Global Change Biology

Global Change Biology (2016) **22**, 2178–2197, doi: 10.1111/gcb.13181

Dispersal limitation drives successional pathways in Central Siberian forests under current and intensified fire regimes

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Abstract

Fire is a primary driver of boreal forest dynamics. Intensifying fire regimes due to climate change may cause a shift in boreal forest composition toward reduced dominance of conifers and greater abundance of deciduous hardwoods, with potential biogeochemical and biophysical feedbacks to regional and global climate. This shift has already been observed in some North American boreal forests and has been attributed to changes in site conditions. However, it is unknown if the mechanisms controlling fire-induced changes in deciduous hardwood cover are similar among different boreal forests, which differ in the ecological traits of the dominant tree species. To better understand the consequences of intensifying fire regimes in boreal forests, we studied postfire regeneration in five burns in the Central Siberian dark taiga, a vast but poorly studied boreal region. We combined field measurements, dendrochronological analysis, and seed-source maps derived from high-resolution satellite images to quantify the importance of site conditions (e.g., organic layer depth) vs. seed availability in shaping postfire regeneration. We show that dispersal limitation of evergreen conifers was the main factor determining postfire regeneration composition and density. Site conditions had significant but weaker effects. We used information on postfire regeneration to develop a classification scheme for successional pathways, representing the dominance of deciduous hardwoods vs. evergreen conifers at different successional stages. We estimated the spatial distribution of different successional pathways under alternative fire regime scenarios. Under intensified fire regimes, dispersal limitation of evergreen conifers is predicted to become more severe, primarily due to reduced abundance of surviving seed sources within burned areas. Increased dispersal limitation of evergreen conifers, in turn, is predicted to increase the prevalence of successional pathways dominated by deciduous hardwoods. The likely fire-induced shift toward greater deciduous hardwood cover may affect climate–vegetation feedbacks via surface albedo, Bowen ratio, and carbon cycling.

Keywords: boosted regression trees, boreal, dark taiga, fire regime, forest regeneration, land surface–climate feedback, postfire succession, residual seed trees, seed dispersal

Received 20 November 2014; revised version received 6 November 2015 and accepted 18 November 2015

Introduction

In the past few decades, the northern high latitudes have experienced the most surface warming of any region on Earth, leading to increased frequency, severity, and size of fires throughout the boreal zone (Chapin *et al*., 2000; Soja *et al*., 2007). Projected global warming, together with an intensified fire regime, might push the boreal forest system across a tipping point beyond which dieback and compositional change will occur (Shvidenko *et al*., 2013). In addition to the direct effects of an intensified fire regime on climate and ecosystems (Randerson *et al*., 2006; Bond-Lamberty *et al*., 2007; Oris *et al*., 2014), indirect long-lasting effects may also occur due to shifts in tree species composition (Johnson, 1996; Chapin *et al*., 2004; Goetz *et al*., 2007; Wirth *et al*., 2008; Johnstone *et al*., 2010; Taylor & Chen, 2011; Rogers *et al*., 2015). A shift in tree species composition from evergreen conifers (e.g., *Picea*

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spp. and *Abies* spp.) toward deciduous hardwoods (broad-leaved, deciduous angiosperms; e.g., *Betula* spp. and *Populus* spp.) would increase surface albedo and evaporative cooling (Amiro *et al*., 2006; Randerson *et al*., 2006, see also Table 1), resulting in negative feedbacks to surface warming (McGuire *et al*., 2006; Goetz *et al*., 2007; Lyons *et al*., 2008). A shift toward greater deciduous hardwood cover also has consequences for carbon and nutrient cycling (Cleve & Viereck, 1981; Gower *et al*., 2001); for example, increased carbon uptake due to faster biomass growth rates (Nikolov & Helmisaari, 1992; Yarie & Billings, 2002). A fire-induced increase in deciduous hardwood forest cover has already been observed in boreal North America (Beck *et al*., 2011) and is expected to occur in other boreal regions as well (e.g. Otoda *et al*., 2012). However, the ecological traits of the dominant tree species differ among boreal regions (Rowe, 1983; Wirth, 2005). It is therefore unclear if all boreal regions will respond to an intensifying fire regime in a similar manner. An improved understanding of the mechanisms that determine the landscape-scale abundance of deciduous hardwoods vs. evergreen conifers in different boreal regions is thus critical for understanding the

Table 1 Ecological characteristics of dominant tree species in Central Siberian dark taiga. Species within each group (deciduous hardwood or evergreen conifer) are similar with respect to fire adaption, regeneration strategy, germination conditions, and biophysical feedbacks

Group	Deciduous hardwoods 'DHs'		Evergreen conifers 'ECs'		
Species	*Betula pendula*	*Populus tremula*	*Abies sibirica*	*Picea obovata*	*Pinus sibirica*
Cover in old growth stands (>200 years)					
Stem density (individuals/m^2)*	0.005 ± 0.004	0.0002 ± 0.0004	0.040 ± 0.013	0.007 ± 0.003	0.003 ± 0.002
Basal area (m^2/ha)*	3.43 ± 1.85	0.12 ± 0.30	19.61 ± 4.77	7.68 ± 3.66	7.35 ± 5.92
Fire adaption and postfire succession strategy					
Fire adaption strategy†	'Invader'	'Edurer'	'Avoider'	'Avoider'	'Avoider'
Fire survival‡	Belowground	Belowground	No	No	No
Successional stage	Early	Early	Late	Late	Late
Shade tolerance	Low	Low	High	High	High
Regeneration strategy					
Seed mass (mg)§	0.27	0.11	10.00	4.53	226
Dispersal vector‡	Wind	Wind	Wind + animal	Wind + animal	Animal
Dispersal distance‡	Long	Long	Short	Short	Intermediate
Resprouting capacity after fire¶	Intermediate	High	No	No	No
Site preferences for germination					
Mineral soil‡	Preferred	Required	Not required	Not required	Not required
Drought‡	Tolerant	Intolerant	Intolerant	Intolerant	Intolerant
Fire‡	Required	Required	Not required	Not required	Not required
Biophysical feedbacks					
Age of reaching 100 cm height (years)¶	15	15	26	27	24
Maximum age (years)**,††,‡‡	125–135	100–150	220–260	300–500	400–800
Wood decomposition k§§	0.135 ± 0.036	0.109 ± 0.034	0.053 ± 0.014¶¶	0.055 ± 0.0135	0.057 ± 0.014
Short-wave albedo (%)***	0.13		0.09		
Bowen ratio (%)†††	0.6		1.03		

*Own data from 6 old growth stands (>200 years) in the Zotino region of Central Siberia; For the calculation of the stem density only adult trees (with a DBH > 15 cm) where included.

†Wirth (2005).

‡Nikolov & Helmisaari (1992).

§Seed information database (http://data.kew.org/sid/).

¶Predicted with a BRT-Model fitted to field data from five burns in the Zotino region of Central Siberia, see Appendix S5.2.

**Komarov (1956).

††Kellomäki (1987).

‡‡Sokolov et al. (1977).

§§Pietsch et al. (2014), k refers to the decay constant in the single negative exponential decay model of Olson (1963).

¶¶There was no species-specific data available for *A. sibirica* and the given value is the mean of available values for the genus *Abies*.

***Median of 'EC' stands ($n = 63$) and 'DH' stands ($n = 24$) estimated from Fluxnet sites (http://www.fluxdata.org).

†††Median of 'EC' stands ($n = 15$) and 'DH' stands ($n = 7$) estimated from Fluxnet sites (Cescatti *et al*., 2012).

long-term consequences of an intensified fire regime for climate–vegetation feedbacks.

Understanding ecosystem response to intensifying fire regimes requires an understanding of how fire interacts with tree life-history traits that determine postfire succession, including susceptibility to fire vs. persistence, postfire seed dispersal and establishment, and growth and survival on decadal to centennial time scales (Noble & Slatyer, 1980). Based on these traits, boreal tree species can be classified according to their fire-adaptation strategy (Rowe, 1983; Wirth, 2005; Rogers *et al.*, 2015). Boreal deciduous hardwood species (mostly *Betula* spp. and *Populus* spp.) rarely survive fire aboveground but often have high postfire recruitment success via root resprouting or soil seed banks within the burned area ('endurer' strategy), or effective colonization from outside the burn due to their large numbers of minute seeds adapted for long-distance dispersal ('invader' strategy; Nikolov & Helmisaari, 1992; Wirth, 2005; Hynynen *et al.*, 2009). In contrast, boreal conifers vary substantially in their postfire recolonization strategies. *Pinus sylvestris* and *Larix* spp., which dominate the light taiga (relatively open stands at far northern latitudes or on poor soils), often survive low to medium intensity fires due to their thick bark ('resister' strategy), and they are therefore associated with frequent surface fires. In contrast, dark taiga conifers (which are all evergreen) include two distinct fire strategies: 'embracers' and 'avoiders'. 'Embracers'(e.g., *Pinus banksiana* and *Picea mariana*) are representative of fire regimes of intermediate frequency and intermediate-to-high severity and can recruit locally from a canopy seed bank stored in serotinous cones. 'Avoiders' (e.g., *Abies balsamea* and *Picea glauca* in North America; and *Abies sibirica*, *Abies nephrolepis*, *Picea abies* and *Picea obovata* in Eurasian dark taiga) have a dense canopy that protects the forest floor from drying, such that the conditions for fire ignition and spread are poor. 'Avoiders' often occur on nutrient-rich soils and are associated with infrequent fires. However, when fires occur in these dense forests, they are often severe and stand-replacing. 'Avoiders' rarely survive fire, lack aerial seed banks, and cannot resprout. Their soil seed bank is usually consumed or rendered inviable by the heat (Johnson, 1975; Greene *et al.*, 1999). Thus, postfire regeneration of dark taiga 'avoider' species relies on seed dispersal from seed sources in unburned areas.

The traits of the dominant tree species in different boreal regions have implications for the potential mechanisms that determine how forests respond to an intensifying fire regime. In North American 'embracer'-dominated forests (e.g. Albani *et al.*, 2005; Johnstone *et al.*, 2010), the transition toward greater deciduous hardwood cover has been attributed to two sets of mechanisms. The first mechanism is that more frequent and larger fires increase the fraction of the landscape that is in an early-successional stage, and thus favors deciduous hardwoods due to their early-successional life-history strategy (Johnstone & Chapin, 2006b; Kurkowski *et al.*, 2008). Because deciduous hardwoods are the dominant early-successional species in most boreal forest regions, this mechanism is likely of broad relevance. The second set of mechanisms that appears to favor deciduous hardwoods in North American 'embracer' forests involves changing site conditions. Increasing fire severity causes changes in physical, chemical, and biological properties of the soil (Certini, 2005), which can affect the competitive balance between different tree species. In particular, the combustion of organic soil layers favors deciduous hardwoods over conifers (Johnstone & Kasischke, 2005; Johnstone *et al.*, 2010) , because the former have smaller seeds and thus less capacity to support initial root growth through a thick organic layer that is prone to desiccation (Leishman & Wright, 2000). Increased thermal nutrient mineralization also favors deciduous hardwoods relative to conifers (Zackrisson *et al.*, 1996; Wardle *et al.*, 1998), and *Betula* germination is stimulated by smoke, increasing its postfire establishment success (Keeley & Fotheringham, 2000). These mechanisms related to site conditions may also be important in boreal regions other than 'embracer'-dominated North American forests. However, the dominance in some dark taiga regions of 'avoider' species (which rely on external seed sources for postfire regeneration) implies that dispersal limitation may also play an important role in postfire succession and thus in the mechanisms that control the landscape-scale balance between deciduous hardwoods and evergreen conifers.

