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Simulating dynamic fire regime and vegetation change in a warming Siberia

Neil G. Williams[1,2*], Melissa S. Lucash[1], Marc R. Ouellette[3], Thomas Brussel[1], Eric J. Gustafson[4], Shelby A. Weiss[1], Brian R. Sturtevant[4], Dmitry G. Schepaschenko[5] and Anatoly Z. Shvidenko[5]

Abstract

Background Climate change is expected to increase fire activity across the circumboreal zone, including central Siberia. However, few studies have quantitatively assessed potential changes in fire regime characteristics, or considered possible spatial variation in the magnitude of change. Moreover, while simulations indicate that changes in climate are likely to drive major shifts in Siberian vegetation, knowledge of future forest dynamics under the joint influence of changes in climate and fire regimes remains largely theoretical. We used the forest landscape model, LANDIS-II, with PnET-Succession and the BFOLDS fire extension to simulate changes in vegetation and fire regime characteristics under four alternative climate scenarios in three 10,000-km^2 study landscapes distributed across a large latitudinal gradient in lowland central Siberia. We evaluated vegetation change using the fire life history strategies adopted by forest tree species: fire resisters, fire avoiders, and fire endurers.

Results Annual burned area, the number of fires per year, fire size, and fire intensity all increased under climate change. The relative increase in fire activity was greatest in the northernmost study landscape, leading to a reduction in the difference in fire rotation period between study landscapes. Although the number of fires per year increased progressively with the magnitude of climate change, mean fire size peaked under mild or moderate climate warming in each of our study landscapes, suggesting that fuel limitations and past fire perimeters will feed back to reduce individual fire extent under extreme warming, relative to less extreme warming scenarios. In the Southern and Mid-taiga landscapes, we observed a major shift from fire resister-dominated forests to forests dominated by broadleaved deciduous fire endurers (*Betula* and *Populus* genera) under moderate and extreme climate warming scenarios, likely associated with the substantial increase in fire activity. These changes were accompanied by a major decrease in average cohort age and total vegetation biomass across the simulation landscapes.

Conclusions Our results imply that climate change will greatly increase fire activity and reduce spatial heterogeneity in fire regime characteristics across central Siberia. Potential ecological consequences include a widespread shift toward forests dominated by broadleaved deciduous species that employ a fire endurer strategy to persist in an increasingly fire-prone environment.

Keywords BFOLDS, Climate change, Fire activity, Fire adaptations, Fire regimes, Forest dynamics, LANDIS-II, Siberia

*Correspondence:
Neil G. Williams
neil.williams2@usda.gov
Full list of author information is available at the end of the article

Resumen

Antecedentes Se espera que el cambio climático incremente la actividad de incendios en toda la zona circumboreal, incluyendo la Siberia central. Sin embargo, pocos estudios han determinado cuantitativamente los cambios potenciales en las características de los regímenes de fuegos, o la posible variación en la magnitud de esos cambios. Además, mientras que las simulaciones indican que los cambios en el clima probablemente van a producir variaciones en la vegetación de Siberia, el conocimiento de la dinámica futura de esos bosques bajo la influencia conjunta de cambios en el clima y regímenes de fuegos permanece largamente en la especulación teórica. Usamos el modelo de paisajes de bosques (LANDIS-II, con sucesiones PnET y el módulo de extensión de fuegos BFOLDS), para simular cambios en la vegetación y en las características de los regímenes de fuego, bajo cuatro escenarios alternativos de clima futuro, en tres paisajes de 10 mil km2 distribuidos a lo largo de un gradiente latitudinal en las áreas bajas de Siberia. Consideramos los cambios en la vegetación basados en las estrategias de historias de fuego adoptadas por tres especies: resistentes, evasoras, y tolerantes al fuego.

Resultados Tanto el área anual quemada, el número de incendios por año, como el tamaño e intensidad de los incendios se incrementaron con las proyecciones del cambio climático. El incremento relativo en la actividad de los incendios fue mayor en el paisaje ubicado más al norte en nuestro estudio, llevando a una reducción en la diferencia en el período de rotación de los incendios entre los paisajes en estudio. Aunque el número de incendios por año se incrementó progresivamente con la magnitud del cambio climático, el tamaño medio de los incendios llegó a su pico máximo en condiciones de cambio climático (i.e. aumento en la temperatura) de leve a moderado en cada uno de nuestros paisajes de estudio, sugiriendo que las limitaciones en el combustible y los perímetros de fuegos pasados se retroalimentan para reducir la extensión de cada incendio en particular, bajo calentamientos extremos, comparados con un calentamiento menos extremo. Observamos un cambio mayor desde bosques dominados por árboles deciduos de hoja ancha tolerantes al fuego (géneros Betula y Populus) en la zona sur y Taiga intermedia bajo un incremento medio o extremo de temperaturas, asociados probablemente con un aumento substancial en la actividad de los incendios. Estos cambios fueron acompañados por un decremento mayor a nivel de edad de las cohortes y en la vegetación total a escala de paisaje.

