are showing slower responses and either no treeline advance or rates of only a few metres per year in Siberia (Scherrer et al., 2020; Kharuk et al., 2013; Wiczorek et al., 2017b; Harsch et al., 2009). Either the different response of regions can be related to site conditions (e.g. Harsch et al., 2009; Mamet et al., 2019), or it is not well understood how complex processes such as seed dispersal or intra-species competition acting on fine and broad scales constrain the response to warming (Corlett and Westcott, 2013; Wiczorek et al., 2017b). Models that do not consider these processes lead to forecasts prone to overestimating treeline advance (compare Pearson et al., 2013; Snell and Cowling, 2015), but it is challenging to consider both small-scale processes and the broad-scale picture.

Models which contain processes to estimate competition between individuals for resources and seed dispersal in a spatially explicit environment and which handle each tree individually are called individual-based spatially explicit models (DeAngelis and Mooij, 2005). These models have become increasingly used lately to assist in formulating conservation management strategies (Zurell et al., 2021). For the northern Siberian treeline ecotone the vegetation model LAVESI was developed, which incorporates a full tree (*Larix*) life-cycle beginning with seed production and dispersal, germination, and establishment of seedlings which then grow based on abiotic (temperature, precipitation, active layer depth) and biotic (competition) conditions (Kruse et al., 2019a, 2016). Although soil nutrients and mycorrhiza are not considered explicitly in the current version, it was shown that it can capture the nonlinear response of the treeline populations well at a regional level on the Taimyr Peninsula (Kruse et al., 2019a, 2016; Wiczorek et al., 2017b).

To cope with the complex forest-tundra ecotone responses, which are not in equilibrium with climate (Hofgaard et al., 2012), we updated and made use of our individual-based spatially explicit model LAVESI. With our simulation study, we explore treeline migration and tundra area dynamics to provide important information as to which tundra areas can survive future warming and where preventive measures for protection would be necessary to conserve the unique Siberian tundra. This study is guided by two questions: **“What are the treeline trajectories in Siberia for different climate mitigation scenarios (RCP)?”** and **“Under which climate scenario can tundra retreat to refugia and recolonize areas after temperatures cool again, and where?”**

Results and Discussion

Treeline migration trajectories under future climate changes

The simulations revealed that treeline advance follows climate warming exponentially reaching 30 km decade⁻¹ in the 21st century with faster rates the warmer the climate scenario (Table 1). When relating and tracking the position of the treeline to the climate (= climate-analogue) we find a severe migration lag of hundreds of years until simulations reach the same position (Figure 1). This behaviour is longer than expected from the properties of treeline-forming larch species with generation times of decades and weak long-distance dispersal rates (e.g. Mamet et al., 2019; Kruse et al., 2019a; Scherrer et al., 2020; Clark, 1998). Other processes, not yet explicitly captured by the model, may constrain the migration process, such as the strong greening of the Arctic (compare Pearson et al., 2013; Berner et al., 2020), the warming and abrupt thaw of permafrost (e.g. Stuenzi et al., 2021; Biskaborn et al., 2019), soil nutrients (e.g. Sullivan et al., 2015), and animal activity (e.g.

Figure 1. The trajectory of the simulated treeline position versus its current position for the Taimyr Peninsula shows a migration lag of the treeline during the first centuries (each line segment represents 25 years) until the simulated treeline is limited by climate. Forests expand their area further and infilling proceeds when climate conditions cool and even overshoot in the long run with cooling back to 20th century temperatures.

90 *Wielgolaski et al., 2017*). Regardless, our simulated rates over the past few decades are generally
 91 in line with the few existing modern observations showing only a slow treeline advance (*Mamet*
 92 *et al., 2019; Hansson et al., 2021; Rees et al., 2020; Shevtsova et al., 2020; Guo and Rees, 2021*).
 93 Rates are especially high in Chukotka, however, in all forcing scenarios (*Table 1*): an observation
 94 that can be attributed to forest patches ahead of the current treeline, which serve as nuclei for
 95 tundra infilling (shown by e.g. *Snell and Cowling, 2015; Kharuk et al., 2013; Kruse et al., 2019a;*
 96 *Harsch and Bader, 2011*).