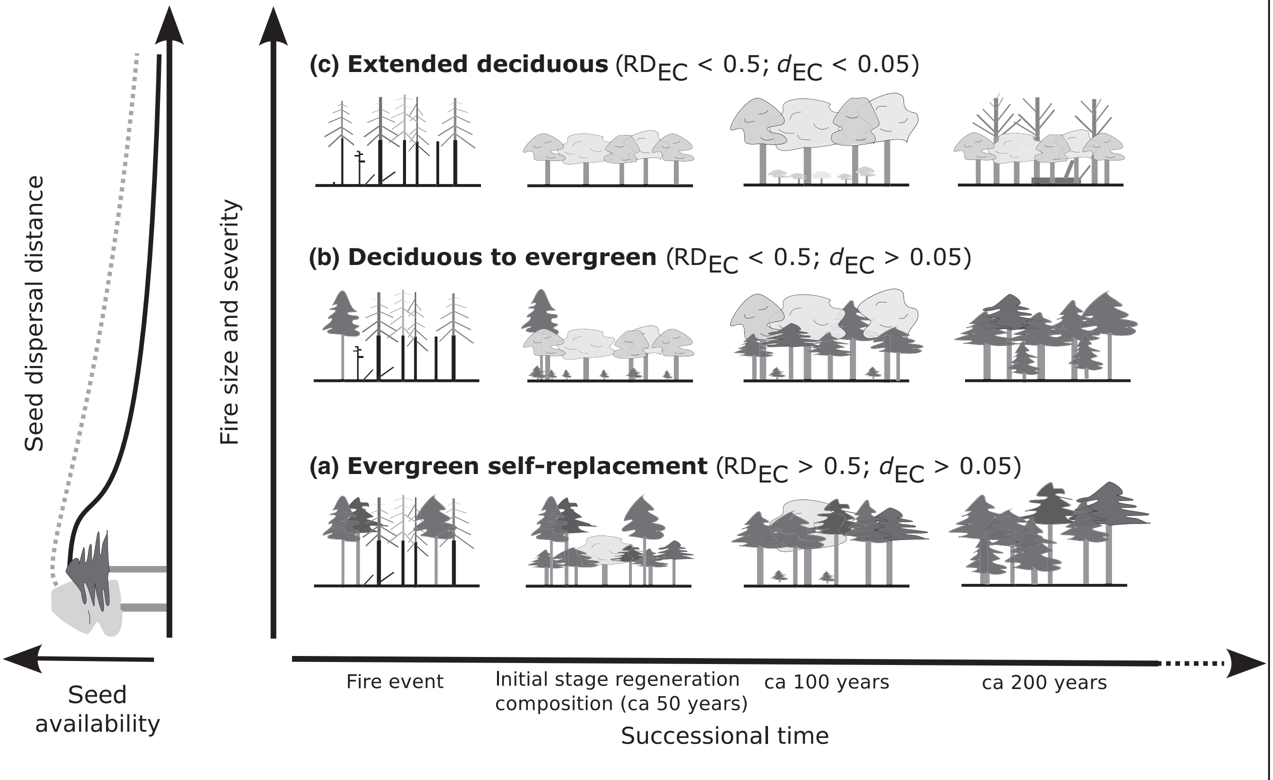
In this study, we explore the potential role of dispersal limitation in causing a shift from evergreen conifers toward deciduous hardwoods under an intensifying regime in 'avoider'-dominated dark taiga forests. Increasing fire size could benefit deciduous hardwoods (due to their relatively long dispersal distances) over evergreen conifer 'avoider' species (shorter dispersal distances). Dispersal limitation has previously been studied as a potential mechanism leading to a fire-induced shift in dominance among different evergreen conifer species in British Columbia and Alaska (e.g. Albani *et al.*, 2005; Wirth *et al.*, 2008). Here, we propose that dispersal limitation, combined with an intensifying fire regime, could similarly lead to a transition toward more deciduous forest cover in regions where the dominant conifers are all evergreen 'avoider' species (Box 1).

To explore the potential role of dispersal limitation in controlling the balance between deciduous hardwoods and evergreen conifers under an intensifying fire

Box 1 Dispersal limitation of evergreen conifers and successional pathways in Central Siberia

In the dark taiga of Central Siberia, deciduous hardwoods (DHs) have an advantage in colonizing burned areas compared to evergreen conifers (ECs). DH recruitment density is typically high following fire because DH species in this region have relatively long seed dispersal distances (*gray dotted seed dispersal curve in left figure below*), have a higher probability to form and regenerate from a soil seed bank, and can also resprout after fire (Zasada *et al.*, 1992). In contrast, EC species in this region are likely dispersal limited on large and severe burns as they have short dispersal distances (*black solid seed dispersal curve*), do not resprout or regenerate from a soil seed bank, and lack serotiny. Increasing fire size and/or severity (both of which result in increased distances between seed trees and burned areas available for recolonization) could therefore shift successional pathways toward greater DH dominance. Two key characteristics of postfire regeneration can be used to determine likely successional pathways (for details, see 'Classification of successional pathways' in Methods and Appendix S5.4):

1. *Evergreen conifer regeneration dominance:* $\mathrm{RD}_{\mathrm{EC}}$ quantifies EC vs. DH regeneration dominance in terms of biomass. Values of 0, 1, and 0.5, respectively, indicate pure DH, pure EC, and equal regeneration.
2. *Evergreen conifer regeneration density:* d_{EC} indicates if EC regeneration is adequate to form a fully stocked mature EC stand ($d_{\mathrm{EC}} > 0.05$ individuals/m^2).



(a) Evergreen self-replacement: Small and/or low-intensity burns require relatively short dispersal distances for postfire regeneration (the figures above illustrate how seed dispersal kernels compare to the distances needed to recolonize fires of varying size and severity). Due to their greater abundance and fire resistance, most surviving seed trees are EC. Near these seed trees, EC recruitment density is high enough to prevent early-successional DH dominance. Once EC trees close the canopy, shade-intolerant DH regeneration is precluded (Taylor & Chen, 2011). This pathway is associated with high $\mathrm{RD}_{\mathrm{EC}}$ (>0.5) and high d_{EC} (>0.05 individuals/m^2).

(b) Deciduous to evergreen: Burns of intermediate size and/or severity require intermediate dispersal distances for postfire regeneration. This situation initially favors DH due to their relatively long dispersal distances and fast growth rate under high-nutrient and high-light conditions immediately after fire, but EC regeneration density is sufficient to eventually form a fully stocked stand. After $\sim$120 years, the abundance of DH declines due to their short lifespan and shade-intolerance. EC regain dominance until the next fire, unless other disturbances occur (e.g., wind-

Box 1 (continued)

throw or insect outbreaks;Schulze *et al.*, 2005; Shorohova *et al.*, 2009; Taylor & Chen, 2001). This is the most common successional pathway in the Central Siberian dark taiga (Schulze *et al.*, 2005), and is associated with low RD_{EC} (<0.5) and adequate d_{EC} (>0.05 individuals/m^2).

(c) Extended deciduous: Large and/or severe burns require long-distance dispersal for regeneration. EC regeneration densities may be inadequate to form a mature EC stand even after several hundred years, despite some level of continuous recruitment. Thus, the transition from DH to EC is delayed relative to the currently dominant 'deciduous to evergreen' pathway. In this case, DH may dominate a stand for hundreds of years (Appendix S5.5), most likely due to vegetative reproduction (Hynynen *et al.*, 2009). This pathway is associated with low RD_{EC} (<0.5) and inadequate d_{EC} (<0.05 individuals/m^2).

regime, we studied postfire regeneration and successional pathways in the dark taiga of Central Siberia. In these closed canopy boreal forests, the dominant conifers are all late-successional, evergreen 'avoider' species (primarily *Abies sibirica*, *Picea obovata*, *Pinus sibirica*). For conciseness, we henceforth refer to these species as evergreen conifers (ECs), but we emphasize that we use the term ECs to refer specifically to dark taiga EC 'avoiders' (unless stated otherwise). In our study region, these EC species co-occur with early-successional deciduous hardwoods (DHs; primarily *Betula pendula*, *Populus tremula*). Postfire succession in this region typically follows a 'deciduous to evergreen' successional pathway (Schulze *et al.*, 2005, see also Box 1b): After a fire, DH and EC species often both colonize burned areas. Due to their faster growth rates under high-resource conditions, DH species overgrow EC species early in postfire succession, and remain dominant until EC species take over after about 120 years due to their greater shade tolerance and longevity (Furyaev *et al.*, 1983; Nikolov & Helmisaari, 1992; Schulze *et al.*, 2005; Wirth, 2005). This creates a landscape mosaic with roughly one-third of the Central Siberian dark taiga area dominated by DH trees, and two-thirds dominated by EC trees (Mollicone *et al.*, 2002).

Using a large field data set together with high-resolution satellite remote sensing data, dendrochronological analysis, and machine-learning-based regression, we test the following hypotheses: (i) postfire succession in the Central Siberian dark taiga is strongly affected by dispersal limitation of EC 'avoider' species; and (ii) site conditions created by fire favor the establishment of DH over EC species, as in North American 'embracer' forests. Both hypotheses rely on mechanisms that would promote a transition toward greater DH cover at the landscape scale under an intensified fire regime. We explore this transition using our quantitative results to assess the potential for shifts toward greater DH cover under plausible future scenarios for intensified fire regimes in the dark taiga of Central Siberia.

Materials and methods

Overview

We tested our hypotheses related to dispersal limitation and postfire establishment conditions by studying postfire regeneration of deciduous hardwoods (DHs) and evergreen conifers (ECs) in the dark taiga of Central Siberia. (As noted in the Introduction, we use the term 'EC' to refer specifically to dark taiga evergreen conifer 'avoider' species.) To quantify the relative importance of factors related to seed dispersal and site conditions, we used machine-learning-based regression to construct models of EC regeneration dominance (RD_{EC}) and density (d_{EC}), two key characteristics of postfire regeneration (see Box 1). Our statistical modeling approach integrates multiple data streams: (i) an extensive data set on postfire regeneration, surviving residual trees, and site conditions measured *in situ* in five burned areas; (ii) dendrochronological tree age and fire history determination (Appendix S5); and (iii) high-resolution satellite images, which we used to estimate the landscape-scale distribution of EC seed sources.

To project successional pathways (Box 1) at the landscape scale under current and intensified fire regimes, we first generated landscape-scale maps of EC seed sources and establishment conditions corresponding to different burn size and severity scenarios. For each of these fire regime scenarios, we used our statistical models to predict EC regeneration dominance and density in each landscape pixel. These two key regeneration metrics were then used to assign a likely successional pathway based on a set of empirical rules, thus allowing us to assess the potential for shifts toward greater DH cover under intensified fire regimes.

Study area and species

Our study area is located in Central Siberia on the east bank of the Yenisei river near the town Zotino. The climate of the Zotino region is continental with −26 °C average January temperatures and temperature minima of <−56 °C. Daily maximum temperatures in summer can reach 36 °C. The region is characterized by the escarpment of the Central Siberian Mountain range, with ridges of 1100 m altitude (Schulze *et al.*, 2005). The mountain range shows a strong geomorphological structure and heterogeneity with many creeks and rivers that are often cut steeply into the landscape (Schulze *et al.*, 2002). Mean annual precipitation ranges from 600–1000 mm (Ivanov, 1990). The loamy, nutrient-rich cambisol soils originate from weathered Cambrian and Paleozoic bedrock composed of granites, quartzite, and calcareous sediments (Schulze *et al.*, 2002).