Conclusiones Nuestros resultados implican que el cambio climático va a incrementar la actividad de los incendios y reducir la heterogeneidad espacial en regímenes de fuego característicos a lo largo y ancho de Siberia. Las consecuencias ecológicas potenciales incluyen un amplio cambio hacia bosques dominados por especies deciduas de hoja ancha tolerantes al fuego, y que emplean una estrategia de tolerancia para persistir en un ambiente progresivamente proclive al fuego.

Background

Fire is a primary control on ecosystem structure and species distribution in the boreal forests of Eurasia (e.g., Nikolov and Helmisaari 1992; Shvidenko and Nilsson 2000 and 2002; Sofronov and Volokitina 2010). Burn frequency, intensity, and behavior influence stand density (Wirth et al. 1999; Ivanova et al. 2017), biomass distribution (Kukavskaya et al. 2014; Ivanova et al. 2020), and soil surface and sub-surface properties (Yevdokimenko 2011; Knorre et al. 2018), modifying the competitive environment and redirecting stand dynamics and long-term succession (Schulze et al. 2005; Shorohova et al. 2009). At larger spatial scales, geographic variability in fire regime characteristics (the frequency, intensity, variability, size, severity, and normative behavior of fires, and the variability in these attributes) interacts with climatic, edaphic, and topographic factors to drive variability in forest type and species composition across Siberia (Wirth et al., 2005; Kharuk et al. 2021). Over long timeframes, changes in vegetation biomass and composition as a direct and indirect (i.e., disturbance-mediated) result of climate change may ultimately feed back to regulate fire regimes (Johnstone et al. 2010a; Parks et al. 2016a). Understanding these relationships between climate, fire regimes, and vegetation is critical to predicting future vegetation dynamics and potential land cover change across the vast circumpolar territories of the northern hemisphere. Such understanding contributes to efforts to mitigate the adverse effects of climate warming on Siberian ecosystems and can be used to improve the land cover inputs to global climate models.

In central Siberia (around 100° E) (Fig. 1), a pronounced north–south gradient in fire activity influences spatial patterns of fire regime characteristics and signals a path for potential fire regime (and vegetation) change over the twenty-first century (Kharuk et al. 2008a; Kharuk & Ponomarev 2017). Substantial variation in solar insolation and ambient air temperature from the northern limit of closed larch (*Larix spp.*) forests (~71° N) to the lowland southern taiga (~50° N) contribute

