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Legacy of the Last Glacial on the present-day distribution of deciduous versus evergreen boreal forests

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Abstract

Issue: Despite their rather similar climatic conditions, eastern Eurasia and northern North America are largely covered by different plant functional types (deciduous or evergreen boreal forest) composed of larch or pine, spruce and fir, respectively. I propose that these deciduous and evergreen boreal forests represent alternative quasi-stable states, triggered by their different northern tree refugia that reflect the different environmental conditions experienced during the Last Glacial.

Evidence: This view is supported by palaeoecological and environmental evidence. Once established, Asian larch forests are likely to have stabilized through a complex vegetation–fire–permafrost soil–climate feedback system.

Conclusion: With respect to future forest developments, this implies that Asian larch forests are likely to be governed by long-term trajectories and are therefore largely resistant to natural climate variability on time-scales shorter than millennia. The effects of regional human impact and anthropogenic global warming might, however, cause certain stability thresholds to be crossed, meaning that irreversible transitions occur and resulting in marked consequences for ecosystem services on these human-relevant time-scales.

KEYWORDS

boreal forests, Glacial refugia, Holocene, *Larix* larch, permafrost ecosystems, Palaeoecology, Siberia, vegetation–climate–fire–soil feedbacks, vegetation states, vegetation trajectories

1 | INTRODUCTION

Contemporary climate has traditionally been assumed to determine the distribution of major plant functional types on global and continental scales (Pan, Birdsey, Phillips, & Jackson, 2013; Woodward, Lomas, & Kelly, 2004). Accordingly, plant functional types form the central structural element of terrestrial biosphere modules in all Earth system models. Any predictions of vegetation change and its feedbacks with other Earth system components are thus particularly sensitive to the implemented climate thresholds of each plant functional type. However, the assumption of a straightforward climate–plant functional type relationship conflicts with the observation that

despite modern climatic conditions being rather similar across most of the boreal areas in eastern Eurasia and northern North America they are covered by different plant functional types: deciduous and evergreen needleleaf trees, respectively (Figure 1). The widespread dominance in eastern Eurasia of *Larix* (larch), a deciduous needleleaf tree, is particularly surprising given that *Larix* is successively replaced by evergreen taxa when growing in mixed stands (Kharuk, Ranson, & Dvinskaya, 2007; Schulze et al., 2012).

Two principal arguments contradict a climatic explanation for most of the vast deciduous needleleaf forests in eastern Eurasia. First, most of the deciduous boreal forest areas in northern Eurasia share climate space [spanned by mean January temperature (T_{Jan}), mean July

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temperature (T_{July}) and mean annual precipitation (P_{ann}) with the evergreen boreal forests in northern North America (Figure 1). My investigations show that c. 81% of the boreal forest area in eastern Eurasia is deciduous needleleaf forests, of which 47% has climate analogues in northern North America that are covered by evergreen forests (Figure 1b,c). (A site in northern North America is considered an analogue for a site in eastern Eurasia if the distance in multivariate climate space between them is < 5% of the distances calculated among all boreal forest sites from eastern Eurasia; see also Supporting Information Supplementary Methods). The remaining 34% of boreal forests covered by deciduous forests have no climate analogues in areas with boreal forests in northern North America. Conversely, most boreal forest sites in northern North America have climate analogues in eastern Eurasia (Figure 1d,e). Accordingly, if contemporaneous climate is decisive for forest type, either large areas of northern North America should be covered by deciduous boreal forests or a much greater area in eastern Eurasia should be covered by evergreen boreal forests.