The area is representative of the Central Siberian dark taiga – a closed canopy boreal forest dominated by *Betula pendula* ROTH and *Populus tremula* L. SYN. during early-successional stages; and *Abies sibirica* LEDEB., *Picea obovata* LEDEB., and *Pinus sibirica* DU TOUR in the late-successional stages. All of the late-successional dominants are evergreen conifer (EC) 'avoider' species (see Introduction for a description of fire adaption types). 'Resister' species do not occur in the dark taiga forests of the Yenisei ridge – *Larix* species are associated with permafrost and/or drier, more fire-prone habitats (Schulze *et al.*, 2012), and *Pinus sylvestris* grows on sandy alluvial soils (Wirth *et al.*, 2002). 'Embracer' species with on-site aerial seed banks are absent from Siberia (Wirth, 2005).

In the Central Siberian dark taiga zone, stand-replacing fires represent the primary disturbance agent, with a mean fire return interval of about 300–500 years (Mollicone *et al.*, 2002; Schulze *et al.*, 2005). Central Siberian 'avoider' forests feature the longest fire return interval of all boreal forest types. The dense canopy of the 'avoider' species and thus the high soil moisture results in poor conditions for the development and spread of fire. But if fires occur – commonly starting after extreme dry spells – they are severe crown fires that kill the trees while surface fires do not occur in this region (Wirth, 2005). Local differences in fire severity and therefore survival of residual seed trees can arise from topographic landscape heterogeneity – the survival of residual seed trees is higher on well drained uplands compared to the moist lowlands, depressions, channels, and creeks (Harden *et al.*, 2000; Jung *et al.*, 2013).

The dark taiga extends along a broad band between 57° and 62°N from European Russia across the Ural mountains to the Yenisei region (Schulze *et al.*, 2002 2005) and covers about 20% of the Eurasian forest area (129.3 Mha; Bartalev *et al.*, 2004 2011; Rogers *et al.*, 2015, see also Appendix S1) This corresponds to roughly 40% of the entire Canadian forest area and to about half of the area of boreal North American 'embracer' forests (Rogers *et al.*, 2015).

Aggregation to deciduous hardwoods and evergreen conifers. We grouped the occurring tree species into the dark taiga evergreen conifers (ECs) and deciduous hardwoods (DHs) because these two functional groups have distinct regeneration strategies as well as distinct biophysical and biogeochemical properties that are relevant for vegetation–climate feedbacks (see Table 1 for a summary). DH species benefit from abundant, small light-winged or hair-coated seeds with a good dispersal ability and can also regenerate from stump or root suckers (Nikolov & Helmisaari, 1992). They have mean dispersal distances of ~50–90 m, but as the dispersal kernels are highly right skewed, very long dispersal events occur frequently (Wagner *et al.*, 2004; Huth, 2009; Hynynen *et al.*, 2009). Therefore, DHs are available on-site after the fire event and are assumed to be not limited by dispersal. In contrast, EC species are all limited by dispersal. *Abies sibirica* and *Picea obovata* are mainly wind dispersed, and due to their larger seed mass compared to DH (see Table 1), their dispersal distances are comparatively short. Mean dispersal distances of the genus *Abies* are ~8–25 m (Clark *et al.*, 1999; Sagnard *et al.*, 2007; Paluch, 2011) and of the genus *Picea* ~13–5 m (for a meta-analysis see fig. 9 of Wirth *et al.*, 2008). *Pinus sibirica* is an exception here, as its seeds are often dispersed by Siberian Jays (Schulze *et al.*, 2005). This is of minor relevance because this tree species was rare (see Table 1).

Sampling sites. During field expeditions in the summers of 2007 and 2008, we examined five burned areas on the eastern side of the Yenisei river near Zotino (Fig. 2). The areas were burned in 1944, 1956, 1958, 1990, and 1999, and are all still in the early stages of succession (Fig. 1). The burns differ in various characteristics (Table 2). The areas were burned in 1944, 1956, 1958, 1990, and 1999 (corresponding to stand ages ranging from 9 to 63 years; see Appendix S5 for dendrochronological methods), and are all still in the early stages of succession (Fig. 1). The burns also differ in size (8–33 km^2) and the basal area of surviving 'residual' evergreen conifer (EC) seed trees within the fire perimeter (BA$_{\text{residual}}$), with mean BA$_{\text{residual}}$ ranging from 8 to 11 m^2/ha (Table 2). In contrast, the mean EC basal area in the surrounding unburned forest ranged from 16 to 32 m^2/ha. Based on our field observations and our visual assessment of satellite images, we classified each burned area as having a low, medium, or high degree of spatial clumping of residual EC seed trees, which affects the spatial distribution of EC seed sources within the burn.

A total of 295 sample plots were established in the five burned areas (Fig. S2.1 – S2.5). The basal area of EC seed trees was measured on all 295 plots ('seed-source plots'), and postfire regeneration was characterized on a subset of 233 'regeneration plots'. The majority of plots were established along 2–3 km transects extending from the unburned forest edge into the center of each burn at intervals of 100–300 m (see Fig. S2.1 – S2.5). A few of the 295 plots (~8%) were located outside the transects in unburned forest around the burn peripheries to characterize external seed sources and conditions that were underrepresented in the transects (e.g., underrepresented site conditions or high distances from EC seed sources). Plot coordinates were determined with a precision of ca. 12 m using GPS.

Field observations

Regeneration plots. In each of the 233 regeneration plots, we quantified stem density for each tree species in six size classes: 5–10, 10–20, 20–50, 50–100, and >100 cm height; and >10 cm DBH. The amount of area sampled was adjusted at each plot for each species × size class combination, with the aim of sampling 10 individuals per species per size class. Sampling began at the plot center and expanded outward, up to a maximum area of 10 × 10 m. For each individual (21 505 in total), we measured either tree height or stem diameter at a height of 0,

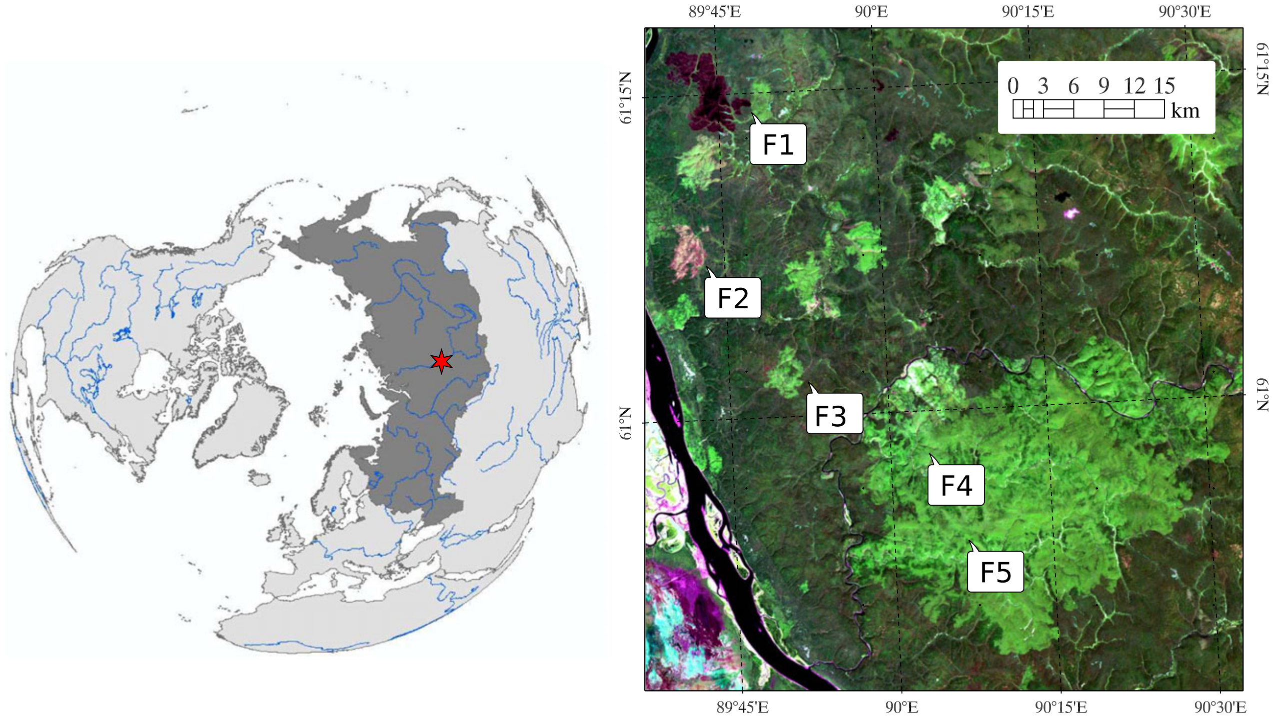


Fig. 1 Locations of the five burned areas along the Yenisei river. The Landsat image (false color, R:4, G:7, B:2) shows newly burned areas in pink and burned areas where the deciduous canopy has already developed in light green. Plot locations within each burned area are shown in Appendix S2 (Fig. S2.1 – S2.5).

Table 2 Summary information for the five studied burned areas (F1–F5). *Stand age* is the age of the burn at the time of field sampling. *Burn size* was determined from QuickBird images (for F4 and F5, minimum areas are reported because complete QuickBird scenes were not available). Mean $BA_{residual}$ is the mean basal area of evergreen conifers (EC) that survived the fire, which was estimated using methods described in Jung *et al.* (2013). *Clumping of*$BA_{residual}$ within each burn was visually assessed from the QuickBird images. *Number of seed-source plots* is the number of plots used as training data for the QuickBird analysis of EC seed sources. *Number of regeneration plots* is the number of plots used to quantify postfire regeneration

Fire area	F1	F2	F3	F4	F5
Stand age (years)	9	17	50	51	63
Burn size (km^2)	23	8	9	≫29	≫33
mean ($BA_{residual}$) (m^2/ha)	11	9	8	10	10
Clumping of $BA_{residual}$	Medium	High	Low	Medium	Medium
Number of seed-source plots	86	71	70	19	49
Number of regeneration plots	53	70	49	19	42

10, or 130 cm (D0, D10, or DBH) and later converted diameters into heights using allometric equations derived from our data (detailed in Appendix S3). Data were collected for both evergreen conifers (ECs) and deciduous hardwoods (DHs) in 214 of the 233 plots, and in 19 additional plots for EC only (due to time limits).

In addition to tree density, we collected data at each regeneration plot to characterize burn severity and site conditions for tree establishment. We visually estimated the fractional cover of herbaceous species on a 4 m^2 subplot at the center of each plot. At five points in each plot (center and four corners), we measured the thickness of the entire *organic* layer and its sublayers, the thickness of the *litter* layer, and the thickness of *charcoal* deposits. We described the topography of each plot by classifying the *shape* of the landform as concave, slightly concave, flat, slightly convex, or convex; and recording the *slope* and *aspect*.

Evergreen conifer seed rain index derived from QuickBird satellite data

We used high-resolution (2.4 m multispectral, 0.6 m panchromatic) QuickBird satellite data to map the basal area of evergreen conifer (EC) seed sources (BA_{source}; see Jung *et al.* (2013) for details). BA_{source} includes the basal area of surviving EC seed trees inside the burn perimeter ($BA_{residual}$), as well as EC trees outside the burn. Maps of $\mathrm{BA}_{\mathrm{source}}$ were then used to derive a spatially explicit EC seed rain index (SRI). We did not attempt to model deciduous hardwoods (DHs) seed rain, because DHs in this region are assumed to not be dispersal-limited due to their minute seeds adapted for long-distance dispersal (Nikolov & Helmisaari, 1992; Hynynen *et al.*, 2009).