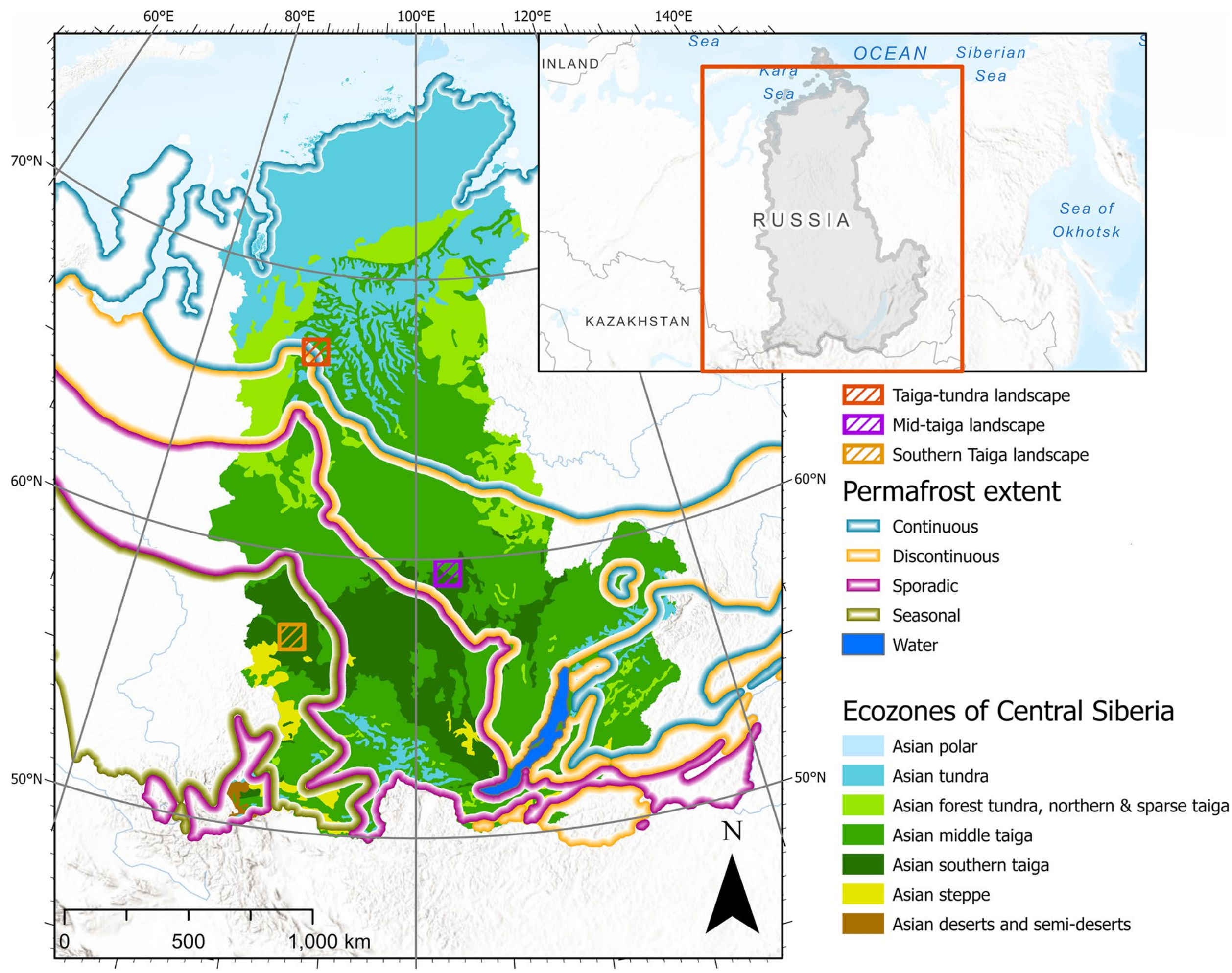

Fig. 1 Location of the Tundra-taiga, Mid-taiga, and Southern taiga study landscapes in central Siberia (demarcated by a gray polygon in the inset map, and covered by ecozones in the main map)

to a generalized increase in fire season length, annual burned area and the number of annual fires from north to south, and a consequent reduction in fire return interval over this space (Ponomarev et al. 2016; Kharuk & Ponomarev 2017). Areas of higher elevation complicate this generalized picture, inducing climate and weather patterns that affect fire probability and plant community composition and structure (Kharuk, et al. 2008b, 2021; Tchebakova et al. 2011). Recent climate warming—and its effect on fuel moisture—is thought to be a driver of increasing fire activity and its release of CO_2 (Shvidenko & Schepaschenko 2013; Ponomarev et al. 2021), as well as a longer fire season (Kirillina et al. 2020). As the climate continues to warm, increasingly hazardous fire weather and fuel moisture levels (Groisman et al. 2007; de Groot, et al. 2013a) and elevated lightning rates (Chen et al. 2021) suggest that weather, fuel conditions, and the supply of ignitions will all become more conducive to fire activity. The effect of these changes may be most evident in northern Siberia, where the pace of climate warming is greatest (IPCC 2021), and fire regimes are dominantly lightning-driven and ignition-limited (Kharuk et al. 2021). Together, these observations imply that fire regime characteristics in northern Siberia may begin to converge with those further south, with consequences for ecosystem structure and composition.

Although tree species diversity in central Siberia is relatively low, the species that are present display diverging life history strategies for persistence in a fire-prone landscape (Wirth 2005). Larch and Scots pine (*Pinus sylvestris*), pyrophilic species that are dominant across 45% and 13% of forestland in Siberia (sensu (Kharuk et al. 2021)), respectively, are highly fire-tolerant due to their thick bark and branch-pruning habit (Nikolov and Helmisaari 1992; Wirth 2005; McRae et al. 2006; Kharuk et al. 2021). These species (also known as “light” conifers) function as "fire resisters" (Wirth 2005; Rogers et al. 2015)—i.e., they are capable of surviving surface fires of low to moderate (larger individuals) intensity relatively unscathed (Rowe 1983; Agee 1993; Wirth 2005)—and on sites not underlain by permafrost, typically experience moderately to highly frequent, low- to moderate-severity surface fires (Ivanova et al. 2010; Kharuk & Ponomarev 2017; Ponomarev et al. 2021). By contrast, the "dark conifers", Siberian fir (*Abies sibirica*), Siberian pine (*Pinus sibirica*), and Siberian spruce (*Picea obovata*) (collectively dominant on 12% of forestland) are thin-barked species with dense, flammable foliage (Wirth 2005; Kharuk et al. 2021). These "fire avoiders"—species that have little to no adaptation to fire and are readily killed by low-intensity burns (Rowe 1983; Agee 1993; Wirth 2005)—occur in areas experiencing fire infrequently, but such fires are often high-severity, stand-replacing events (Wirth 2005; Rogers et al. 2015). Broadleaved deciduous species in the birch (*Betula*) and *Populus* genera (12% of Siberian forests, Kharuk et al. (2021)) are similarly intolerant of fire, but able to resprout and disperse large volumes of seed over long distances, helping them persist in (a "fire endurer" strategy) and rapidly recolonize burned areas—rapid recolonization of burned sites has also been described as a "fire invader" strategy, but we use "fire endurer" here as *Betula* and *Populus* employ both of these strategies to varying degree (Rowe 1983; Agee 1993; Wirth 2005; Rogers et al. 2015). Given the influence of fire on the current distribution of these three "fire response groups," changes in fire regimes over the twenty-first century are likely to alter the spatial distribution of fire resisters, fire avoiders, and fire endurers.