Second, *Larix* dominance has hitherto been explained as the advantage of deciduousness in a cold climate (Givnish, 2002; Zanne et al., 2014). For example, Givnish (2002) put forth that "...winter loading by high winds, ice, and snow should force evergreens to build more massive stems and branches and give deciduous plants an advantage". Indeed, winters are exceptionally cold in some parts of the *Larix*-dominated area in eastern Eurasia (Figure 1b,d). Therefore, winter temperature has been used as a limit for the evergreen boreal plant functional type in vegetation models (Zhu et al., 2015), but there is contradictory experimental and observational evidence. Siberian *Larix* taxa, *Abies sibirica* and *Picea obovata* are all classified in the maximum category with respect to frost hardiness, in that they can withstand temperatures of the coldest month below -45°C (Bannister & Neuner, 2001). It has even been demonstrated that, once frozen, tissue of these taxa can survive immersion in liquid nitrogen (Strimbeck, Schaberg, Fossdal, & Schröder, 2015). This is in line with the finding that *Pinus* and *Picea* taxa occur in many stands in central and northern Yakutia (sometimes even dominant; see single light blue dots in Figure 1b,d), which are among the coldest winter areas in the world, but they are absent from more favourable areas, such as the northern Russian Far East. Furthermore, the growth of most *Pinus* and *Picea* individuals investigated along a latitudinal gradient in eastern Siberia was not positively correlated with the increase in winter temperature during the 20th century but instead with early summer warming (Lloyd, Bunn, & Berner, 2011). Likewise, a remote-sensing study revealed that evergreen taxa expanded into *Larix* forests in central Siberia during the last two decades despite the particularly low winter temperatures during this time (He et al., 2017).

This all suggests that contemporary climate is not a suitable explanation for *Larix* dominance in eastern Eurasia and that the basic mechanisms that control the distribution of boreal forest types remain poorly understood. Potential future changes in boreal ecosystem services cannot therefore be predicted and thus remain uncertain, which is a matter of local, regional and global concern because the forest types differ with respect to crucial ecosystem services, including carbon stocks, climate feedback, permafrost stability, biodiversity and economic benefits.

2 | THE GLACIAL LEGACY HYPOTHESIS

Here, I propose that the huge deciduous boreal forests in eastern Eurasia represent a legacy of the Last Glacial. Support for this idea comes from an investigation of a Plio-Pleistocene pollen sequence (3.4–2.1 Myr) from the northern Russian Far East, where Herzschuh et al. (2016) found that glacial environmental conditions are more relevant for the subsequent interglacial composition of the boreal forest than the contemporaneous interglacial climate, implying a millennial-scale vegetation–climate lag. Through multivariate analyses, they showed that *Larix* forests dominated only in those interglacials that were preceded by cold glacials, whereas spruce and pine forests were common during interglacials that followed milder glacials. By analogy to this palaeoecological evidence, it can be hypothesized that deciduous and evergreen boreal forests represent alternative quasi-stable states that occur in similar climate conditions today but were determined by different conditions during the Last Glacial. I investigate this hypothesis and its wider implications in the following sections.

3 | WHY DID DECIDUOUS BOREAL FORESTS ESTABLISH ONLY IN EASTERN EURASIA?

After the Last Glacial, boreal forests expanded into formerly glaciated areas in the northern part of North America and into tundra areas in most of Eurasia. In North America, all major boreal taxa survived close to the southern margin of the Laurentide Ice Sheet and/or in Alaska (Roberts & Hamann, 2015) and jointly invaded the open areas during the post-glacial period (Figure 2). Therefore, most areas currently covered by boreal forests were initially colonized by evergreen taxa, mostly *Picea*, whereas *Larix* was only co-dominant, if at all, at the very beginning of forest establishment (Warren et al., 2016; Figure 2) (*Larix* has still a wide distribution range in North America [Mamet, Brown, Trant, & Laroque, 2019] but is mostly only present with low abundances.). Northern refugia are now considered to have played a crucial role in post-glacial continental-scale reforestation in Eurasia and Alaska (Feurdean et al., 2013). In most of Eurasia, *Larix* survived the Last Glacial in northern refugia that were widespread across the periglacial continent (Polezhaeva, Lascoux, & Semerikov, 2010; Semerikov, Semerikova, Polezhaeva, Kosintsev, & Lascoux, 2013), from where it is likely to have colonized the open tundra areas during the late glacial (Figure 2). *Picea* and *Pinus* survived in widespread northern refugia only in western Eurasia (Binney et al., 2009, 2017; Tian et al., 2018; Tsuda et al., 2016; Väliänta, Salonen, Heikkilä, 2015), from where they colonized the area together with *Larix* and became dominant later on. In contrast, eastern Eurasia, which is currently dominated by deciduous needleleaf trees, had rather few northern refugia of evergreen tree conifers, possibly only of *Picea* (Binney et al., 2009; Edwards, Armbruster, & Elias, 2014).

