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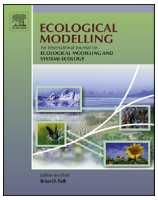

Treeline dynamics in Siberia under changing climates as inferred from an individual-based model for *Larix*

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ABSTRACT

Siberian boreal forests are expected to expand northwards in the course of global warming. However, processes of the treeline ecotone transition, as well astiming and related climate feedbacks are still not understood. Here, we present '*Larix* Vegetation Simulator' LAVESI, an individual-based spatially-explicit model that can simulate *Larix gmelinii* (Rupr.) Rupr. stand dynamics in an attempt to improve our understanding about past and future treeline movements under changing climates. The relevant processes (growth, seed production and dispersal, establishment and mortality) are incorporated and adjusted to observation data mainly gained from the literature. Results of a local sensitivity analysis support the robustness of the model's parameterization by giving relatively small sensitivity values. We tested the model by simulating tree stands under modern climate across the whole Taymyr Peninsula, north-central Siberia (c. 64–80° N; 92–119° E). We find tree densities similar to observed forests in the northern to mid-treeline areas, but densities are overestimated in the southern parts of the simulated region. Finally, from a temperature-forcing experiment, we detect that the responses of tree stands lag the hypothetical warming by several decades, until the end of 21st century. With our simulation experiments we demonstrate that the newly-developed model captures the dynamics of the Siberian latitudinal treeline.

1. Introduction

Taxa forming the boreal treeline (Holtmeier and Broll, 2005) are expected to expand their distribution area northwards under a future warmer climate (Pearson et al., 2013). This tundra-to-taiga transition will be accompanied by an albedo decrease (Bonan, 2008), which in turn will raise regional temperatures. Such positive feedback can significantly contribute to global warming as revealed by Earth-system modelling studies (Stocker et al., 2013). However, the detailed tree population processes that ultimately determine the timing and magnitude of tree responses to a given climate signal are still not fully understood. For example, seed dispersal limitations and slow reproduction rates will lead to leading-edge vegetation-climate disequilibrium that could last for decades or centuries (Lenoir and Svenning, 2015). Furthermore, one should keep in mind that a limited or delayed reaction to the temperature signal is also possible because increased temperatures could lead to decreased growth rates due to drought stress generally in more southerly treeline stands or on slopes (Lawrence et al., 2015; Barber et al., 2000). This can, however, be buffered by permafrost meltwater that is an important direct source of moisture for larches (Sugimoto et al., 2002), but if this meltwater accumulates in depressions it can hinder growth due to water stress (Lawrence et al., 2015; Kharuk et al., 2015). Additionally, fires play a role in larch population dynamics in the northern parts of central Siberia (Sofronov et al., 2000), with frequency decreasing from high fire return intervals of around 100 years in the south (61° N) to low intervals of 350 years in the northernmost forests (Kharuk et al., 2011).

Hitherto, time-series of population dynamics from treeline areas of reasonable temporal length are lacking. Vegetation-plot studies along treeline transects can portray tree-stand characteristics and recruitment patterns under different climates and thus can provide hints about future changes. However, the complexity of the treeline response to climate can best be disentangled with

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the help of numerical modelling. Among the various vegetation model types available, an individual-based spatially-explicit model could be most suitable for simulating vegetation dynamics at the treeline. Such models can capture the most relevant processes with respect to the establishment, structure, and expansion of tree stands, including individual tree ageing, competition among different life stages, seed dispersal, and seed-bank establishment. For example, Martínez et al. (2011) successfully applied an individual-based spatially-explicit model of alpine treelines to evaluate the importance of krummholz for treeline range expansion.

Treelines are known as tundra-taiga ecotones (Holtmeier and Broll, 2005; MacDonald et al., 2008) that are often defined by tree heights of between 2 m and 8 m at the latitudinal upper and lower tree limit (Holtmeier, 2009). We use the term treeline here for a region spanning from the limits of dense northern taiga forests in favourable habitats to trees that reach a maximum height of 2 m due to deteriorating conditions. The vast Siberian treeline is unique with respect to its sole composition of *Larix* Mill., a deciduous needle-leaf tree genus (Abaimov, 2010; Franz, 1973b). Evidence from other treeline areas cannot, therefore, simply be applied to Siberia. There are three *Larix* species forming the treeline up to ~72.5° N: *Larix sibirica* Ledeb. from roughly 60–90° E, *Larix gmelinii* (Rupr.) Rupr. towards the east where continuous permafrost prevails between 90 and 120° E, and *Larix cajanderi* Mayr. from 120 to 160° E. These species are well adapted to the harsh north Siberian permafrost environment experiencing cold winters up to −40 °C and short summers with only 60–90 days exceeding the freezing point. The regional temperature regime causes a maximum summer active-layer depth ranging only between 0.3–0.6 m in some areas (Franz, 1973a).