97 After the initial migration lag we can see from our millennium-long simulations that the tree-
 98 line reaches more advanced positions than the climate analogue (*Figure 1, Table 1, Appendix 1*
 99 *Figure 1, Appendix 1 Figure 2, Appendix 2 Figure 1, Appendix 2 Figure 2*). This strong overshooting
 100 was unexpected especially in scenarios with cooling temperatures back to the 20th century level.
 101 However, we designed our model to be pattern-oriented and is based on observations that, once
 102 established, trees can endure periods of unfavourable environments (compare *Kruse et al., 2016*).
 103 This leads to the survival of trees ahead of the treeline acting as nuclei for tundra colonization
 104 when conditions improve (*Väliiranta et al., 2011; Snell and Cowling, 2015*). This is backed by ob-
 105 servations of slower than expected retreat of elevational treelines because trees can persist until
 106 dramatic events cause the death of all well-established trees (*Scherrer et al., 2020*).

107 **Tundra area dynamics caused by forest expansion**

108 The area loss over time roughly follows a negative exponential function, which is steeper the
 109 warmer the climate scenarios is (*Figure 2, Appendix 2 Figure 1*). The quickest loss, already by
 110 ~ 2100 CE, is seen in the intermediate warming scenario RCP 4.5 (+3 °C July temperatures) and
 111 the extreme RCP 8.5 (July temperatures +14 °C). For these scenarios, tundra retreats to its mini-
 112 mum cover of 5.7% by the middle of the millennium (Fig. 2b). Even under mitigation scenario RCP
 113 2.6 the tundra area is reduced to 32.7% or in the very ambitious scenario 2.6* to only 54.9%. Other
 114 simulation studies show 50% loss during the 21st century (*Callaghan et al., 2005; Kaplan et al.,*

Figure 2. Forest position and tundra area at year 3000 CE for different climate mitigation scenarios and under potential cooling back to 20th century temperatures after peak temperatures have been reached. The area of tundra changes over time and can only partly recover when temperatures cool and forests recede (plots next of the maps show years 2000-3000 CE). Only tundra areas above the treeline (Walker et al., 2005) are considered; Map projection: Albers Equal Area.

Figure 2-video 1. The development of the forest position and tundra area can be seen in a video supplement presenting the state in 10-year steps.

2003; Pearson et al., 2013) but not the dynamics of the long run until the end of 3000 CE, as shown by our study.

Cooling back to the 20th century levels led to a slight tundra re-expansion of a few percent of the area by the end of the simulations. While re-expansion is small for RCP 2.6* and 2.6, and largest for RCP 4.5 on the Taimyr Peninsula where forests retreat from areas of ~ 200 000 km² in the final 200 years of the simulation, under RCP 8.5 the effect of the cooling led to no tundra releases. In consequence, only if humans act ambitiously in limiting global warming to well below +2 °C (RCP 2.6, 2.6*), and temperatures actually cool after the maximum, do simulations show that ~10-30% of the tundra area could persist in the north and can re-expand after the mid-millennium maximum treeline extent. However, due to the overshooting effect, less than 10% of the area remains unforested. All in all, the expansion is in accordance with other studies and will likely put especially cold-climate tundra types at risk of extinction (e.g. Pearson et al., 2013; Walker et al., 2005).