The approach to mapping $\mathrm{BA}_{\mathrm{source}}$ (Jung *et al.*, 2013) relies on a training data set of *in situ* measurements of $\mathrm{BA}_{\mathrm{source}}$, comprised of the 295 seed-source plots (see 'Sampling sites' above). In each seed-source plot (14 × 14 m), we inventoried all EC trees with $\mathrm{DBH} > 10$ cm, and we estimated $\mathrm{BA}_{\mathrm{source}}[\mathrm{m}^2/\mathrm{ha}]$ as

$$\mathrm{BA}_{\mathrm{source}} = \sum_{i=1}^{N} \mathrm{BA}_i \cdot p_{\mathrm{prefire}\ i}, \tag{1}$$

where BA_i is the basal area of tree *i*, and $p_{\mathrm{prefire}\ i}$ is the probability that tree *i* recruited prefire (obtained from a statistical model based on dendrochronological and allometric data; see Appendix S4). Depending on the context, $\mathrm{BA}_{\mathrm{source}}$ may refer to ground data (Eqn (1)) or to seed-source basal area estimated from ground-calibrated QuickBird images (see below).

To map $\mathrm{BA}_{\mathrm{source}}$ across the landscape, we built a statistical model (using the Random Forest algorithm, Breiman, 2001) for $\mathrm{BA}_{\mathrm{source}}$ using 101 potential predictor variables derived from QuickBird data, including burn i.d. (equivalent to a site-level random effect); different vegetation indices (NDVI, EVI, EVI2, MSAVI); and the mean, variance, coefficient of variation, and percentiles (1st, 5th, 10th, 25th, 75th, 90th, 95th, 99th) for the panchromatic channel and all multispectral channels. An optimal subset of predictor variables was selected using a genetic algorithm to propose different combinations of predictors for the Random Forest algorithm (Jung & Zscheischler, 2013). The Random Forest algorithm requires only three parameter settings: the number of regression trees (set to 120), the minimum number of observations in each node (set to 1, determined empirically), and the number of variables used to find the split at each node (set to the recommended default of one-third the number of predictor variables).

$\mathrm{BA}_{\mathrm{source}}$ was estimated for each pixel (2.4 m) in the QuickBird scenes using the trained model. The cross-validation correlation between observed and predicted $\mathrm{BA}_{\mathrm{source}}$ was 0.53, and increased to 0.65 when 7 outliers (2.5 percent of largest absolute residuals) were removed. $\mathrm{BA}_{\mathrm{source}}$ predictions are accurate for basal areas <10 m^2/ha, but tend to saturate around 20 m^2/ha (see fig. 2 of Jung *et al.*, 2013).

To calculate the EC seed rain index (SRI) for each location in the landscape (i.e., each QuickBird pixel), we combined the maps of predicted $\mathrm{BA}_{\mathrm{source}}$ with a seed dispersal kernel $k(r)$ that provides the probability that a seed disperses a distance *r* from its source

$$k(r) = [1/((2 \cdot \pi)^{1.5} S \cdot r^2)] e^{-(\ln(r/L))^2/(2 \cdot S^2)}, \tag{2}$$

where *S* and *L* are the shape and scale parameters in the log-normal seed dispersal kernel (Greene *et al.*, 2004). Given the remoteness of our field sites, it was impractical to monitor seed traps to parameterize Eqn (2). Because dispersal kernels are not available for our study region, we used parameter values reported by Greene *et al.* (2004) for North American *Picea engelmannii* ($S = 1.14$, and $L = 43.3$). The dominant EC species in our system, *Abies sibirica* and *P. obovata*, have similar dispersal traits to *P. engelmannii* (see Table 1 and Wirth *et al.*, 2008), and we therefore expect their dispersal kernels to be similar. More generally, we expect our main conclusions are robust to errors in the dispersal kernel (see Discussion).

To calculate SRI, we use $\mathrm{BA}_{\mathrm{source}}$ as an index for seed production (Ribbens *et al.*, 1994), and we sum the kernel-based seed contributions of all pixels *j* to a given location, excluding pixels beyond a radius of 1000 m because $k(r_j)$ is negligible beyond this distance. SRI is thus a distance-weighted measure of EC basal area in the landscape surrounding a given location

$$\mathrm{SRI}(x, y) = \sum_{j: r_j < 1000\,m} \mathrm{BA}_{\mathrm{sourcej}} \cdot k(r_j), \tag{3}$$

where r_j is the distance between the location (*x*,*y*) and pixel *j*. After calculating SRI for every landscape pixel, we then scaled it from 0 to 1, with values near 0 and 1 indicating low and high expected seed rain, respectively.

Quantifying the effects of different factors on postfire regeneration

We quantified how evergreen conifer (EC) regeneration dominance and density – two key regeneration characteristics (see Box 1) – depend on a set of predictor variables related to seed dispersal and site conditions using boosted regression trees (BRT). Below, we describe the two response variables, the predictor variables (summarized in Table 3), and the BRT analysis.

Characterizing regeneration. To quantify EC regeneration dominance ($\mathrm{RD}_{\mathrm{EC}}$) in each plot, we first calculated the sum of squared heights SSH – separately for EC and DH species – as

$$\mathrm{SSH} = \sum_{i=1}^{N} \frac{h_i^2 \cdot p_{\mathrm{postfire}\ i}}{A_i}, \tag{4}$$

where *N* is the number of individuals (either EC or DH); h_i is the height of individual *i* in the plot; A_i is the sample area for individual *i*; and $p_{\mathrm{postfire}i}$ is the probability that individual *i* recruited after fire (see Appendix S4). $\mathrm{RD}_{\mathrm{EC}}$ is then calculated as

$$\mathrm{RD}_{\mathrm{EC}} = \frac{\mathrm{SSH}_{\mathrm{EC}}}{(\mathrm{SSH}_{\mathrm{EC}} + \mathrm{SSH}_{\mathrm{DH}})}. \tag{5}$$

EC regeneration density (d_{EC}) was calculated as

$$d_{\mathrm{EC}} = \sum_{i=1}^{N} \frac{p_{\mathrm{postfire}i}}{A_i}. \tag{6}$$

Because small differences in d_{EC} are expected to be ecologically important when d_{EC} is near zero, we used a $\log_{10}(d_{\mathrm{EC}} + 0.001)$-transformation to emphasize these differences in the BRT analysis (see below).

Predictor variables. SRI (Eqn 3) provides an index of EC seed rain based on the spatial distribution of EC basal area. *Stand age*, defined as the difference between the year of the data

Table 3 Summary of response and candidate predictor variables used in boosted regression tree (BRT) analysis; *n* is the number of plots where the variable was measured. Missing data for predictor variables are handled with surrogate splits within the BRT analysis (Feelders, 1999)

Category	Variable name	Range	*n*
Responses	Evergreen conifer regeneration dominance – RD_{EC} (unitless)	0.00–1.00	214
	Evergreen conifer regeneration density – d_{EC} ($1/m^2$)	0.00–11.48	233
Predictors	Evergreen conifer seed rain index – SRI (unitless)	0–1	233
	Stand age (years)	9–63	233
	Charcoal layer thickness (cm)	0.00–3.50	183
	Organic layer thickness (cm)	0.00–11.30	183
	Litter layer thickness (cm)	0.00–5.10	183
	Shape	Categorical*	224
	Slope (°)	0–18.4	186
	Aspect ($\cos(\alpha \cdot \pi/180)$)	−1 to 1	186
	Soil moisture (unitless)	1.00–5.00	161
	Soil type	Categorical†	85

*Categories: flat, slightly convex, convex, slightly concave, concave.

†Categories: brown soils, gley soils, kolluvisols, pseudo gley soils.

collection and the year of the fire, is the time available for seed dispersal, establishment, and succession. *Charcoal layer thickness*, *organic layer thickness*, and *litter layer thickness* are mean values of five measurements per plot (see 'Field Observations', above) and are indicators of fire severity. *Shape*, *slope aspect*, and *soil type* were used to characterize site conditions. We also calculated a *soil moisture index* for each plot based on the herbaceous vegetation. Each herbaceous species was assigned a 'moisture indicator value' anging from 1 to 5 (similar to Cajander, 1949; Ellenberg *et al.*, 1992; Ellenberg & Leuschner, 2010, see Appendix S6). These were weighted by fractional cover to obtain a mean moisture value per plot.

Statistical analysis with boosted regression trees (BRT). The BRT method is a flexible regression technique based on machine learning – BRT does not require *a priori* information on functional relationships (Elith *et al*., 2008). BRT analysis was executed with the gbm library (Ridgeway with contributions from others, 2013) in the R statistical software package (R development Core Team, 2013). For each of two models (one for each response variable: RD_{EC} and d_{EC}), we proceeded as follows: First, we started with the full model containing all candidate predictor variables (Table 3) with the following settings: a Gaussian error distribution, a bag fraction of 0.5, a tree complexity of 2, and a learning rate of 0.001. We used a cross-validation procedure to identify the appropriate number of trees associated with the chosen learning rate as recommended by Elith *et al.* (2008). We then used a stepwise procedure for model simplification that reduces the number of predictor variables without substantial gains of the cross-validation error. After identifying the most parsimonious models, we again estimated the optimal number of trees. We used three metrics to characterize the relative importance of the predictors in the final models: 'relative influence', 'permutation', and 'leave out'. The 'relative influence' and 'permutation' measures of variable importance characterize the sensitivity of the trained model to a predictor (Ridgeway with contributions from others, 2013) . The 'leave out' measure assesses redundancy among variables by eliminating them sequentially and quantifying the changes in predictive performance. The functional response of a BRT model to each predictor can be visualized with partial dependency plots, which show how the response variable depends on each predictor while controlling for variation in the other predictors (Friedman, 2001).

Predicting successional pathways under current and intensified fire regimes

We used the fitted BRT models to predict evergreen conifer (EC) regeneration dominance (RD_{EC}) and density (d_{EC}) in each landscape (QuickBird) pixel in each burned area. Predictions of RD_{EC} and d_{EC} were based on the value of the seed rain index (SRI) in a given pixel and assumed a stand age of 60 years; all other predictor variables were assigned their most likely values given SRI and a stand age of 60 years. We chose a stand age of 60 years because this is within the range of observations (7–63 years postfire) and because demographic data suggest that this age is sufficient to make robust predictions of successional trajectories at our site (see Appendix S5). We used predictions of RD_{EC} and d_{EC} to assign each pixel to one of three successional pathways (see Box 1 and 'Classification of successional pathways' below), which allowed us to predict the relative dominance of each successional pathway under the current fire regime (based on the actual BA_{source} map in each burned area) and under scenarios of intensified fire regimes (based on simulated BA_{source} maps; see 'Intensified fire regime scenarios' below).

Classification of successional pathways. We assigned each landscape pixel to one of three successional pathways based on predicted EC regeneration dominance (RD_{EC}) and density (d_{EC}) 60 years postfire (Box 1): 'evergreen self- replacement', 'deciduous to evergreen', and 'extended deciduous'. Locations where EC regeneration is dominant ($RD_{EC} > 0.5$) are classified as 'evergreen self-replacement'. Locations where deciduous hardwood (DH) regeneration is dominant ($RD_{EC} < 0.5$) are classified as 'deciduous to evergreen' if d_{EC} at 60 years postfire exceeds a threshold required to form a fully stocked mature EC forest, and as 'extended deciduous' if d_{EC} is below this threshold (see below for derivation of the threshold). We note that the 'extended deciduous' pathway does not necessarily imply a self-replacing DH forest (which would be impossible to verify with the available data), but merely a prolonged period of DH dominance compared to the 'deciduous to evergreen' pathway.

To determine the d_{EC} threshold to form a fully stocked mature EC forest (i.e., to distinguish the 'deciduous to evergreen' and 'extended deciduous' pathways), we inventoried six mature EC stands in our study region (>200 years) and determined the density of EC canopy trees (DBH > 15 cm) to be 0.06 ± 0.01 individuals/m^2. Therefore, we set the d_{EC} threshold as 0.05 individuals/m^2. In Discussion, we explore the validity of the above assumptions and their potential impact on our main results (see Discussion section 'Robustness of predicted shifts in successional pathways').