The question remains, why did these *Picea* refugia not function as kernels of post-glacial population spread, like *Larix*? It has been suggested that glacial refugial populations are highly adapted to local adverse conditions (Edwards et al., 2014). The ability of

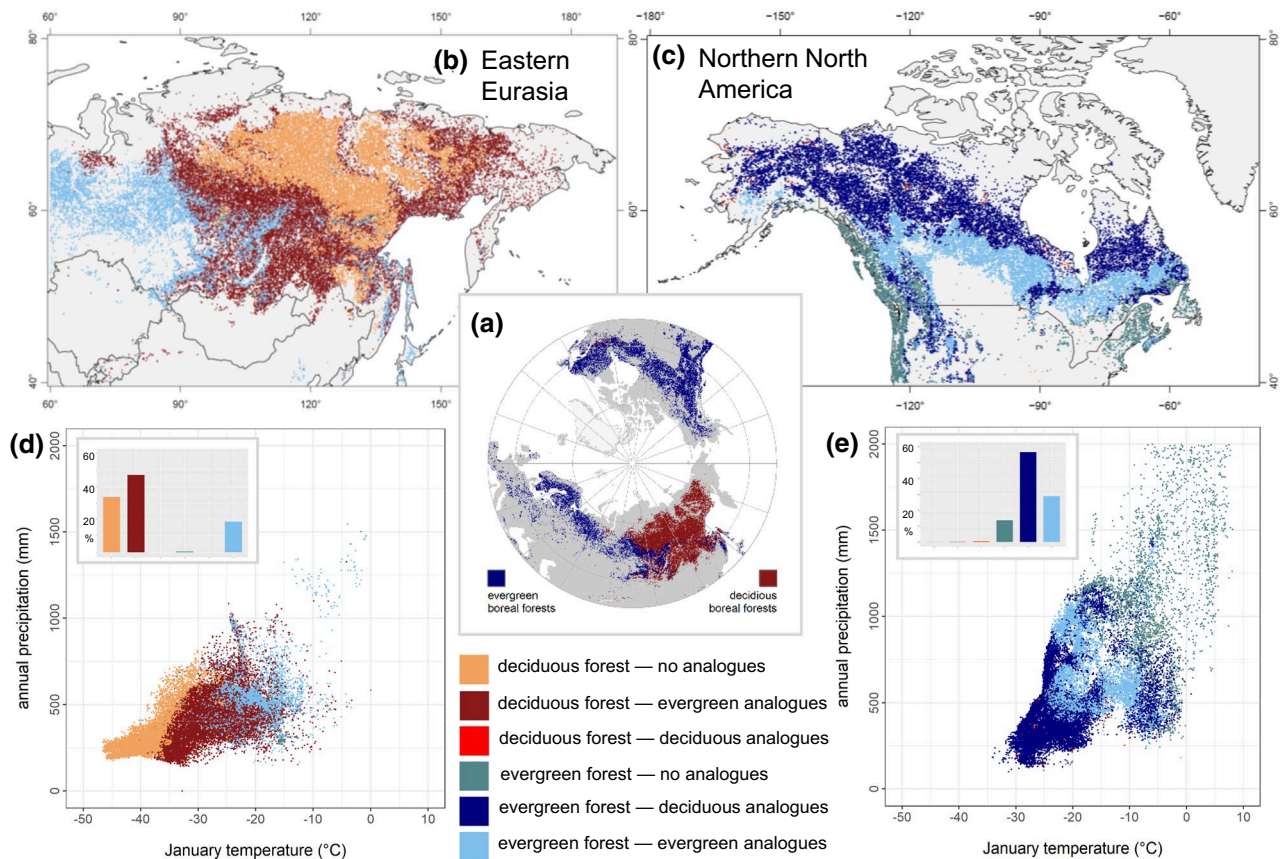


FIGURE 1 Distribution of boreal forests in eastern Eurasia and northern North America in climate space. (a) Distribution of deciduous (*Larix*) and evergreen (mainly *Pinus*, *Picea* and *Abies*) boreal forests in the Northern Hemisphere. Distribution of deciduous and evergreen boreal forests in geographical and climate space in eastern Eurasia (b,d) and northern North America (c,e). Colour indicates the dominant forest type for each continental area and its corresponding forest type in areas with analogous climate on the other continent (or without analogous climate). For example, dark red indicates an area dominated by deciduous forests in Siberia that, in a climatically similar area in northern North America, is covered by evergreen forests [Colour figure can be viewed at wileyonlinelibrary.com]