Increasing fire activity in a warmer climate strengthens the competitive advantage of fire resisters but may present recruitment challenges for even these fire-adapted species in the southern taiga. Larch dominance across much of southcentral Siberia is substantially maintained by fire, without which shade-tolerant fire avoider species—Siberian fir and Siberian spruce, in particular—can eventually replace it on sites with sufficient soil moisture (Kharuk et al. 2005; Shorohova et al. 2009; Schulze et al. 2012). Modeling of future species distributions with and without fire supports this assessment (Shuman et al. 2017). However, increasing fire frequency in forests dominated by the fire resister, Scots pine—a species that is often found on xeric sites with the highest fire frequencies in Siberia (Kharuk et al. 2021)—is already a cause of regeneration failure in parts of southcentral and southeastern Siberia (Kukavskaya et al. 2013, 2016). This increased fire frequency has been implicated as a driver of projected Scots pine range contraction under extreme climate warming (Sannikov et al. 2020) and may induce transitions from forests dominated by fire resisters in southern Siberia to steppe communities dominated by grasses (Tchebakova et al. 2009; Kukavskaya et al. 2016). Such transitions are particularly likely following high-intensity fires on sites that experience moisture deficits during critical periods of the growing season (Chu et al. 2017; Shvetsov et al. 2019; Barrett et al. 2020). In such settings, disturbance acts as a catalyst for transition to vegetation types better adapted to future climate (Gustafson et al. 2010; Halofsky et al. 2020).

At higher latitudes, climate warming may instead increase the growth and survival of fire avoider species (Tchebakova et al. 2016). Fire-avoiding conifers in the mid- and northern taiga of central Siberia have lower cold tolerance than larch and lack physiological adaptations to survive in the continuous permafrost zone, reducing their competitiveness (e.g., Kharuk et al. 2005, 2021; Wirth 2005; Tchebakova et al. 2011). However, increasing regeneration of fire avoiders in northcentral Siberia (Kharuk et al. 2005) and at upper treelines in southcentral Siberia (Kharuk et al. 2009; Petrov et al. 2019) suggest that warmer conditions and permafrost thaw over the twenty-first century will facilitate the expansion of fire avoiders, especially Siberian pine. This is most likely along river drainages, where the deeper soil active layer, additional moisture, and shelter from desiccating winds increase the competitiveness of fire avoiders (Kharuk et al. 2005). However, the extent to which the expansion of suitable habitat for fire avoiders will offset mortality from concomitant increases in fire activity remains unclear.

Even more uncertain is the potential influence of changes in climate and fire regimes on fire endurer species (for example, silver birch (*Betula pendula*) and Eurasian aspen (*Populus tremula*)) in central Siberia. In contrast to boreal North American forests (e.g., Johnstone et al. 2010b), future changes in deciduous hardwood extent and biomass in central Siberia are little studied. A warmer climate may increase competitiveness at the northern edge of the present-day fire endurer distribution (Kharuk et al. 2014), but may also reduce competitiveness in southern Siberia if higher temperatures increase moisture stress (Brédoire et al. 2020). In Alaska, increasing fire frequency may substantially increase deciduous hardwood presence (Mack et al. 2021), but there is a need for additional research to ascertain the likelihood of similar changes in Siberia.

Simulation models provide a means of identifying possible changes in fire regimes and vegetation under climate change, but a major challenge in central Siberia is scaling these effects from forest stands to vast landscapes, while also accounting for mechanistic ecosystem responses to the novel future conditions (Gustafson et al. 2010; Puettmann 2021). Previous studies have effectively coupled forest gap models with simulation of fire effects to identify changes in species biomass and structure across Siberia at coarse (> 20 km) spatial resolution (Shuman et al. 2017), or have implemented bioclimatic models in combination with fire weather metrics to estimate future climatic envelopes and fire potential under alternative climate change scenarios (Tchebakova et al. 2009). These studies do not, however, provide quantitative projections of future fire regime characteristics. Additional studies are required to characterize changes in fire regimes as the climate warms and to evaluate future vegetation demographic responses to these changes while accounting for the direct (e.g., warming, CO_2 enhancement) and indirect (e.g., permafrost thaw) effects of climate change on vegetation.

To this end, we simulated fire regime characteristics and plant fire response group dominance under climate change in central Siberia using the LANDIS-II forest landscape model. LANDIS-II is well-suited to exploring vegetation responses to climate change and disturbance, by permitting differential physiological responses to change as a result of interactions between unique combinations of plant functional traits, changes in resource availability, and disturbances (Lucash et al. 2018; Serra-Diaz et al. 2018). Spatial interactions between cells in a landscape is possible via physical processes such as seed dispersal, and disturbance propagation between cells. These attributes enable realistic characterization of vegetation and allow for emergent responses to change, which is a major advantage when investigating the unknowns presented by global change phenomena (Puettmann 2011; Gustafson 2013).

We focused on three 10,000-km^2 study landscapes spanning a broad (12°) latitudinal and vegetation gradient, but all representing lowland biophysical settings. Fire regimes and forest dynamics were simulated from 2015 to 2099 under four alternative climate scenarios representing mild to extreme warming (plus a contemporary climate baseline scenario). Our specific research hypotheses were as follows:

1. Annual burned area, maximum fire size, the number of fires per year, and average fire intensity will increase, and fire rotation period will decrease in all study landscapes as the magnitude of climate warming scenario increases.
2. Changes in fire regime characteristics (hypothesis (1)) will be most pronounced in the northernmost study landscape because the rate of climate warming and the relative increase in fuel availability will be greatest at higher northern latitudes.
3. The relative importance (i.e., the contribution to total vegetation abundance and biomass, defined in the "Vegetation" section of the "Methods" section) of fire avoider species will:
   a. Increase through time in the northernmost study landscape as the beneficial effect of climate warming to tree growth outweighs fire-induced mortality.
   b. Decrease through time in the southernmost landscape as more frequent fire reduces opportunities for late-successional (fire avoider) species to gain dominance.
4. The relative importance of fire resister species will increase in southern landscapes, as the competitive advantage of high fire tolerance outweighs increased fire-induced mortality.
5. The relative importance of fire endurer species will decrease in the southernmost study landscape due to increasing moisture limitations, but remain constant or increase in other landscapes as climate warming increases competitiveness.
6. Average cohort age and age-class diversity will decrease across southern landscapes as a consequence of more frequent, high-severity fire.