Intensified fire regime scenarios. To assess the influence of an intensified fire regime on successional pathways, we repeated the successional classification analysis described above, but with increased burn size (increased distances from the burn interior to seed sources at the unburned forest edge) and/or severity (decreased EC residual basal area, $BA_{residual}$). The intensified fire regime scenarios are based on the QuickBird-derived BA_{source} maps (which include $BA_{residual}$, as well as EC basal area around the unburned edge) for three burned areas (F1–F3) that differ in the degree of spatial clumping of $BA_{residual}$ (Fig. S2.1 – S2.5). For each of these burns, we separated the burned area from the unburned forest edge by manual digitization and then adjusted the burn size and $BA_{residual}$ (i.e., burn severity) as described below to create nine scenarios (three sizes × three severities) for each of the three burns (F1–F3, see Fig. 2).

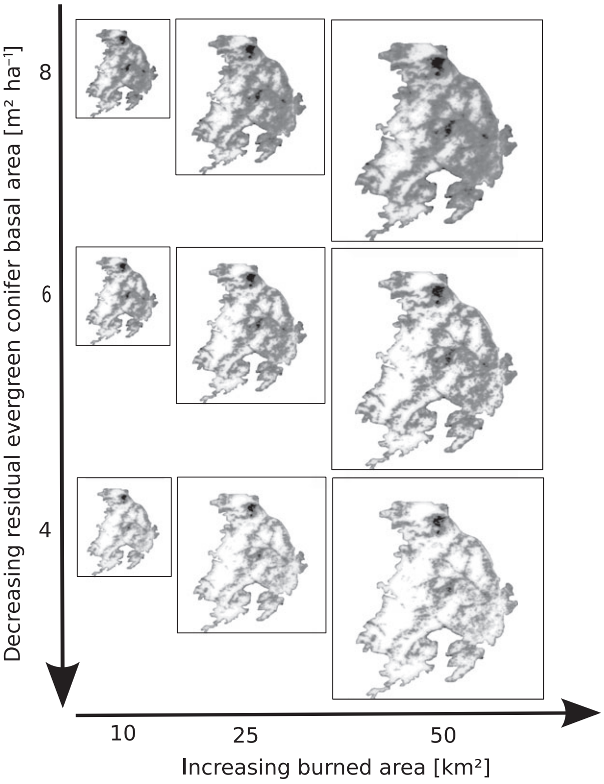


Fig. 2 Overview of the intensified fire regime scenarios, in which *burned area* was increased and the basal area of evergreen conifer (EC) seed sources (residual trees that survived the fire) decreased to reflect increased fire severity. Darker shading indicates higher residual EC basal area.

We adjusted the burn sizes (the area inside the unburned forest edge) to predefined areas A (10, 25 and 50 km^2) by adjusting the spatial resolution x of the BA_{source}-map by

$$x = \sqrt{\frac{A}{np}}, \tag{7}$$

where np is the number of pixels inside the burned area.

To represent increased burn severity, we decreased the mean $BA_{residual}$ from the observed values (about 10 m^2/ha; Table 1) to predefined, hypothetical values of 8, 6, and 4 m^2/ha. Our approach to determining the spatial distribution of $BA_{residual}$ for each target mean was motivated by the observation that some topographic positions (e.g., ravines) are unlikely to burn (Jung *et al.*, 2013) and the high vulnerability of small, thin-barked trees to fire. Thus, rather than uniformly reducing $BA_{residual}$ throughout each burned area, we reduced $BA_{residual}$ in pixels where it was already low. Specifically, we set $BA_{residual}$ of all pixels that were below a threshold pt to a background value (smallest $BA_{residual}$ predicted for any pixel in the burns we studied). We determined pt using an iterative search that matched the mean $BA_{residual}$ in each of the three burns (F1 – F3) to each predefined target basal area (8, 6, and 4 m^2/ha).

Results

Postfire regeneration patterns

Overview of regeneration patterns. Evergreen conifer (EC) regeneration dominance (RD_{EC}) and density (d_{EC}) both increased with the EC seed rain index (SRI; Fig. 3). Although RD_{EC} tended to be low (<0.5 in 93% of our regeneration plots), values ranged from zero (pure deciduous hardwood, DH) to one (pure EC), and d_{EC} was sufficient to form a fully stocked EC stand (d_{EC} > 0.05 individuals/m^2) in 80% of the 233 regeneration plots.

Factors affecting evergreen conifer regeneration dominance. The most parsimonious BRT model for RD_{EC} had a cross-validation correlation of 0.69 and included five predictor variables: SRI, soil moisture index, charcoal layer thickness, stand age, and organic layer thickness (Fig. 4). SRI was clearly the most important factor affecting RD_{EC}. Depending on the value of SRI, RD_{EC} spanned almost the full range of possible values (0–1; Fig. 4). In contrast, RD_{EC} depended only weakly on the other predictor variables (Fig. 4). SRI was the only factor capable of yielding RD_{EC} predictions above 0.5.

Factors affecting evergreen conifer regeneration density. The most parsimonious BRT model for evergreen

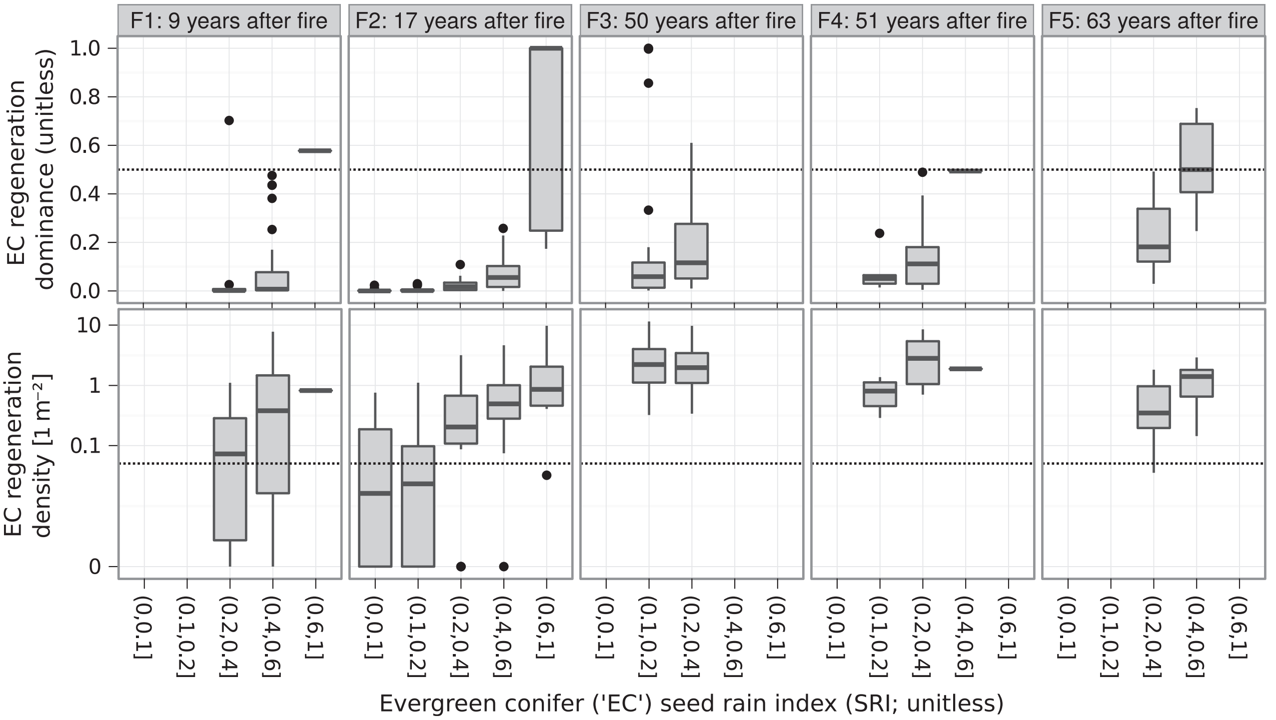


Fig. 3 Evergreen conifer (EC) regeneration dominance RD_{EC} and EC regeneration density d_{EC} in relation to the EC seed rain index SRI) in the five studied burns (F1–F5). The burns are arranged from left to right in order of increasing stand age (time since fire). RD_{EC} and SRI are unitless and are scaled from 0 to 1. Horizontal dashed lines show thresholds used to distinguish successional pathways (Box 1): $RD_{EC} > 0.5$ indicates 'evergreen self-replacement', and $d_{EC} < 0.05$ individuals/m^2 indicates 'extended deciduous'. The cohort age structure of EC regeneration is shown in Appendix S5.3, Fig. S5.3. Lines in boxes represent medians, boxes represent 25% and 75% quartiles, whiskers represent extremes up to 1.5 times the interquartile range, and circles are outliers.

regeneration density d_{EC} had a cross-validation correlation of 0.68 and included nine predictor variables: SRI, stand age, soil moisture index, shape, aspect, slope, and the thickness of the charcoal, litter, and organic layers (Fig. 5). Again, SRI was the most important predictor variable, followed by stand age (positive effect) and soil moisture (negative effect; Fig. 5). SRI was the only factor capable of reducing d_{EC} predictions below the threshold of 0.05 individuals/m^2 needed to form a fully stocked EC stand.

Current and predicted successional pathways

Current successional pathways. Based on our classification of successional pathways (Box 1) and the values of evergreen conifer (EC) regeneration dominance RD_{EC} and density d_{EC} in our regeneration plots, 74% of plots were classified as 'deciduous to evergreen', 7% as 'evergreen self-replacement', and 19% as 'extended deciduous' .

We predicted a successional pathway for each pixel in burns F1, F2, and F3 (Fig. 6) by combining the classification scheme (Box 1) with BRT model predictions of RD_{EC} and d_{EC}. 'Deciduous to evergreen' was the predicted pathway in nearly all pixels in F1 and F3, and in most pixels in F2 (Fig. 6). The 'evergreen self-replacement' and 'extended deciduous' pathways were predicted to occur where SRI was very low and very high, respectively, conditions which occurred primarily in F2 due to the high degree of spatial clumping of $BA_{residual}$. Compared to F1 and F3, F2 has intermediate stand age, small size, and similar mean $BA_{residual}$ (Table 2). Thus, the degree of clumping of $BA_{residual}$ appears to be the primary cause of differences in successional pathways among burns F1–F3, which may partially reflect the limited variation in mean $BA_{residual}$ among these three burns.