Concluding opportunities for tundra conservation

Following our simulation results, tundra is reduced to ~5.7% of its current area at maximum forest expansion under the most likely scenario RCP 4.5 after an initial migration lag. Only ambitious strategies to mitigate climate warming (for example RCP 2.6) could prevent such an extensive loss and retain ~32.7% of the current tundra. In both cases, the northern refugia are located in Chukotka and the Taimyr Peninsula, currently covered by High Arctic and Arctic tundra types which have relatively high biodiversity (Arctic Climate Impact Assessment, 2004). A WWF report (Kremer et al., 2009) finds that the current total cover of protected northern areas is insufficient to achieve the requisite 30% protection necessary for biodiversity conservation (Secretariat of the United Nations Convention on Biological Diversity, 2021). Especially cold-climate tundra types on Siberian islands and in Chukotka are under-protected (e.g. Pearson et al., 2013; Walker et al., 2005) and thus further protected areas need to be established.

Although the large refugia could enable tundra species survival and later recolonization (analogous forests, Harsch et al., 2009; Clark, 1998; Stralberg et al., 2020), the diversity in these ~ 2500 km distant fragments is threatened by the fundamental disadvantages of a small population (inbreeding/genetic drift, Ohsawa and Ide, 2008; Charlesworth and Charlesworth, 1987; Mona et al., 2014; May et al., 2013). A network of connected systems would be necessary with protection of potential refugia (e.g. Morelli et al., 2020) distributed across the ~ 4000 km wide tundra area. Due to its

individual-based nature, LAVESI can be a tool to assess population genetics and aid in the optimal placement of migration corridors and areas to protect (cf. *Zurell et al., 2021*).

Methods

Model description and improvements

The model LAVESI is an individual based and spatially-explicit model that was developed to study the treeline ecotone growing on permafrost soils on the Taimyr Peninsula (*Kruse et al., 2016; Wieczorek et al., 2017b; Epp et al., 2018*) and since then it has been improved and modified for different purposes including for migration-rate studies (*Kruse et al., 2019a*). To achieve the most realistic model, each life-history stage of the larch individuals is handled explicitly, and the model's processes adapted to observed patterns of surveyed tree stands for the dominant larch tree species, *Larix gmelinii* and *Larix sibirica*. The source code was updated to version 1.2 on the crutransects branch to be sufficiently light in terms of memory allocation and include landscape (developed in parallel for Chukotka mixed alpine-latitudinal treeline simulations in *Shevtsova et al., 2021; Kruse et al., 2021*). The model is freely available on Github <https://github.com/StefanKruse/LAVESI>. The source code of the version used in this manuscript will be additionally permanently stored on Zenodo on final publication.

Model performance

During simulation runs, each Environment grid cell of 20x20 cm needs 10 bytes, an element of the Tree-structure 64 bytes and the Seed-structure 32 bytes. In total, for very dense scenarios it needs for each square km ~ 11 GB RAM. The parallelization was updated and instead of Standard Template Library (STL) list containers for tree and seed elements a vector structure was implemented to allow better support for OpenMP (<https://www.openmp.org>) parallelization for scaling on a High-Performance Cluster and the realization of large-scale transect simulations as needed for this study. The computation speed depends on the number of trees and reaches ~ 3.5 s yr⁻¹ km⁻² for very dense forests on 8 cores that can be reduced when using more cores *Figure 3*. However, due to overheads, scaling is not 1:1. Of the internal functions of LAVESI the mortality is most computationally intensive, as each seed and tree need to be handled individually.

Transect setup

At four representative locations of the Siberian treeline within 100 – 170 °E, we placed linear transects, starting at a field site, and allowed open tree stands to establish up to the shoreline (*Figure 4*). From west to east: (1) Taimyr Peninsula, 573 km long, site 13-TY-09-VI, 72.15067° N 102.09771° E (*Wieczorek et al., 2017b,c*), (2) Buor Khaya Peninsula, 137 km long, 14-OM-20-V4: 70.52671° N 132.91426° E (*Liu et al., 2020*), (3) Kolyma River Basin, 146 km long, 12-KO-02/I: 68.38916° N 161.46617° E (*Wieczorek et al., 2017a*), (4) Chukotka, 626 km long, EN18022: 67.40102° N 168.34801° E (*Kruse and Stoof-Leichsenring, 2016; Kruse et al., 2019b*). While the first three locations in the west cover predominantly flat terrain, the easternmost location in Chukotka has mountainous stretches.