Picea to adapt to local climate conditions since its establishment in Canada on a millennial time-scale is confirmed by genetic analyses of modern populations (Prunier, Laroche, Beaulieu, & Bousquet, 2011). Populations in glacial refugia probably had reduced genetic diversity (Bai & Zhang, 2015; Mee & Moore, 2014), an idea supported by investigations of small modern *Picea* refugia (Wehenkel & Sáenz-Romero, 2012). Gene flow via pollen or seeds might, to some extent, have counteracted genetic erosion in the refugia. However, genetic studies of modern *Picea* using a mitochondrial marker (i.e., one that is maternally inherited) indicate that gene flow between populations via seeds is limited (Aizawa et al., 2007), which accords with the known dispersal limitation (Tautenhahn et al., 2016) that is likely to originate from the relatively heavy seeds of *Picea*. Transmission of paternally inherited core and chloroplast genes among distant glacial populations was probably also restricted because *Picea* has, compared with other wind-pollinated trees, low pollen productivity and low pollen dispersal abilities (Sjögren, van der Knapp, Huusko, & van Leeuwen, 2008). Additionally, outbreeding depression (known for Pinaceae; Goto, Iijima, Ogawa, & Ohya, 2011) might have amplified genetic erosion when pollen reached refugia from a genetically distant population.

Such genetically exhausted glacial tree populations might not have been able to expand when conditions became more generally favourable, but instead lost out to large incoming populations of the same or different species that harboured a much deeper reservoir of genetic variation (Davis, Shaw, & Etterson, 2005). Such a situation would, for example, explain why genetically isolated *Picea* occurrences, such as in the Magadan area (Koropachinskii, Potemkin, Rudikovskii & Kuznetsova, 2012; Kravchenko, Eckart, & Larionova, 2016), remained small or became even smaller during the post-glacial period. However, such genetic drawbacks might not be applicable to *Larix* because its reproductive traits appear well adapted to survival in northern refugia. For example, *Larix* can exchange genetic information over long distances, probably via wind-distributed seeds, which allow maternal and paternal heritable information to be transmitted more easily. This is indicated by modern genetic analyses, which have shown that *Larix* tree line populations across the whole of northernmost Siberia seem to be well connected genetically (Kruse, Epp, et al., 2018; Oreshkova, Belokon, & Jamiyansuren, 2013; Polezhaeva et al., 2010). Furthermore, owing to clonal growth (Wieczorek et al., 2017) in harsh conditions, the population diversity in large refugia