Successional pathways under intensified fire regimes. Our scenario analysis explored how fractional coverages of potential successional pathways are predicted to depend on burn size, mean residual EC basal area ($BA_{residual}$; which decreases with fire severity), and the degree of clumping of $BA_{residual}$ (which increases with topographic heterogeneity). Of the three factors, mean $BA_{residual}$ had the strongest overall effect, with a large increase in the areal coverage of the 'extended deciduous' pathway as mean $BA_{residual}$ decreased from 8 to

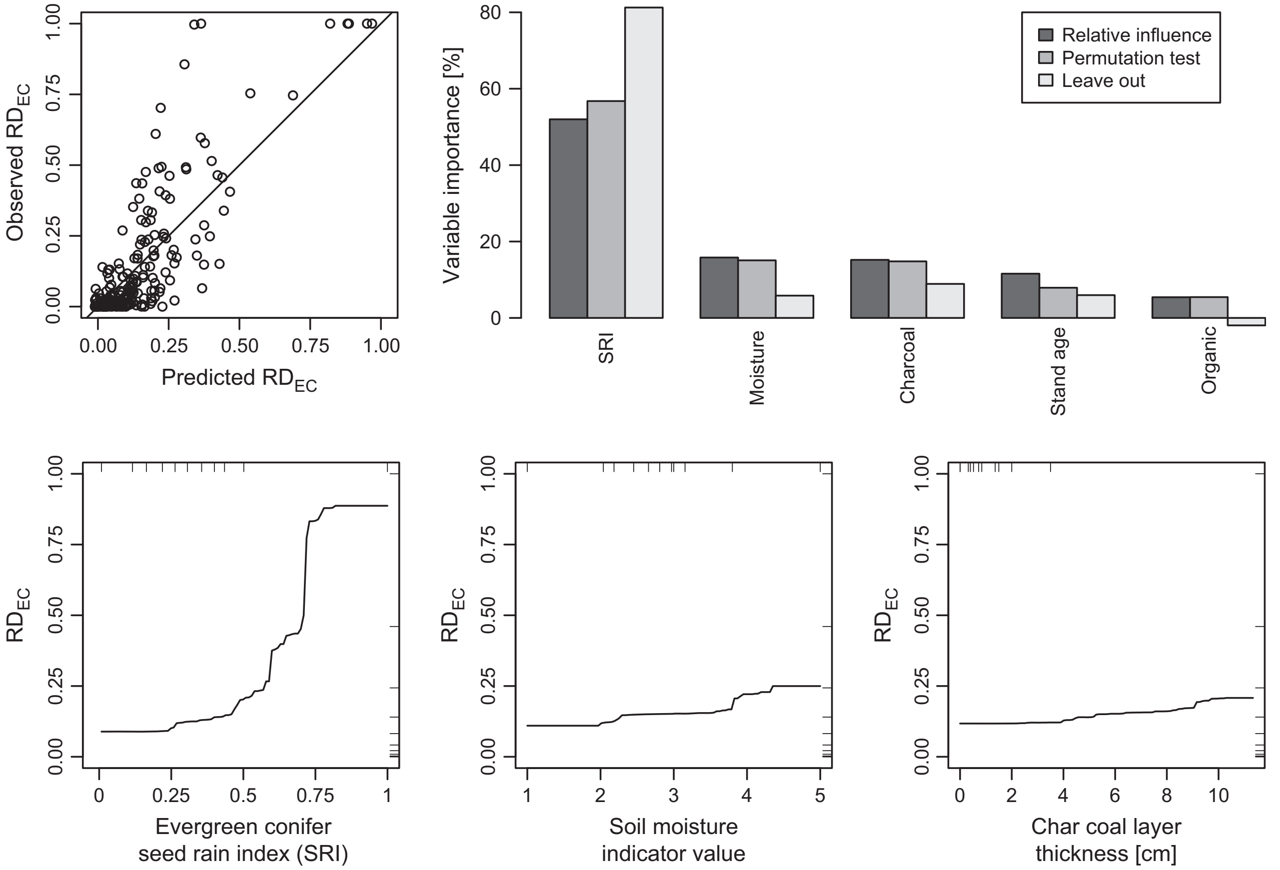


Fig. 4 Boosted regression tree (BRT) model for evergreen conifer (EC) regeneration dominance RD_{EC}. Top row: observed vs. predicted RD_{EC} and importance measures for predictor variables included in the most parsimonious model. Bottom row: partial dependency plots for the three most important predictors. Partial dependency plots show the dependence of the response variable on a given predictor variable while controlling for variation in other predictors. Tick marks along the top and right axes show decantiles of the observed data. The evergreen conifer seed rain index SRI is unitless and is scaled from 0 to 1. Partial dependency plots for all predictors are in Appendix S7.

4 m^2/ha (Fig. 7). Areal coverage of the 'deciduous to evergreen' pathway decreased and coverage of 'extended deciduous' and 'evergreen self-replacement' both increased with increasing clumping of $BA_{residual}$ (Fig. 7). This effect of $BA_{residual}$ clumping was strongest when mean $BA_{residual}$ was high (8 m^2/ha; see Fig. 7 left column), consistent with the strong effect of $BA_{residual}$ clumping under the current fire regime (Fig. 6 and Table 2: mean $BA_{residual}$ ranged from 8 to 11 m^2/ha in burns F1–F3). Finally, areal coverage of the 'extended deciduous' pathway increased with burn size, but the effect was relatively weak (Fig. 7).

Discussion

Based on a combination of *in situ* measurements, high-resolution satellite imagery, and machine-learning-based regression, our analysis shows a clear effect of dispersal limitation on postfire regeneration of evergreen conifers in the Central Siberian dark taiga – a boreal forest region where conifers are the late-successional dominants, all conifers are evergreen, and all have an 'avoider' fire-adaptation strategy (Table 1; we use the abbreviation 'EC' to refer to this group of dark taiga evergreen conifers). Under the current fire regime, our results suggest that spatial variation in the density of postfire EC seed sources (i.e., mature EC trees that survive fire) can lead to departures from the dominant 'deciduous to evergreen' successional pathway (Box 1). However, under current conditions, EC dispersal limitation that is severe enough to delay the transition from deciduous hardwood (DH) to EC dominance (typically around 120 years postfire) appears to be rare. In contrast, under scenarios of larger and/or more severe fires, our results suggest that EC dispersal limitation will become more severe, leading to an increase in the prevalence of the 'extended deciduous' pathway across the landscape and thus a shift toward greater DH

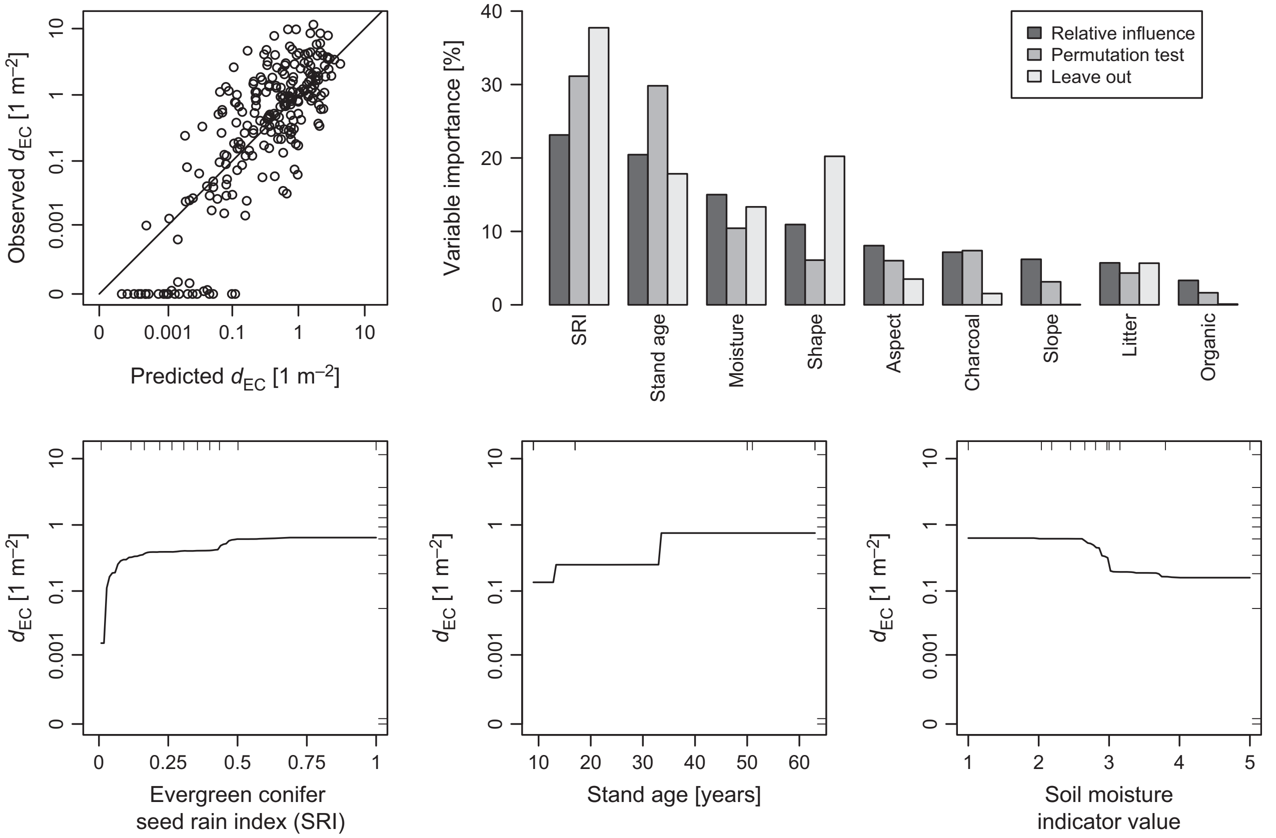


Fig. 5 Boosted regression tree (BRT) model for evergreen conifer regeneration density d_{EC}. See Fig. 4 legend for details. Partial dependency plots for all predictors are in Appendix S8.

cover. In contrast to some systems where conifers are more flammable than deciduous hardwoods (e.g., in much of boreal North America; Johnson, 1996; Hély *et al.*, 2000b) , DH forests are likely more flammable than EC forests in the Central Siberian dark taiga (see below for details). Therefore, a shift toward DH cover in this region is likely to amplify a climate-induced intensification of the fire regime.

Below, we discuss the following: the evidence supporting the above conclusions; mechanisms leading to increased DH cover at the landscape scale under an intensified fire regime; the robustness of our results; the applicability of our results to other boreal forest systems; and potential biogeochemical and biophysical implications of our results for climate–fire–vegetation feedbacks.

Factors affecting postfire regeneration

Our study suggests that in the Central Siberian dark taiga, seed dispersal limitation of evergreen conifers (EC) has a stronger effect on postfire regeneration than site conditions. Here, we review the evidence from our study for both types of effects, and we compare our results to those from other boreal systems.

Effects of site conditions on postfire regeneration. Site effects on postfire regeneration in the Central Siberian ‘avoider’-dominated forests we studied are similar in direction but weaker in magnitude compared to North American boreal ‘embracer’-dominated forests, where altered site conditions due to increasing fire severity favor DH over EC recruitment. For example, exposure of mineral soil due to combustion of the organic layer increases DH germination rate in Alaska (Johnstone & Chapin, 2006a; Johnstone *et al.*, 2010; Beck *et al.*, 2011). Similarly, a thin postfire organic layer also appears to favor DH regeneration in our Central Siberian study, as implied by a positive effect of organic layer thickness on EC regeneration dominance (RD_{EC}); however, this effect was weaker than observed in North American ‘embracer’ forests.