Climate forcing

Temperature and precipitation time series were constructed using the following steps:

1. Extract climate data in 10 km steps along transects beginning at the position of the field sites for each of the four focus regions from the grid cells of CRU TS 4.03 by distance weighted interpolation (*Harris et al., 2020*).
2. Establish a yearly $\delta^{18}\text{O}$ and ice layer thickness series for 501 to 1900 from the yearly resolution ice-core data from Severnaya Zemlya (north of the Taimyr Peninsula, available for years 934 to 1998 *Opel et al., 2013*), the only closest annual resolution archive allowing both temperature and precipitation reconstructions independent of plant-based proxies (pollen or tree rings). This was achieved by sampling 25-year long blocks of yearly resolution data from the

Figure 3. The computation speed increases with the number of available threads and reaches a plateau caused by overheads. The processes of LAVESI scale differently and the process Environment is computationally the heaviest and thus relatively faster with more cores while processes such as Mortality show no clear benefit of more threads. Data were aggregated for 100 years at three different population dynamics stages: e=empty, m=mature old growth, d=densification.

- 192 pre-industrial (< 1800 *CE*) and adding this variability to the AN86/87 core which dates back
- 193 to 4703 *BCE* (Arkhipov et al., 2008).
- 194 3. Adjust this locally to the 10 *km* steps climate data series per transect by building linear models
- 195 of yearly temperature and precipitation for the overlapping years 1901-1998 and use this to
- 196 estimate mean values for the period 501 to 1900.
- 197 4. Sample 15-year long blocks from CRU and adjust the mean temperature by the difference of
- 198 the sampled block from the estimated mean values to achieve monthly data series.
- 199 5. Prolong this series by coupled climate model long runs until 2300 *CE* with model output with
- 200 MPI-ESM-LR prepared for CMIP5 for scenarios RCP 2.6, RCP 4.5, and RCP 8.5 and additionally
- 201 a scenario that warms only half the values of RCP 2.6, which is here called RCP 2.6*.
- 202 6. Extend these trends for 2100-2300 until 2500 *CE* and repeat in the following either the climate
- 203 data of 1901-1978 in a loop which in this study is called 20th century cooling or copy the period
- 204 2300 – 2500 until 3000 *CE*.

205 July temperatures (Figure 4), which have the strongest impact in the model, increase in these

206 scenarios by a median of +1.2 °C (RCP 2.6*), +1.8 °C (2.6), +2.1 °C (4.5) and up to +5 °C (8.5) com-

207 pared to 1970-2000 until 2100, which partly cools until 2300 to +0.6 °C (RCP 2.6*), +0.5 °C (2.6) and

208 reaches higher levels for the two warmest scenarios to +3.1 °C (4.5) and up to +14.4 °C (8.5).

209 Wind speed and direction data were obtained at 6-hourly resolution for 1979-2018 from Eraln-

210 terim5 (data set description in Dee et al., 2011) for each of the transects and supplied with the

211 model. In a prior version, these data were only available for the Taimyr Peninsula and only for

212 years until 2012.

213 Tree growth on transects

214 We implemented sensing of the environment for each individual tree via its y-position along the

215 transect which is made up of 10 *km* spaced climate data. The maximum possible growth at a certain

Figure 4. Transects (blue lines) were placed starting in the treeline at field sites and extending to the shoreline of the Arctic Ocean (map); only tundra areas above the treeline (Walker et al., 2005) are considered. The land area was grouped into four regions equidistantly separated between the transects (lower plot) and plots show climate forcing for 501-3000 CE based on RCP scenarios in these regions at the extremes and middle part of the transects; numbers give mean values for modern and future strongest warming under RCP 8.5. Map projection: Albers Equal Area.

position (see initial publication Kruse et al., 2016) is calculated by interpolating the possible growth under the climate using the two closest climate variables.