Methods

Study sites

Our three study landscapes—"Taiga-tundra," "Mid-taiga," and "Southern taiga"—are located in the Russian territory of Krasnoyarsk Krai (a small portion of the Mid-taiga landscape falls within Irkutsk Oblast). We chose locations situated in ecotones between biomes to capture a broad range of fire-vegetation relationships and facilitate the identification of climate change-induced ecosystem transitions for a companion study (Brussel et al., Assessing Siberia's response to global change through the lens of tipping points, in preparation) (Fig. 1). Specific landscape locations were identified using a data-driven approach that incorporated expert opinion. While the approach was not fully randomized, it ensures that our study landscapes are representative of a broad range of climate, permafrost continuity, ecosystem composition, and fire regime characteristics found in central Siberia (Table 1).

Gradients in elevation between and within each study landscape were intentionally minimized during the site selection process to limit the confounding influence of elevation on plant community composition (Kharuk et al. 2005, 2009).

Climate data that was used in simulations under a historical (baseline) climate, obtained from the Global Soil Wetness Project Phase 3 (GSWP3) dataset (Dirmeyer et al. 2006) (Sect. 2.5.1), was summarized for the period 1980–2014 to provide annual mean values averaged across each study landscape. Climate in all study landscapes is strongly continental (Table 2), becoming progressively

Table 1 Biophysical characteristics for the Taiga-tundra, Mid-taiga, and Southern taiga study landscapes in central Siberia. Dominant plant species are depicted as the post-calibration "initial community" map inputs to LANDIS-II

Landscape	Elevation, mean/ standard deviation (m)	Permafrost condition	Bioclimatic zone	Dominant landcover types	Dominant tree species (simulation year 0) (% biomass)
Taiga-tundra	361/180	continuous – discontinuous transition	Mid-taiga–northern taiga–tundra transition	Shrubland, forestland, open woodland, grass/herb cover	*Larix* spp. (47)*, Picea obovata* (27), *Pinus Sibirica* (10)
Mid-taiga	354/40	discontinuous	Southern taiga–mid-taiga transition	Forestland, grassland, burned area	*Pinus sylvestris* (38), *Larix* spp. (31), Abies sibirica (11)
Southern Taiga	252/44	seasonal	Southern taiga, minor steppe	Forestland, agricultural land, grassland	*Picea obovata* (23), *Betula pendula* (22), *Pinus sylvestris* (21), *Populus tremula* (12)

Table 2 Average annual climate statistics (1980–2015) for the Taiga-tundra, Mid-taiga, and Southern taiga study landscapes in central Siberia

Landscape	Mean Jan. min. temp.[a] (°C)	Mean Jan. max. temp. (°C)	Mean July min. temp. (°C)	Mean July max. temp. (°C)	Mean annual temp. (°C)	Total annual ppt.[b] (mm)	Mean annual rh[c] (%)
Taiga-tundra	−33.17	−26.63	7.42	17.69	−9.72	649.29	59.00
Mid-taiga	−28.63	−15.17	12.31	24.46	−4.87	381.42	55.69
Southern taiga	−33.92	−13.78	9.82	24.55	0.44	516.50	51.77

[a] Temperature

[b] Total precipitation,

[c] Relative humidity

warmer from the north (Taiga-tundra landscape) to south (Southern taiga landscape) (Dirmeyer et al. 2006). By contrast, total annual precipitation generally decreases from west to east and was lowest in the Mid-taiga landscape.

Although all study landscapes shared a common set of tree species at the start of simulations, the relative dominance of these species varied widely between landscapes (Table 1). Fire resisters were the dominant fire response group in the Taiga-tundra and Mid-taiga landscapes, by biomass, while in the Southern taiga fire endurers, fire avoiders, and fire resisters accounted for similar proportions of total landscape vegetation biomass (see Table 1 for species dominance and Table 4 for fire response group composition). Woody shrubs (*Alnus fruticosa*, *Betula nana*, and *Salix spp.*) are important seral and riparian forest species in central Siberia, but made up a small proportion of total landscape aboveground biomass. At the start of simulations, this vegetation type was only widespread in the Taiga-tundra landscape, where a shallow active layer (seasonally thawed surface permafrost) creates perennially wet conditions. Non-woody ground vegetation can play an important role in fire spread and related successional trajectories in boreal systems (Johnstone et al. 2010a; Volokitina et al. 2021), and, in these landscapes, included herbs, forbs, lichens, feather mosses, and sphagnum. This ground vegetation was a particularly important component of the Taiga-tundra landscape, where open forest and herb and moss-dominated systems were dominant land cover types, by extent, at the start of simulations.