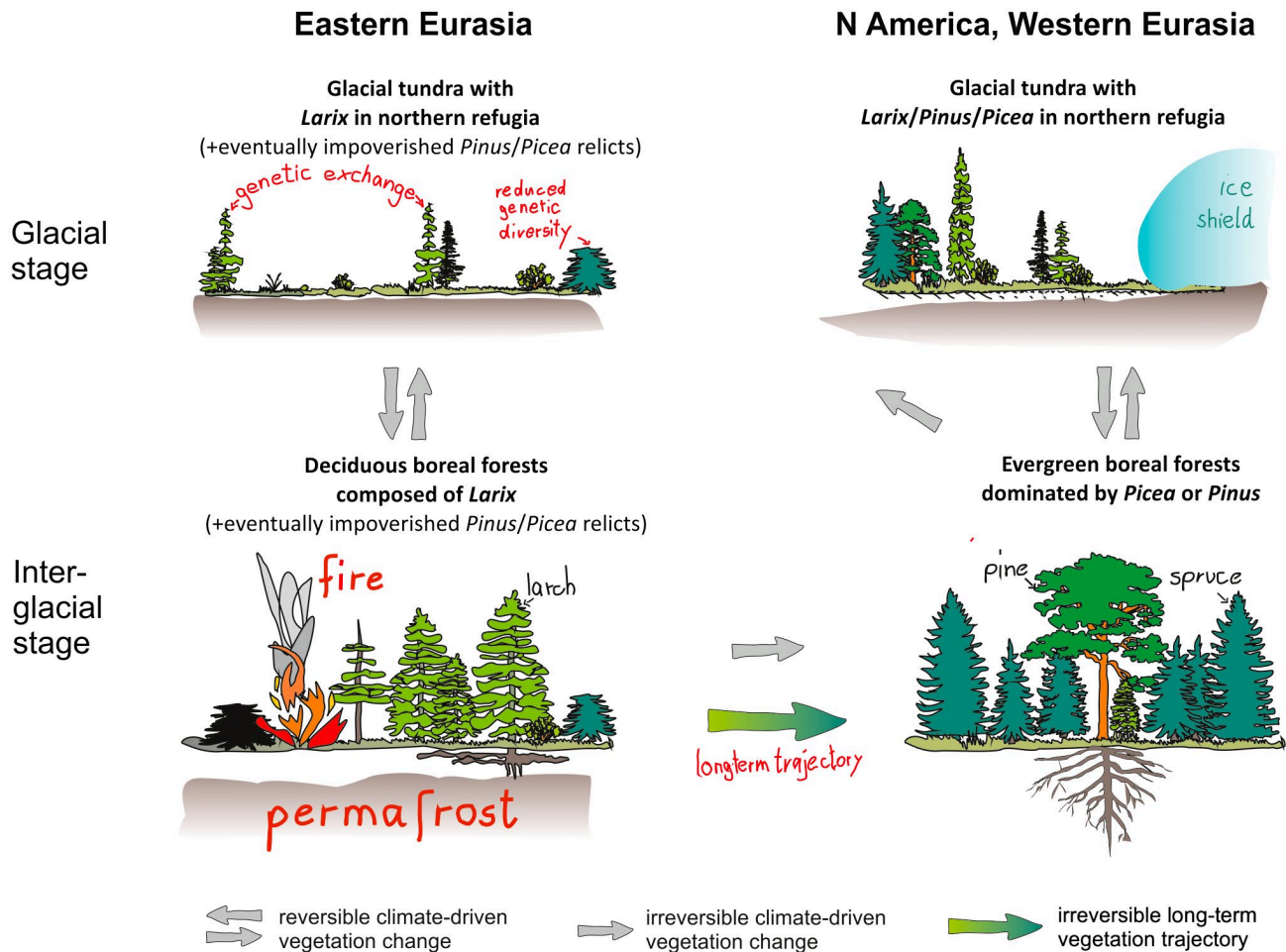


FIGURE 2 Illustration of the concept of “boreal forest bi-stability and glacial legacy”. The hypothesis is that deciduous and evergreen boreal forests represent alternative quasi-stable states that occur in similar climates today, but which came about because of the different characteristics (gene pool) of the northern tree refugia, as a legacy of the preceding glacial stage. Once established, Asian larch forests stabilized because of their unique vegetation–fire–permafrost–climate system that inhibits the invasion of evergreen taxa. However, the long-term vegetation trajectory causes the irreversible transition of deciduous into evergreen boreal forests. This is mainly because the larch is a poor competitor compared with evergreen spruce and pine when growing in mixed stands. Asian larch forest would be able to re-establish only after a new forest-free glacial stage. Given that both boreal forest types are stable only across a certain climate range, a warmer and drier climate in the future might cause their transition into steppe, which is also irreversible for Asian larch forests [Colour figure can be viewed at wileyonlinelibrary.com]

is probably better preserved than would have been the case if small groups had reproduced sexually. This can be concluded from the analyses of Kruse, Epp, et al. (2018), who revealed that clonal tree stands ahead of the Siberian forest-line (representing relicts of the extended early Holocene area) showed a higher diversity than the currently expanding forest-line located farther south. However, the impact of reproductive traits on long-term population dynamics is still a poorly investigated research field. (There is no convincing evidence that pine trees survived glacial conditions in northeastern Asia, and these were, accordingly, excluded from above discussion.)