Charcoal layer thickness in our study showed a weak negative effect on d_{EC} and a weak positive effect on RD_{EC}. These opposing effects result from a stronger negative effect of charcoal layer thickness on DH

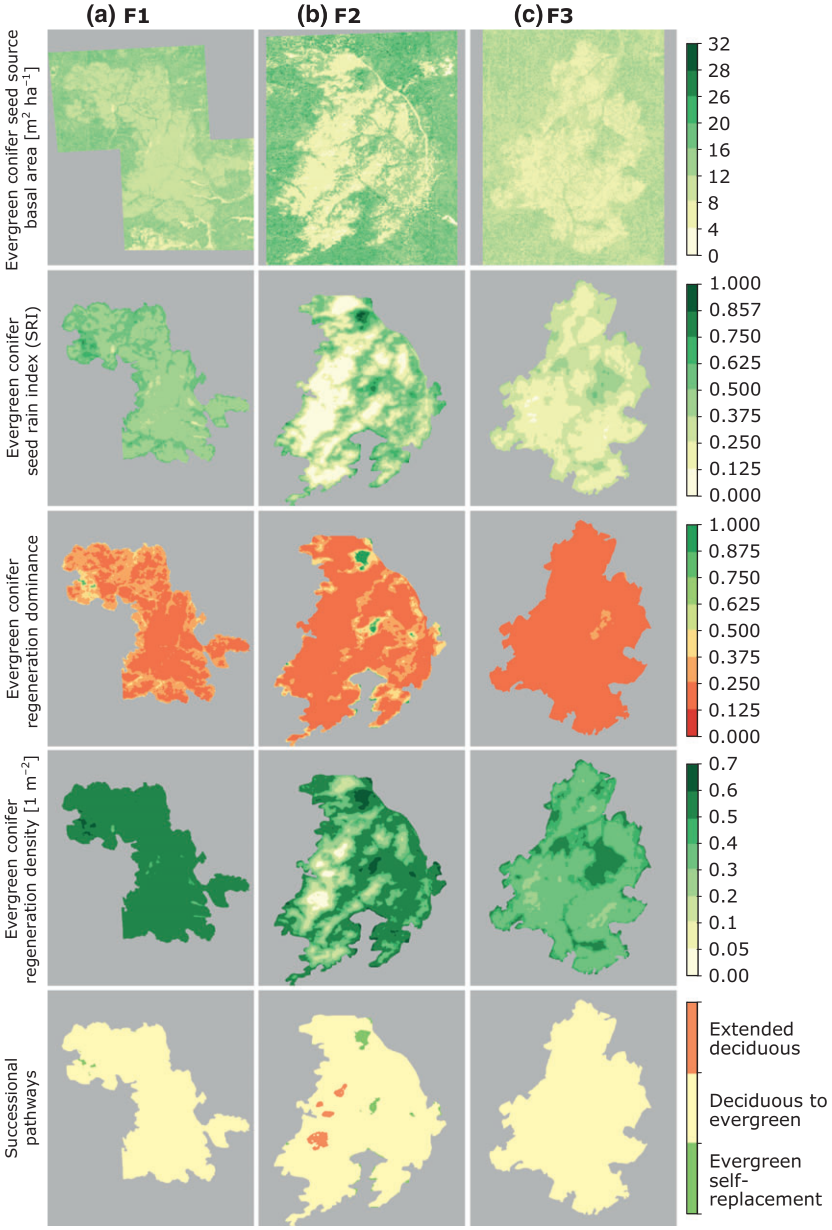


Fig. 6 Evergreen conifer (EC) seed-source basal area BA_{source} (which includes residual EC trees within the burn, as well as EC trees around the periphery of the burn), EC seed rain index SRI (unitless; scaled from 0 to 1), EC regeneration dominance RD_{EC} (unitless), EC regeneration density d_{EC}, and predicted successional pathways for three burned areas that differ in the degree of clumping of residual EC basal area: F1: 23 km^2 burned, mean BA_{source} of 11 m^2/ha with medium clumping, F2: 8 km^2 burned, mean BA_{source} of 9 m^2/ha with high clumping, F3: 9 km^2 burned, mean BA_{source} of 8 m^2/ha with low clumping. The corresponding maps for burned areas F4 and F5 are in Fig. S10.1 in Appendix S10.

regeneration density compared to EC regeneration density in combination with a negative effect of charcoal layer thickness on DH growth conditions (which could affect RD_{EC} via tree size). At present, it is unclear if the charcoal effects are due to direct effects on physical–chemical properties of the soil, or if they are actually caused by correlated factors such as fire severity or prefire soil organic matter content (which could affect both charcoal thickness and postfire regeneration).

As with charcoal layer thickness, higher values of our soil moisture index were associated with both decreased d_{EC} (perhaps due to low recruitment rates under waterlogged conditions) and increased RD_{EC} (suggesting greater tolerance of wet conditions for EC compared to DH). Consistent with our results, drier

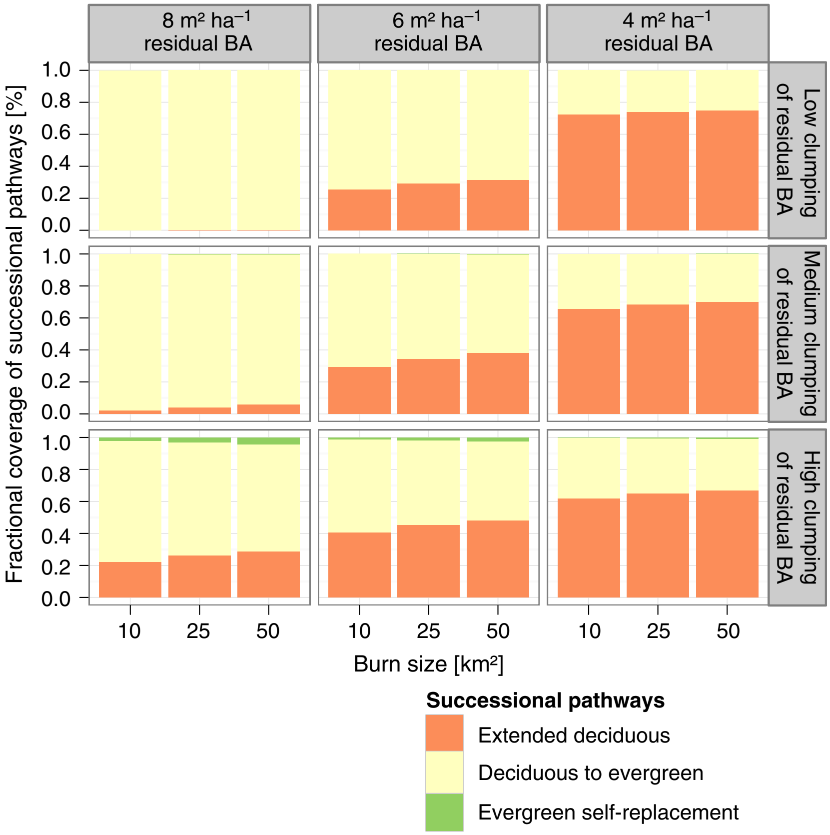


Fig. 7 Predicted successional pathways under fire regime scenarios for burn size, mean evergreen conifer (EC) residual basal area ($BA_{residual}$; which decreases with burn severity and reflects the abundance of surviving EC seed sources), and the degree of clumping of $BA_{residual}$ (reflecting topographic landscape heterogeneity; low, medium, and high levels of clumping were derived from burns F3, F1, and F2, respectively; see Fig. 6). $BA_{residual}$ decreases from left to right in the figure so that the fire regime (burn size and severity) intensifies from left to right.

soils promote DH regeneration dominance in North American 'embracer'-dominated forests (Johnstone *et al.*, 2010). However, in the Central Siberian dark taiga landscape, moisture and other site effects were weak compared to the effects of dispersal limitation on postfire EC regeneration, which we now discuss.

Effects of evergreen conifer seed availability on postfire regeneration. Evergreen conifer (EC) seed availability, and thus dispersal limitation, appears to be the main driver of EC postfire regeneration success in the Central Siberian dark taiga landscape. The primary support for this conclusion is from the boosted regression tree (BRT) analysis, which identified the EC seed rain index (SRI) as the most important predictor variable for both RD_{EC} and d_{EC} (Figs 4 and 5). Although some predictors (e.g., stand age) were correlated with SRI, no other variables could account for the information contained in SRI (see Appendix S5.4 for a detailed discussion of the temporal dynamics of postfire recruitment). Multiple factors contribute to uncertainty in SRI, including the stochastic nature of seed dispersal (Tufto *et al.*, 1997), uncertainties in applying the single dispersal kernel from Greene *et al.* (2004) to three EC species in our study area, and uncertainty in the spatial distribution of EC seed sources used to estimate SRI. Thus, errors in SRI are likely greater than errors in other, more-easily measured predictor variables (e.g., stand age and organic layer thickness). Given the potentially large errors in SRI, and given that errors in predictor variables tend to bias their estimated effects toward zero (Fuller, 1987; Lichstein et al., 2014), the relative importance of SRI inferred from our analysis is likely conservative. Therefore, our conclusion that SRI (and thus EC dispersal limitation) is a key factor controlling forest dynamics in the Central Siberian dark taiga is likely robust.

The importance of dispersal limitation for postfire recruitment of boreal conifers likely depends on characteristics of both the burn (e.g., size and severity) and the species (e.g., 'embracer', 'resister' , or 'avoider' strategy; Rowe, 1983; Wirth, 2005). Unlike the 'avoider' species that dominate Central Siberian dark taiga, 'resister' species often survive fire and are therefore unlikely to be dispersal-limited except following very severe fires with few surviving seed sources. In contrast, dispersal limitation of 'embracer' species would not be expected following large, severe burns due to their serotinous cones. For example, in British Columbia, distance to seed source appears to limit the postfire distribution of the 'avoider' *Picea glauca*, but not the 'embracer' *Picea mariana* (Albani *et al*., 2005). Similarly, the 'embracer' *Pinus contorta* had high recruitment densities in large, severe burns in Yellowstone National Park, USA (Turner *et al*., 1997). In contrast, dispersal limitation appeared to occur for the 'resister' *Larix sibirica* following severe fire in northern Mongolia (Otoda *et al*., 2012), but not for the 'resister' *Pinus sylvestris* following surface fire in Central Siberia (Tautenhahn *et al*., 2012). The role of dispersal limitation in the above studies appears consistent with our understanding of how species fire-adaptation strategies interact with burn size and severity. However, the relative roles of dispersal limitation vs. site conditions in controlling postfire recruitment in different contexts is uncertain, because few studies to date have simultaneously quantified both site and seed-source effects on postfire recruitment in boreal forests. This highlights a critical data gap in our understanding of the mechanisms controlling boreal forest responses to intensifying fire regimes.

Consequences of dispersal limitation for successional pathways under intensified fire regimes

To explore the implications of evergreen conifer (EC) dispersal limitation for potential shifts in deciduous hardwood (DH) vs. EC forest cover in Central Siberia, we estimated the landscape distribution of successional pathways under current and hypothetical future intensified fire regimes. Our classification of successional pathways is based on postfire regeneration (d_{EC} and $\mathrm{RD}_{\mathrm{EC}}$) and a conceptual model of succession in Central Siberian dark taiga (Box 1). Although the classification involves simplifying assumptions and extrapolation of regeneration patterns to later stages of succession, the main conclusions we derive from the classification appear to be qualitatively robust (see the following section on 'Robustness of predicted shifts in successional pathways').

Our results suggest that as burn size and severity increase, dispersal limitation of EC regeneration will become more prevalent and severe, because an increasing fraction of the landscape will become spatially isolated from EC seed sources. Our analysis suggests that dispersal limitation of EC regeneration under plausible future fire scenarios can substantially increase the landscape cover of the 'extended deciduous' successional pathway relative to the currently dominant 'deciduous to evergreen' pathway (Fig. 7), which implies a shift toward greater DH cover. In our analysis, increased burn severity had stronger effects than increased burn size on predicted successional pathways. This is because in the system we studied, most EC postfire regeneration appears to originate from residual seed sources (surviving EC trees) within the burn. By reducing the prevalence of these residual seed sources, increasing burn severity can have a dramatic impact on postfire regeneration and the resulting successional pathway. In addition to increased burn size and severity, an increase in fire frequency (which we did not study) would be expected to cause a further shift toward greater DH cover in Central Siberian dark taiga, as in other boreal regions (Johnstone & Chapin, 2006b; Beck *et al*., 2011). This is because DH species tend to dominate early in succession, and the fraction of the landscape in an early-successional state increases with fire frequency. Together, increased fire frequency, size, and severity have strong potential to cause a transition from EC- to DH-dominated forests in the Central Siberian dark taiga.