Observed fire regime characteristics in these study landscapes are largely consistent with the latitudinal trends in fire activity described by Kharuk et al. (2021) (Table 3). Historic fire occurrence in our study landscapes was derived from the *Global Fire Atlas* (Andela et al. 2019), while fire severity (assessed using dNBR) was calculated from the *Fire Intensity and Burn Severity Metrics for Circumpolar Boreal Forests, 2001–2013*, dataset (Rogers et al. 2015). Over the 2003–2016 observational period, annual burned area and the number of fires per year were highest in the Southern taiga landscape (mean annual burned area of 16,232 ha) and lowest in the Taiga-tundra landscape (mean annual burned area of 1101 ha). For context, remote sensing-derived estimates of fire activity across Siberia (defined sensu Ponomarev et al. 2021 to exclude the Russian Far East) put the mean annual burned area at approximately 16×10^6 ha for the 2016–2020 period. Approximately 60% of total annual Siberian burned area occurs on forested land (Kharuk et al. 2021), the majority of this

Table 3 Historic fire regime characteristics for the Taiga-tundra, Mid-taiga, and Southern taiga study landscapes. All characteristics except fire severity (see footnote) are calculated from the Global Fire Atlas (Andela et al. 2019) for the period 2003–2016

Landscape	Annual burned area (ha)	Av. number of fires per year	Av. fire size (ha)	Max. fire size (ha)	Fire rotation period (years)	Fire severity (dNBR)[a]
Taiga-tundra	1101	2	236	32,134	908	0.1
Mid-taiga	7749	12	627	30,205	129	0.14
Southern taiga	16,232	61	265	14,920	61	0.02

[a] dNBR represents the spatial mean across each landscape from the gridded *Fire Intensity and Burn Severity Metrics for Circumpolar Boreal Forests, 2001–2013* (Rogers et al. 2017) dataset. Minimum and maximum dNBR values across the circumpolar region recorded in this dataset are – 0.5 and 0.8, respectively, with higher dNBR values indicating higher burn severity (and hence, higher vegetation mortality)

Table 4 Fuel type classification supplied to the Dynamic Fuels System and BFOLDS LANDIS-II extensions for simulations in three central Siberian study landscapes for the period 2015–2099

Surface fuel type	Description	Species[a]	Age range (years)	Fire intensity-mortality threshold (kW m^{-1})	Key literature
C-2	Young fire avoiders	ABSI, PIOB, PISI	0–40	400	(Alexander et al. 1991; Wirth 2005; Fryer 2014; Miquelajauregui et al. 2016)
C-2	Mature and old fire avoiders	ABSI, PIOB, PISI	41–280	1500	
C-4	Young fire resisters	LASP, PISY	0–40	700	(Ivanova et al. 2020; Kukavskaya et al. 2014; McRae et al. 2005; Wirth 2005)
C-7	Mature and old fire resisters	LASP, PISY	41–300	5000	
D-1	Young fire endurers	BESP, POTR	0–30	200	(Quintilo et al. 1991; Uchytil 1991; Howard, 1996)
D-1	Mature and old fire endurers	BESP, POTR	31–120	700	
D-1	Shrub fire endurers	ALFR, BENA, SASP	0–120	400	(Quintilo et al. 1991; Tollefson 2007)
O-1a	Ground layer fire avoiders (wet-mesic)	Sphagnum moss	0–220	1000	(Kharuk et al. 2021; Kidnie et al. 2010; Volokitina et al., 2021)
O-1b	Ground layer fire endurers (dry-mesic)	Grass and herbs	0–200	100	

[a] Species acronyms: ABSI, *Abies sibirica*; ALFR, *Alnus fruticosa*; BENA, *Betula nana*; BESP, *Betula tree* spp.; LASP, *Larix* spp.; PIOB, *Picea obovata*; PISI, *Pinus sibirica*; PISY, *Pinus sylvestris*; POTR, *Populus tremula*

in forests dominated by larch species (Larix spp) (Krylov et al. 2014; Ponomarev et al. 2021). Also consistent with Siberia-wide fire regime characteristics, maximum historic fire size in our study landscapes was highest in the northernmost landscape, and lowest in the southernmost (Kharuk et al. 2021; Ponomarev et al. 2021). Mean dNBR estimates for our study landscapes are lower than those derived for Eurasia as a whole or for individual forest types in Eurasia (Rogers et al. 2015) and are toward the lower end of the dNBR range in a recent study of fires in Siberia during 2021 (Ponomarev et al., 2022)). However, differences in the spatial scale at which these dNBR values were obtained—values presented for our study landscapes were obtained from a relatively coarse 0.25 degree pixel resolution data product—limit comparability of dNBR calculated for our study landscapes with values from other studies.

LANDIS-II model description

We used the forest landscape model, LANDIS-II (v. 7.0), a process-based simulation environment in which model landscapes are composed of square cells of a user-defined size, wherein vegetation is represented by species-age cohorts rather than individual stems (Scheller et al. 2007). Succession and disturbance are simulated using a wide range of optional "extensions" (modules) to the LANDIS-II core, while deterministic climate change scenarios can be accommodated via a Climate Library (Lucash and Scheller 2021) that supplies and synchronizes climate inputs across all extensions in a given simulation.