With respect to post-glacial boreal forest establishment, four conclusions can be drawn from the above literature review:

1. Evergreen and deciduous needleleaf taxa are seldom co-dominant but typically form certain forest states in space and

time (Figure 1), supporting the idea of bi-stability of boreal forests (Figure 2).

2. Evergreen boreal forests were able to replace larch forests during the post-glacial but rarely vice versa, pointing to a hysteresis effect or trajectories.
3. Evergreen trees probably took advantage of their competitive strength when recolonizing deglaciated areas from continuous mixed forests or widespread refugia (e.g., North America and western Eurasia).
4. When recolonizing from small northern refugia (i.e., north-eastern Eurasia), only *Larix* expanded, possibly because it had preserved its genetic diversity better than the evergreen taxa during the glacial and could thus react more flexibly to warming during the late glacial.

Briefly, I propose that the post-glacial vegetation trajectories in boreal areas are defined by the characteristics of northern tree refugia resulting,

to some extent, from genetic constraints and indirectly from the glacial climate (Figure 2). However, given that empirical evidence is still too rare and modelling evidence is entirely absent, this statement represents evidence-based speculation rather than confirmed knowledge. There might also be an alternative explanation for the present larch dominance in Siberia despite the available climate space for evergreen taxa. It could be that this is not a legacy of glacial climate but a legacy of early Holocene cold winter climate, which, in accordance with current theory (Givnish, 2002; Zanne et al., 2014), supported the establishment of deciduous *Larix* because it can cope with extremely low winter temperatures. Since then, the invasion of evergreen taxa lag behind winter warming related to the Holocene increase in winter insolation. In any case, the assumption that the current climate is the main explanation of the present boreal forest tree distribution requires re-examination.

Accordingly, research priorities include the re-analyses of available pollen datasets (Bigelow et al., 2003; Binney et al., 2017; Tian et al., 2018) to identify stable states, legacies and post-glacial vegetation trajectories in boreal areas. Furthermore, genetic constraints on boreal tree taxa migration need to be explored through high-resolution genomic/genetic analyses of modern populations (Polezhaeva et al., 2010; Semerikov et al., 2013) or, even better, through direct tracking of past population dynamics (Epp et al., 2018; Schmid et al., 2017; Zimmermann et al., 2017) with ancient DNA analysis of sedimentary archives. Even more challenging than gaining empirical data might be the implementation of appropriate simulation studies. A suitable vegetation model needs both to run on large temporal and spatial scales and to resolve small-scale tree population processes, including seed dispersal and genetic adaptation. Such a model is not yet available. Generally, individual-based models focusing on boreal tree taxa dynamics are more appropriate than dynamic global vegetation models for further development. Among all the available individual-based models for boreal trees, only LAVESI (Kruse, Wieczorek, Jeltsch, & Herzschuh, 2016) currently handles seed and pollen dispersal (Kruse et al., 2019; Kruse, Gerdes, Kath, & Herzschuh, 2018) explicitly, which might be decisive in the accurate simulation of tree migration. Variable traits have hitherto not been implemented in individual-based models but are at a population scale in dynamic global vegetation models (Sakschewski et al., 2016).

4 | HOW DID DECIDUOUS FORESTS STABILIZE IN EASTERN EURASIA AND THUS RESIST REPLACEMENT BY EVERGREEN TAXA?

In mixed forest stands, light-demanding *Larix* trees are out-competed by evergreen taxa (Kharuk et al., 2007; Schulze et al., 2012) i.e., evergreen taxa are assumed to represent the late successional stage). Given their wide distribution, it is not yet known how *Larix* forests, once established, hinder their replacement by evergreen forests and thus maintain vegetation–climate disequilibrium.