The larch species *Larix gmelinii* (Rupr.) Rupr. dominates the areas to the west of the Verkhoyansk Mountain Range ~90-130° E and its sister species *L. cajanderi* Mill. grows in north-east Siberia Figure 4 (Abaimov, 2010). Hence, the already implemented species *L. gmelinii* was set to be present in the simulations and simulations tuned to fit observations. To initiate growth 100 000 seeds were introduced at the cold end with a distance based on a negative exponential kernel for the first 50 years. Similarly, extinction on a transect was prevented by permanently introducing 1000 seeds per 200 km length. Further seed introduction from the non-explicitly simulated hinterland was estimated on a 500 m long stretch at the cold site linking the production and release height to climate.

Model tuning and validation

Simulation runs were forced with the prepared climate data for the transects for validation of the shape of the treeline as simulated by the model. The results of year 2000 were compared to field data that was positioned along the temperature gradient on the simulated transects by using the

respective CRU TS temperature data for each grid cell of each plot (example **Figure 4**). The field data collection included disturbed sites (e.g. in Chukotka) leading to very high stem counts, which are the number of trees exceeding 1.3 m in height per ha. The model could be tuned by introducing a local adjustment based on elevation lapse rates of the relevant climate values used internally, which is necessary as the climate data may lead to over/underestimations locally in a model that does not consider local topography: an issue that is especially relevant in the mountainous region of Chukotka. We made a moderate fit with the following amendments

- Taimyr Peninsula: $T_{Jan} = -1.17^{\circ}C$, $T_{Jul} = -0.84^{\circ}C$ and $P_{Year} = -5.4\text{ mm}$
- Buor Khaya Peninsula: $T_{Jan} = -0.23^{\circ}C$, $T_{Jul} = -2.48^{\circ}C$ and $P_{Year} = -28.9\text{ mm}$
- Kolyma River Basin: $T_{Jan} = +3.14^{\circ}C$, $T_{Jul} = +1.26^{\circ}C$ and $P_{Year} = +85.7\text{ mm}$
- Chukotka: $T_{Jan} = +4.46^{\circ}C$, $T_{Jul} = +4.30^{\circ}C$ and $P_{Year} = +8.2\text{ mm}$

From the individuals present along the simulated transects, the northernmost positions of the treeline are calculated. For the four focus regions these are +66, +88, +98, and +16 km beyond the treeline start location at year 2000 (**Appendix 1 Figure 2**), which are partly ahead of the observed positions based on visual inspection of satellite data $\sim +30, +30, +80$, and +15 km beyond the field location selected as the starting point.

Simulation setup and data processing

We ran three simulation repeats for each transect with the climate series prepared for this study as initial tests showed robust simulation results. To consider the available area from the start to the shoreline, we used 800 km-long and 300 km-long transects and 20 m wide wrapping for the east and west boundary of each simulated stretch, thereby representing a slice of a continuous treeline.

The positions of three key variables are extracted in 10-year steps: single-tree stands, tree-line stands, and forestline stands, which are defined as the northernmost position of stands with $> 1\text{ stem}$ (tree $> 1.3\text{ m}$ tall) per ha, the northernmost position of a forest cover not falling below 1 stem ha^{-1} , and the northernmost position of a forest cover not falling below 100 stems ha^{-1} (see Fig. 2 in *Kruse et al., 2019a*, for a graphical representation), respectively. The determined treeline at year 2000 is used as a baseline for expansion and subtracted from the following years' values. The resulting values for each of the three key variables are used in 10-year steps to interpolate with a weighted average the expansion starting at the current treeline (e.g. *Walker et al., 2005*).