Spatial variation in the abiotic environment is approximated via "ecoregions" representing areas of homogenous climate and site characteristics, factors that may also influence the transmission of disturbances and biological responses to these stressors.

In this study, we paired the LANDIS-II v 7.0 core model with PnET Succession v 5.0 (Gustafson and Miranda 2022), while fire was simulated using BFOLDS v 2.1 (Perera et al. 2014; Ouellette et al., BFOLDS Fire Regime Module v2.1 User Guide for LANDIS-II Extension, in preparation) and Dynamic Fuel System v3.0 (Sturtevant et al. 2009). Model outputs were produced using the Biomass Community v 2.0 (Scheller 2020), Output Biomass Reclass v 3.0 (Scheller & Domingo 2020), and Output PnET v 5.0 (Gustafson and Miranda 2022) extensions.

LANDIS-II model description: PnET-Succession extension

The PnET-Succession extension simulates vegetation establishment, growth, competition, and mortality. PnET-Succession uses physiological first-principles to model cohort growth as a competition for light and water and is particularly suited to simulations that incorporate climate change by virtue of its direct, process-based simulation of photosynthesis in response to available light and soil moisture, temperature, and atmospheric carbon dioxide concentrations (Gustafson & Miranda., 2022).

In PnET, vegetation responses to environmental drivers are scaled from leaves to landscape grid cells using a “big-leaf” approach (Aber et al. 1992). The cohorts on each grid cell each have a dynamic biomass density of foliage, subdivided into vertically stacked sublayers, each of which is conceptualized as a single “big leaf” representing cohort foliage. Photosynthesis is simulated for each sublayer (leaf), accounting for light attenuation and water availability, and the fixed carbon is allocated to cohort pools of wood, root, and reserves. Cohort productivity is determined by foliar nitrogen (Aber et al. 1983). Stress associated with lack of resources is dynamically simulated based on available light and water, and species-specific tolerances to shade, temperature, and moisture shortages or overabundance (waterlogging) (Gustafson & Miranda 2022). A “bucket” model is used to simulate soil water balance based on incoming precipitation, interception, percolation, runoff, and permafrost effects on soil hydrology (Gustafson & Miranda 2022). Soil water balance is computed dynamically (monthly), enabling responsive growth, survival, and mortality pathways among vegetation present on site. Tree species-age cohorts compete for water and light resources. Competitive interactions among cohorts within and between cells, and direct linkages with the abiotic environment, enable the propagation of fine-scale processes to drive community change at large spatial scales.

New cohorts establish on sites through the interaction of site conditions—notably light and moisture availability—with physiologically based establishment probabilities and seed rain from neighboring cells. Seeds are produced annually from cohorts of reproductive age, with dispersal distance controlled by species-level input parameters. Model parameters are also used to describe the capacity of individual species for establishment via seeding, resprouting, or serotiny. This is particularly relevant to regeneration following disturbance, such as fire, which is modeled according to species physiological traits with respect to seed dispersal and establishment mechanisms.

LANDIS-II model description: BFOLDS fire extension

We used the BFOLDS (Boreal Forest Landscape Dynamics Simulator) v2.1 (Perera et al. 2014: Ouellette et al., BFOLDS Fire Regime Module v2.1 User Guide for LANDIS-II Extension, in preparation) and Dynamic Fuel System v 3.0 (Sturtevant et al. 2009) extensions to simulate wildfire processes.

BFOLDS incorporates core fire spread and fuel classification concepts from the Canadian Fire Behavior Prediction system (CFBP) (Forestry Canada, 1992) in a mechanistic framework that does not constrain fire dynamics to a predefined range of tolerable outcomes. Fire ignition, spread, and extinguishment pair CFBP fire behavior algorithms with fire weather indices derived from the Canadian Fire Weather Index System (van Wagner & Pickett, 1985). These synthetic fire weather indices describe various aspects of fuel moisture conditions (Fine Fuel Moisture Code (FFMC), Duff Moisture Code (DMC), and Drought Code) and fire behavior (Initial Spread Index, Buildup Index, and Fire Weather Index) (de Groot 1998). Weather inputs used to calculate these fire weather indices are supplied to BFOLDS by the LANDIS-II Climate Library (Lucash and Scheller 2021) at daily temporal resolution, and a diurnal effect is applied to FFMC (Lawson et al. 1996) and wind speed (unpublished data). Hourly wind speed was modified using a multiplier based on diurnal variations in mean hourly wind speed by month in the boreal forests of northern Ontario (2001–2003, unpublished data). Meanwhile, the fuel classification used by BFOLDS (and derived from the CFBP) is defined within the Dynamic Fuel System (Sturtevant et al. 2009) extension, providing consistency between the fuel types used in fire simulation and those produced by other LANDIS-II disturbance extensions. Fire simulation in BFOLDS is, therefore, both flexible and highly mechanistic, enabling fire regimes to emerge as a result of dynamic interactions within the model.