If the climate envelope shifts north, forests in Siberia will probably densify and expand northwards. Such a general relationship is corroborated by results from palaeoecological investigations of glacial/interglacial and Holocene treeline transitions (Andreev et al., 2011; MacDonald et al., 2008) and the few available field observations of modern tree-population processes at the treeline (Golubeva et al., 2013; Kharuk et al., 2006). Computer simulations that could help to understand the underlying processes at the Siberian treeline are rare. A rather detailed approach for northern boreal forests was recently published by Brazhnik and Shugart (2015, 2016): their forest gap model SIBBORK includes a 3-D light environment and allows for complex interactions between boreal forest species and their environment. Simulations suggest a 2 °C increase in annual temperature will cause northwards range expansion of larch forests and steppe formation in the south (Brazhnik and Shugart, 2015). Zhang et al. (2013) applied the LPJ-GUESS in cohort mode to simulate high-latitude arctic vegetation. Their results suggest that the treeline will advance polewards in the future and be accompanied by reduced albedo in winter months due to strong densification. Similarly, the application of the ArcVeg model to the Yamal Peninsula (Yu et al., 2009) led to the conclusion that a significant increase in biomass will occur when climate warms by 2 °C. Despite their detailed implementation of abiotic processes, such as radiation, water table level and available nutrients, which affect growth, and the computation of these on daily time steps, such models are optimized for a global application and as a consequence the life-cycle stages are highly generalized (Sato et al., 2007; see, for example, Sitch et al., 2003). These models might therefore miss important details of relevance to local stand dynamics, which could enhance or diminish the pressure of climate change via biotic interactions (e.g. seedling establishment under unfavourable abiotic conditions triggered by facilitation, Martínez et al., 2011). To study complex ecosystems where individual-based processes cause observed patterns, individual-based models are widely used in ecology (DeAngelis and Mooij, 2005; Grimm and Railsback, 2005; Jeltsch et al., 2008; Martínez et al., 2011; Peck, 2004; Seidl et al., 2012), but have not been available for larch forests growing on permafrost. As a consequence, we set up a rather simple model framework and successively implemented processes which generate patterns such as those observed at reference sites, until we created a final model that is able to capture the observed patterns. With our focus on understanding local stand interactions that can cause larger scale population dynamics, seeds and tree individuals are handled individually and have explicit coordinates. This model allows for spatially-explicit interactions among all life-history phases of larches and is therefore a handy tool to realistically simulate responses of population dynamics in a changing environment (past-to-present or present-to-future). Additionally, information can be inherited from one parent individual to the offspring, so a fruitful future study could be to implement different genetic markers and validate the model against results of population genetics that try to infer the phylogeography of a species (for example central and far-east Siberian species: Semerikov et al., 2007; Polezhaeva et al., 2010).

Here we present an individual-based model (LAVESI = *Larix* Vegetation Simulator) to simulate the relevant processes of *Larix gmelinii* population dynamics at the arctic treeline in Siberia. First, we calibrated LAVESI and checked the influence of parameterization on model performance by conducting a sensitivity analysis. Second, we simulated tree stands forming the modern treeline area on the southern Taymyr Peninsula, north-central Siberia, emphasizing stand density in our analysis. And, finally, we investigated the response of population density and structure of tree stands to a variety of hypothetical warmer and colder climate scenarios.

2. Material and methods

2.1. Reference sites

Field data were collected from two replicate plots at each of five sites. The five sites used in this study were visited during the vegetation periods of the summers of 2011 and 2013 (M. Wieczorek et al., submitted; Table 1, Fig. 1). Locations are situated along a southwest to northeast transect across the treeline and are representative of tree growth at the treeline, which passes through the Khatanga River flood basin at one of the most northerly locations for tree growth at around 73° N. At each site, larch individuals in two plots of at least 20 × 20 m were examined; variables such as height, basal diameter and diameter at breast height were measured, number of cones estimated and the position of trees recorded.

2.2. Description of the model LAVESI

Following the approach of pattern-oriented modelling (Grimm and Railsback, 2005) focusing on forest stand densities of several reference sites, we started with a simple growth model and successively added functions to allow the model to simulate those observations. Based on literature about larches growing at the treeline in Siberia (e.g. Osawa and Kajimoto, 2010), we designed the basic framework to represent the life-cycle of different species of larches as completely as possible from seeds to mature trees. This version was adapted for the specific deciduous larch *Larix gmelinii* (Rupr.) Rupr. that grows in single species stands on prevailing permafrost and under harsh cold climates in northern central Siberia (Naurzbaev et al., 2002). Dendrochronological analyses show that tree growth in these areas mainly depends on temperature, especially summer temperature (Abaimov, 2010), and to some extent on precipitation (Sidorova et al., 2010). Thus, we coupled the simulations to monthly temperature and precipitation series as driving forces. Within one simulation step, which is one year, a variety of processes become consecutively invoked: growth, seed produc-