We used R version 3.6.1. (*R Core Team, 2019*) for data handling, statistical analyses and graphical representation. The 30 arc sec WorldClim 1.4 data (*Hijmans et al., 2005*) along the transects and 2.5 minutes of a degree elevation for mapping was downloaded through the geospatial package raster version 3.0-12. (*Hijmans, 2020*). Additional geospatial packages sf version 1.4-2 and rgdal version 1.4-7, (*Pebesma, 2018; Bivand et al., 2019*) were used to reproject the treeline shape to Albers Equal Area projection and calculate weighted average buffers at each 10 km-step along the treeline and merge the buffer polygons for each of the advancement values for the three key variables (single trees, treeline, forestline). The treeline constructed by the circumarctic vegetation map consortium (CAVM, *Walker et al., 2005*) is provided in segments that were simplified in QGIS version 3.10 (*QGIS Development Team, 2020*). For tundra area assessment, the land area polygons of Russia accessed via R package maps version 3.3.0 (*code by Richard A. Becker et al., 2018*) were cleaned and the islands in the Arctic Ocean excluded. Linear models for temperature and precipitation reconstruction and climate lapse rates were established with functions from the R base package (*R Core Team, 2019*).

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Competing interests

The authors declare no competing interests.

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473 Appendix 1

474 Migration rates

475 **Appendix 1 Table 1** provides a summary of simulated treeline advance and the correspond-
 476 ing position at the same year of the climate analogue. **Appendix 1 Figure 1** shows the posi-
 477 tion of the climate-analogue treeline position at the four transects and **Appendix 1 Figure 2**
 478 gives an overview of the simulated maximum positions of the single-tree stands, the treeline
 479 and the forestline at the same transects.

Appendix 1 Figure 1. Forest expansion dynamics along the four transects (columns) extrapolated based on July temperatures (climate-analogue) for climate data based on RCP scenarios (rows). A general rapid expansion of the forestline (continuous cover from south > 1 tree ha⁻¹, green) can be seen. Blue colour at the top represents the shoreline.

Appendix 1 Figure 2. Forest expansion dynamics along the four transects (columns) forced with climate data based on RCP scenarios (rows). A general quick expansion of single tree stands (maximum position of $> 1 \text{ tree ha}^{-1}$, light green) and the forestline (continuous cover from south $> 1 \text{ tree ha}^{-1}$, green) followed by the treeline (continuous cover from south $> 100 \text{ tree ha}^{-1}$, dark green) is seen. Blue colour at the top represents the shoreline.

Appendix 1 Table 1. Summary of simulated vs. climate envelope-based treeline advance. Climate envelope solely based on July temperatures (following *MacDonald et al., 2008*). Values in bold reach the shoreline, but note that because of technical reasons the step sizes of the climate are in 10 km steps.