Expansion of late-successional taxa is often hampered by recurrent disturbances (Dantas, Hirota, Oliveira, & Pausas, 2015). Fire

is the most obvious disturbance in boreal forests (Helbig, Pappas, & Sonnentag, 2016; Rogers, Soja, Goulden, & Randerson, 2016). A Northern Hemisphere-wide remote-sensing study revealed that fire regimens differ markedly between forests dominated by *Larix* (a fire resister) and those dominated by evergreen taxa, such as *Picea* (a fire avoider), despite rather similar climatic conditions (Rogers et al., 2016). It was shown that *Larix* forest fires are less severe, probably because of their high leaf water content, but are more frequent, possibly as a result of effective fuel accumulation (Rogers et al., 2016), which might be attributable to high early-stage growth rates compared with evergreen taxa (Shuman et al., 2017). These traits and related small-scale population dynamics are likely to play an important role in maintaining fire systems and thus inhibiting the invasion of *Picea obovata* and *Picea mariana* (both fire avoiders) into *Larix*-dominated forests in eastern Siberia and the Russian Far East, respectively (Furyaev, Vaganov, Tchebakova, & Valendik, 2001; Schulze et al., 2012; Tautenhahn et al., 2016). In contrast, the occurrence of *Pinus sylvestris* might not be affected generally by the *Larix*-induced fire regimen, because it is a fire resister itself (McRae et al., 2006), although its low early-stage growth rate might hinder its expansion (Shuman et al., 2017). Such modelling and field data from Siberia all indicate that *Larix* dominance coincides with high fire frequency in eastern Eurasia (Kharuk, Ranson, Dvinskaya, & Im, 2011; Schulze et al., 2012; Shuman et al., 2017).

A second major barrier to evergreen boreal tree expansion is permanently frozen soil (permafrost; Osawa, Zyryanova, Matsuura, Kajimoto, & Wein, 2010). Eastern Eurasian *Larix* species are the only tree taxa that can grow on permafrost soils with very small active-layer depths (i.e., late-summer thaw depth of < 30 cm), owing to their ability to develop an adventitious rooting system (Kajimoto, 2010). In boreal northern Asia, such small active-layer depths are observed only below *Larix* forests, whereas forest-free areas resulting from land use or steppe expansion have deeper active-layer depths (Fedorov et al., 2017). This fits with the finding that forest-protected permafrost islands occur within permafrost-free lowlands in the discontinuous permafrost zone of northern North America (Baltzer, Veness, Chasmer, Sniderhan, & Quinton, 2014; Fisher et al., 2016; Morse, Wolfe, Kokelj, & Gaanderse, 2016). Respective studies from eastern Eurasia are rare. Chang et al. (2015) showed that *Larix* can decouple permafrost from climate very effectively, probably because of its low water-use efficiency (Kloppel, Gower, Treichel, & Kharuk, 1998) and strong upper soil organic matter accumulation related to its below-ground oriented biomass production (Kajimoto et al., 2006; Vedrova, 2005). Deep-rooting evergreen taxa, such as *Pinus sylvestris*, are therefore unable to invade their territory owing to the high permafrost table.

The control of the nutrient regimen by the founding community could, hypothetically, be a third mechanism that allows the self-stabilization of deciduous taxa. It is assumed that deciduous taxa maximize carbon recycling, in contrast to evergreen taxa, which maximize nitrogen recycling (Weng, Farrior, Dybzinski, & Pacala, 2017) as confirmed by the low nitrogen content of litterfall of evergreen taxa (Vedrova, 2005). However, data that directly support such feedback cycles are currently lacking for boreal forests of eastern Eurasia.

To summarize, once established, Asian larch forests are likely to stabilize through a complex vegetation–fire–permafrost soil–climate feedback system, which results in a shallow active-layer depth, a high fire frequency and, possibly, in a nutrient regimen maximizing carbon recycling that hinders the establishment of evergreen needleleaf taxa (Figure 2). Rare modelling evidence so far suggests that feedbacks provide some protection for larch forests against invasion by evergreen taxa (Shuman et al., 2017; Zhang, Yasunari, & Takesi, 2011). The inference of feedbacks is strongly dependent on the processes that are incorporated into the models used and their parameterization, requiring a broader empirical base than is currently available for northern Asia, in particular with respect to differences among deciduous and evergreen forest in nutrient cycling. Accordingly, a quantification of the feedbacks in the coupled forest fire–permafrost–climate system along broad environmental gradients is highly desirable.