In addition to the main effects of an intensified fire regime on dispersal limitation and successional pathways in Central Siberia, our analysis also revealed an interaction between the fire regime and spatial clumping of EC seed sources. Within a landscape (with given vegetation, climate, and weather), the distribution of residual seed trees is largely controlled by topographic moisture effects (Duffy *et al*., 2007; Dillon *et al*., 2011). Uplands tend to be better-drained and more prone to severe fire than moist lowlands, depressions, and channels (Harden *et al*., 2000; Jung *et al*., 2013). In our study region, DH forests often occupy plateaus and ridges (Danilo Mollicone, Personal communication), where fires are likely severe and EC seed rain is likely limited by a scarcity of residual seed sources. Thus, topographically complex landscapes (high degree of seed-source clumping) contain a relatively large area where dispersal limitation of EC recruitment is severe, even under the current fire regime (Fig. 6). In contrast, topographically simple landscapes (low degree of seed-source clumping) – where severe EC dispersal limitation is rare under the current fire regime – have the lowest DH cover under current conditions and thus the greatest potential shift toward DH dominance under intensified fire regimes (Fig. 7).

Robustness of predicted shifts in successional pathways

Our discrete classification of successional pathways (Box 1) is a simplification of a more complex and continuous reality. The predicted shift toward greater prevalence of the 'extended deciduous' pathway under an intensified fire regime (Fig. 7) should thus be interpreted more broadly as a shift toward greater deciduous hardwood (DH) dominance. The robustness of this predicted shift depends on our classification method: if BRT-model-predicted EC regeneration density (d_{EC}) at 60 years postfire is above a threshold of 0.05 individuals/m^2, then a landscape pixel is classified as the 'extended deciduous' pathway, and is otherwise classified as either the 'deciduous to evergreen' or 'evergreen self-replacement' pathway (depending on the level of EC regeneration dominance; Box 1). Classification of the 'extended deciduous' pathway depends on four key assumptions, which we now examine. The first assumption is the d_{EC} threshold of 0.05 individuals/m^2. This value was chosen to be smaller than the observed mean EC tree density in mature forests (0.06 individuals/m^2), and is thus conservative with respect to predicting shifts toward greater DH cover. The second assumption is that predicted d_{EC} at 60 years postfire is accurate. The BRT-model-based classification underestimates the frequency of the 'extended deciduous' pathway relative to observations (see also Appendix S9); thus, the predicted shift toward deciduous tree cover is again conservative. The third assumption is that d_{EC} at 60 years postfire is a good indicator of EC density at 120 years postfire, when the transition to EC dominance typically occurs in the 'deciduous to evergreen' pathway (Box 1). Whether late-successional EC trees regenerate primarily as a postfire cohort (Gutsell & Johnson, 2002; Johnstone *et al.*, 2004; Schulze *et al.*, 2005; Shorohova *et al.*, 2009; Johnstone *et al.*, 2010), or later in succession via continuous regeneration (Chen *et al.*, 2009; Ilisson & Chen, 2009; Otoda *et al.*, 2012) is unclear, and may differ among boreal systems. In our study, analysis of EC age structure, using dendrochronological and biometric data collected at our sites (Appendix S5.2), suggests that continuous regeneration and mortality are roughly in balance from 60 to 120 years postfire (Fig. S5.2, Appendices S5.3 and S5.4). Thus, if d_{EC} at 60 years postfire is below the threshold to form a fully stocked EC stand, then d_{EC} would likely also be below this threshold at 120 years postfire. The fourth assumption is that the predicted successional athways are not altered by subsequent intermediate disturbances such as surface fires, wind-throw, and insect outbreaks. Insect outbreaks (which only occur further south according to Kharuk, 2009) and surface fires (for which the dark taiga is too dense and moist, Wirth, 2005) are of minor importance in the study system, and wind-throw occurs only locally (Schulze *et al.*, 2002). If the frequency or severity of these disturbances were to increase in the future, we would expect this to shift the landscape age distribution toward more early-successional stands, which should increase DH cover (Johnstone & Chapin, 2006b).

In summary, examination of the above assumptions suggests that our classification of successional pathways probably yields a conservative estimate of the increase in DH cover under intensified fire regimes. Thus, our conclusion that an intensified regime in Central Siberian dark taiga would lead to an increase in DH cover appears qualitatively robust to potential errors in our classification scheme.

Applicability of our findings to other boreal forest systems

Our main result, increasing deciduous hardwood (DH) forest cover due to increasing dispersal limitation of evergreen conifer (EC) regeneration under an intensifying regime, is not applicable to all boreal systems. Previous studies from North American 'embracer'-dominated forests (Johnstone *et al.*, 2010; Beck *et al.*, 2011) also found that an intensifying fire regime leads to increased DH cover. However, in these 'embracer' forests, the mechanism leading to increased DH cover was not EC dispersal limitation, because the dominant conifers (*Picea mariana*, *Pinus contorta*, and *Pinus banksiana*) have serotinous aerial seed banks. Rather, in these systems, intensification of the fire regime leads to increased DH cover via changing site conditions (e.g., reduced organic layer thickness). Dispersal limitation is also probably uncommon in Eurasian 'resister' communities (*Larix* spp. and *Pinus sylvestris*), where the dominant conifers tend to form self-replacing stands (Furyaev *et al.*, 2001). 'Resister' species frequently survive fire due to their thick bark and a low thermal diffusivity of the bark. Thus, there are typically sufficient residual seed trees to facilitate rapid recolonization of burned areas (Berner *et al.*, 2012; Tautenhahn *et al.*, 2012), and frequent surface fires kill non-fire-resistant species (Wirth, 2005; Schulze *et al.*, 2012). The above scenarios differ markedly from the 'avoider'-dominated dark taiga that we studied, which highlights the importance of functional composition in shaping the mechanisms and responses to intensifying fire regimes.

Although far from universal, the dispersal limitation mechanism documented in our study is in principle relevant in all boreal forest systems where late-successional stages are dominated by EC 'avoider' species with short dispersal distances. Roughly 20% of the Eurasian boreal forest area is dominated by EC 'avoider' species (129.3 Mha; Bartalev *et al.*, 2004 2011; Rogers *et al.*, 2015, see also Appendix S1), including *Picea obovata*, *Abies sibirica* and *Pinus sibirica* in the Central Siberian dark taiga, *Abies nephrolepis* and *Picea ajanensis* in the far east, *Abies alba* and *Picea abies* in Central Europe, and *Picea jezonensis* and *Abies sacchalinensis* in Japan. 'Avoider'-dominated forests also comprise about 10% of the forest area in North America (38.2 Mha; Rogers *et al.*, 2015), including *Abies lasiocarpa* and *Picea engelmanii* in the Rocky Mountains, *Abies balsamea* and *Picea glauca* in the southern North American boreal zone, and *Picea rubra* and *Abies balsamea* in the east.

Biogeochemical and biophysical implications of increasing deciduous hardwood cover

An intensifying fire regime is expected from increased fuel accumulation (due to longer growing seasons, higher temperatures, and CO^2 fertilization) and more frequent and/or severe droughts (Shvidenko *et al.*, 2013). Signs of intensifying fire regimes have already been detected in North American boreal forests and Siberia (Goetz *et al.*, 2007; Soja *et al.*, 2007; Shvidenko *et al.*, 2013).

With this intensifying fire regime, changes in boreal forest composition from evergreen conifers (EC) toward deciduous hardwoods (DH) can be expected in the future, which in turn may have multiple biogeochemical and biophysical consequences. A negative biogeochemical feedback via enhanced carbon sequestration is expected on decadal timescales because DH grow more rapidly than EC in many boreal regions (e.g. Yarie & Billings, 2002), including Central Siberia (Schulze *et al.*, 2005). On the other hand, increasing DH cover may induce positive feedbacks to climate change via reduced soil carbon storage, because DH litter decomposes faster than EC litter (Johnstone *et al.*, 2010). Although the net carbon cycle feedback is uncertain, increased DH cover – with higher albedo and more evaporative cooling than EC – should cause a negative biophysical feedback to regional warming (Bonan *et al.*, 1995; Amiro *et al.*, 2006; Randerson *et al.*, 2006; McMillan & Goulden, 2008; Rogers *et al.*, 2015). We tentatively conclude that the net feedback to climate change due to biogeochemical and biophysical effects of increasing DH cover is negative. However, this conclusion is uncertain, and further investigation of the above processes is needed. Furthermore, the above negative feedbacks may be opposed by positive fire–vegetation feedbacks in the Central Siberian dark taiga, which we now discuss.

Potential fire–vegetation feedbacks initiated by increasing deciduous hardwood cover

There is increasing recognition of strong interactions between fire regimes and species traits, where species distributions are dictated by the fire regime, which in turn is shaped by the properties of the dominant species (e.g. Wirth, 2005; Schulze *et al.*, 2012; Rogers *et al.*, 2015). In North American *Picea mariana*-dominated landscapes, an increase in deciduous hardwood (DH) cover leads to longer fire return intervals because of a lower potential for fire initiation and spread in DH forests (Hély *et al.*, 2000a; Cumming, 2001; Krawchuk *et al.*, 2006). In contrast, in Central Siberia, EC trees do not typically maintain fire-promoting ladder fuels as they do in other systems (Schulze *et al.*, 2005; Wirth, 2005). We expect that an increase in DH cover in Central Siberia could lead to increased frequency of surface fires due to drier litter and soil under the relatively open DH canopy. Such surface fires would be expected to disproportionately kill EC rather than DH saplings, because DH saplings are more resistant to surface fires in Central Siberia (Voinov & Sofronov, 1976; Kellomäki, 1987), in part due to their faster growth rates and thus larger size. Invasion by 'resister' species seems unlikely since *Pinus sylvestris* and *Larix* spp. are typically confined to sandy alluvial soils and permafrost, respectively (Wirth, 2005; Schulze *et al.*, 2012). Thus, a fire-induced shift toward DH dominance may be self-reinforcing in the dark taiga of Central Siberia. Understanding feedbacks between climate change, fire regimes, and vegetation composition in the boreal forest is an important area of research with potentially far reaching implications for regional climate and the Earth system. Our results imply an important role for seed dispersal in determining these feedbacks in 'avoider'-dominated boreal forests.

Acknowledgements

We thank Danilo Mollicone, Marina Bryukhanova, Alexey Panov, and Sergey Verkhovets for their help preparing the expeditions. This work would not have been possible without the hard work in the field of Jan Hertwig, Waldemar Ziegler, Ulrich Pruschitzki, Norman Gentsch, Luisa Hiese, Sergey Titov, Vladimir Kislitsyn, Kolya Savaronsky, and Roman Bachman. Henrik Hartmann, Angela Günther, and Corinna Höhl assisted with dendrochronological analysis. Miguel Mahecha, Jannis van Buttlar, and Ulrich Weber helped with R and the artwork. Corinna Buendia gave helpful comments on a early stage of the manuscript. We thank three anonymous reviewers for their valuable input. The project was funded by the Max Planck Society. Anatoly Prokushkin was supported by the RSF grant 14-24-00113.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Spatial distribution of fire adaption strategy types in Russia.
Appendix S2. Plot locations in the burned areas.
Appendix S3. Allometric conversion of D0, D10, and DBH into heights.
Appendix S4. Quantifying the probability that individuals recruited pre-vs. postfire.
Appendix S5. Temporal dynamics of postfire recruitment.
Appendix S6. Soil moisture indicator values for herbaceous species.
Appendix S7. Boosted regression tree (BRT) model for evergreen conifer regeneration dominance RD_{EC}.
Appendix S8. Boosted regression tree (BRT) model for the evergreen conifer regeneration density d_{EC}.
Appendix S9. Evaluation of predicted successional pathways.
Appendix S10. Maps of fire areas F4 and F5.