Transect	Scenario	Maximum potential expansion based on climate	Simulated maximum expansion	Treeline migration rate 2000-2100 km decade ⁻¹	Treeline migration rate 2000-2300 km decade ⁻¹
Taimyr	RCP 2.6*	210 km 2090	192.2±18.5 km 2733.3±161.7	0.8±0.7	1.5±0.1
	RCP 2.6*c	210 km 2090	135.3±1.4 km 2356.7±57.7	3.4±2.9	1.9±0
	RCP 2.6	320 km 2090	344.8±2.9 km 2730±86.6	11.5±2.3	9±0
	RCP 2.6c	320 km 2090	331.3±1.4 km 2283.3±28.9	8.6±1.2	8.6±0.1
	RCP 4.5	410 km 2297	544.5±0 km 2383.3±5.8	23.4±0.2	10.6±0.1
	RCP 4.5c	400 km 2221	405.3±3.8 km 2566.7±230.9	24.7±0.2	11.2±0.1
	RCP 8.5	560 km 2082	544.5±0 km 2160±0	29.1±0.5	16.1±0
	RCP 8.5c	560 km 2082	544.5±0 km 2140±0	28.4±0.4	16.2±0
Buor Khaya	RCP 2.6*	130 km 2040	94.5±0.9 km 2306.7±75.1	0.1±0.2	0.2±0
	RCP 2.6*c	130 km 2040	91±0.9 km 2496.7±317.5	0±0	0±0
	RCP 2.6	130 km 2020	120.2±1.4 km 2246.7±11.5	1±0.3	1.1±0
	RCP 2.6c	130 km 2020	122.3±0.3 km 2633.3±92.4	0.9±0.6	1.2±0.2
	RCP 4.5	140 km 2133	124.5±0 km 2303.3±5.8	0.6±0.5	1.3±0.1
	RCP 4.5c	140 km 2133	124.5±0 km 2286.7±11.5	0.2±0.1	1.2±0.1
	RCP 8.5	140 km 2038	124.5±0 km 2120±0	3.2±0	1.2±0
	RCP 8.5c	140 km 2038	124.5±0 km 2123.3±11.5	3±0.3	1.1±0
Kolyma	RCP 2.6*	130 km 2012	120.8±0.3 km 2330±0	1.2±0.1	0.7±0
	RCP 2.6*c	130 km 2012	119±0.9 km 2216.7±11.5	1.1±0.2	0.7±0
	RCP 2.6	150 km 2094	134.3±0.3 km 2230±0	2.1±0.1	1.2±0
	RCP 2.6c	150 km 2094	113.5±17.3 km 2103.3±92.4	1.3±0.6	1±0.1
	RCP 4.5	150 km 2284	134.5±0 km 2256.7±11.5	2±0.1	1.2±0
	RCP 4.5c	140 km 2121	134.5±0 km 2306.7±5.8	1.6±0.5	1.2±0
	RCP 8.5	150 km 2072	134.5±0 km 2143.3±5.8	2.2±0.2	1.2±0
	RCP 8.5c	150 km 2072	134.5±0 km 2140±0	2.2±0.1	1.2±0
Chukotka	RCP 2.6*	300 km 2047	285.2±8.4 km 2173.3±28.9	25.1±0.1	8.8±0.1
	RCP 2.6*c	300 km 2047	285.7±3.2 km 2203.3±28.9	25.3±0.2	9.2±0.1
	RCP 2.6	350 km 2047	363.5±0 km 2423.3±5.8	30.8±1	11.3±0.2
	RCP 2.6c	350 km 2047	358.8±6.4 km 2290±86.6	30.9±0.2	11.3±0.2
	RCP 4.5	380 km 2144	604.5±0 km 2746.7±28.9	27.2±1.2	12±0
	RCP 4.5c	380 km 2144	377±0 km 2296.7±5.8	28±0.2	11.9±0.1
	RCP 8.5	610 km 2107	604.5±0 km 2160±0	29.1±0.3	19.6±0
	RCP 8.5c	610 km 2107	604.5±0 km 2150±0	29.2±0.1	19.7±0

Appendix 2 Figure 1. Trajectories for all four regions. Numbers are the first year when the simulated treeline position is equal to or farther north than the modern climate-analogue position. Colour of line segments ranges from yellow for year 2000 to blue in 3000 CE. Further description in caption of **Figure 1** in main text.

Appendix 2

Treeline migration trajectories

Appendix 2 Figure 2 shows the treeline trajectories of the position based on simulations and the climate-analogue position at the four transects and the time when the simulated positions reach the first time the same position of the climate-analogue. **Appendix 2 Figure 1** includes additionally the information of the current temperature in 25-year segments.

Appendix 2 Figure 2. Trajectories for all four regions clockwise: Taimyr Peninsula, Chukotka, Kolyma, and Buor Khaya Peninsula. Colour of line segments ranges from yellow for year 2000 to red in 3000 or blue in year 3000 under the cooling scenario. Further description in caption of *Figure 2* in main text.

Appendix 3

Tundra area dynamics

Appendix 3 Figure 1 gives an overview of the tundra area development in 100-year time steps for each of the eighth climate scenarios.

Appendix 3 Figure 1. Forest expansion for 100-year time steps and all scenarios. Modern tundra areas will become covered by at least open larch tundra forests under different climate scenarios and nearly reach the shoreline in warmest conditions.