5 | HOW WILL DECIDUOUS BOREAL FORESTS CHANGE IN THE FUTURE?

Boreal forest simulations for the 21st century in northern Asia yield contradictory results (Shuman, Shugart, & O'Halloran, 2011; Tchebakova, Parfenova, Korets, & Conrad, 2016; Zhang et al., 2011). All the models assume that the distribution of boreal biomes is mainly a function of current bioclimatic limits. In contrast, I assume that future natural vegetation change in a particular area is likely to follow a long-term vegetation trajectory (Figure 2). By analogy with the past, this would imply that broad-scale vegetation change is rather limited on human-relevant time-scales.

Natural biotic constraints, however, might become ineffective in the face of expanding regional human impact, such as fire management (Mollicone, Eva, & Achard, 2006), land use-related impacts on the permafrost regimen (Fedorov et al., 2017) and unintentional seed dispersal and plantations of evergreen taxa. Thus, it needs to be a research priority to identify the effects of regional human activities on the complex vegetation–fire–permafrost–climate system.

Larix forests are stable over a wide climatic range; hence, they are largely resistant to climate change. However, as a result of anthropogenic global warming, northern Asia is likely to experience an unprecedented climate in the future (IPCC, 2014). This might cause certain thresholds to be crossed, resulting in, for example, *Larix* self-stabilization becoming ineffective and climate becoming the major driver of vegetation in northern Asia. Accordingly, the determination of the climatic range across which *Larix* forests are able to persist is highly necessary. Likewise, it needs to be investigated how the exceedance of climate thresholds would result in deviance from natural vegetation trajectories, particularly those that might lead to an irreversible loss of larch forests.

Boreal forests, which make up roughly one-third of the world's total forested area (Pan et al., 2011), provide crucial ecosystem services (Gauthier, Bernier, Kuuluvainen, & Shivdenko, 2015). These services differ markedly between the evergreen boreal forests and the deciduous boreal forests (Bonan, 2008; Hugelius et al., 2014; Krestov, 2003).

Even the characteristics of lakes depend strongly on the surrounding forest type (Herzschuh et al., 2013). Deciduous and evergreen boreal forests also differ markedly with respect to their climate–vegetation feedback functions (Bonan, 2008). The potentially central role of *Larix* forests in protecting the vast permafrost carbon pool in north-eastern Asia from thaw has hitherto been overlooked completely.

In summary, change in Asian larch forests is likely to be governed by long-term trajectories and is therefore largely resistant to natural climate variability on human-relevant time-scales. The effects of regional human impacts and anthropogenic global warming might, however, cause certain stability thresholds to be crossed, meaning that irreversible transitions occur and having marked consequences for ecosystem services.

6 | CONCLUSION

My overall concept is that deciduous and evergreen boreal forests represent alternative quasi-stable states that occur in similar climate conditions today but were determined by different environmental conditions and different gene pools in the northern refugia during the Last Glacial. This means that tiny genetic variations in the past determined the continental-scale vegetation variation of today. My concept of “boreal forest bi-stability and glacial legacy” would exemplify the conclusion of Montcrieff, Hickler, and Higgins (2015) that both environmental history and contemporary climate have a strong influence on present-day biome distributions. If this concept applies, the establishment of a new scientific framework for the consideration of long-term ecological and genetic processes in Earth system science is required. Such a framework will build on important ecological concepts, namely the palaeoclimate legacy on the biosphere (Svenning, Eiserhardt, Normand, Ordonez, & Sandel, 2015), disturbance and succession (Pulsford, Lindenmayer, & Driscoll, 2016) and alternative stable states (Scheffer et al., 2009). Further investigation of the proposed concept will also foster the ongoing discussion on bi-stability of other vegetation types, such as between savannah and forest vegetation in the tropics (Oliveras & Malhi, 2016). However, these discussions urgently require further data and modelling evidence.

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DATA AVAILABILITY STATEMENT

This study is based exclusively on open data from open sources [i.e., European Space Agency Climate Change Initiative landcover map (www.esa-landcover-cci.org) and WorldClim2 dataset (www.worldclim.org/version2)]. R code for climate space analysis can be obtained upon request from the author.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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