Fire ignition in BFOLDS combines an empirically derived ignition seed (defined below) with simulated fuelbed characteristics and weather. No differentiation is made between lightning-caused ignitions and those of anthropogenic origin. For each day in a user-defined fire season, the number of potential daily ignitions (“ignition sparks”) is calculated by drawing a random number from a Poisson distribution, the mean of which is supplied by the user for each day in the fire season and for all fire seasons in the simulation period (we refer to this number as an “ignition seed”). Ignition sparks may be distributed across the simulation landscape at random or with spatial biasing toward specific areas. Ignition sparks only result in fires if (a) burnable fuel is available (i.e., the cell is not rock or water) and (b) duff moisture levels (defined using Duff Moisture Code (DMC)) are below a user-defined threshold controlled by the *IgnitionDMCLimit* parameter (Supplement S1).

Fire spread from ignited cells on the landscape occurs mechanistically via the interaction of fuels with weather and topography. Each pre-defined fuel type in the model (see below) has characteristic fire behavior, governed by a system of equations (van Wagner & Pickett, 1985; Perera et al. 2014) that relate fuel available to burn with fire weather, slope, and aspect. Fire behavior models in BFOLDS simulate both surface fire and crown fire for all fuel types in which crown fire is possible, with transition between these two modes contingent on suitable fuel, weather, and topographic conditions. For each ignited cell, fire intensity, fuel consumption, and potential rate of spread are calculated at each timepoint. Fire spreads to nearby cells (including adjacent and non-adjacent cells) containing burnable fuels when the calculated rate of spread is sufficient for fire to reach target cells. When the calculated rate of spread is below the threshold required for fire spread, ignited cells "smolder", and are scheduled for re-evaluation, typically within 3 h.

Fires can be extinguished in several ways. All fires are automatically extinguished at the end of the fire season. On an individual cell basis, fires are extinguished at any timepoint if DMC for that cell drops below a critical threshold, governed by two model parameters, *DMCSpreadLimitMean* and *DMCSpreadAdjustment* (Supplement S1). Finally, fire spread may be prevented (and fire eventually extinguished) by a neighborhood of cells that cannot burn—because of unsuitable substrate (e.g., rock, water)—or have recently burned (i.e., no fuel).

Fuel types are defined by the user, based on the 17 surface fuel types from the CFBP (Forestry Canada, 1992), and are also used in the LANDIS-II Dynamic Fire and Fuel System extensions (Sturtevant et al. 2009). Fuel types included in the CFBP include evergreen conifer (fuel types C-1 to C-7), deciduous (D-1) and mixed (M-1 to M-4) forests, slash (S-1 to S-3), and grasses (O-1a, O-1b). Although these fuel types are based on Canadian forest types, they encompass a wide range of fuel structures, from dense, young stands to crown-fire dominated black spruce systems and open, frequent-fire ponderosa pine (*Pinus ponderosa var. ponderosa* C. Lawson)—Rocky Mountain Douglas-fir (*Pseudotsuga menziesii var. glauca* (Beissn.)) forests. Fuel types are defined by the user in the Dynamic Fuels extension input file using species and age criteria, and each unique fuel type is associated with a single CFBP surface fuel type. Age is used here as a surrogate for the differences in fire resistance conferred by vegetation size (LANDIS does not generate physical dimensions for simulated cohorts) (Table 4). Fuel types may be composed of individual species or many species, based on the structure and composition of forests in the simulation landscape. Definition of these fuel types and their assignment to CFBP surface fuel types should be completed using knowledge of species fire ecology and fire behavior in the forests in the simulation landscape, and with reference to CFBP fuel type descriptions (Forestry Canada, 1992). Detailed information on fire behavior in fuel types present on the simulation landscape may also be used to further tailor the input parameters of CFBP fire spread equations for any of the 17 CFBP surface fuel types to better match simulated fire behavior with empirical observations from the study landscape. During simulations, each cell is assigned to a single fuel type at any given instant in time based on the species-age cohorts present in the cell and the fuel type definitions supplied to the Dynamic Fuels extension. Mixed fuel types are generated internally within the model based on the proportion of conifer and hardwood components present in model cells.

Fuel types defined in the Dynamic Fuels extension are also assigned a fuel type-specific fire intensity-mortality threshold in the BFOLDS input file. The fire intensity-mortality threshold (kW m^2) represents the fire intensity required for mortality in the species and ages comprising the fuel type (see Table 4 for the fire intensity-mortality thresholds used in this study). During fire events, mortality is evaluated at the scale of individual model cells by comparing the simulated fire intensity to the fire intensity-mortality threshold for the fuel type assigned to the burned cell. If the intensity-mortality threshold is exceeded, all cohorts on the cell are killed. Thus, at the scale of model cells, fire events may result in 0% mortality (fire burns through the cell, but vegetation is not killed—a very low-severity fire), or 100% mortality (i.e., a high-severity fire). However, at the scale of individual fires (or forest stands), the outcomes may be infinitely varied as a result of differences in the spatial arrangement of fuels (and fuelbed conditions), fire weather, and topography, and the consequences for location and proportion of cells in which mortality occurs. A corollary of this approach to evaluating fire effects is the importance of defining a model cell size that is appropriate to the research questions being asked.

Model parameterization, calibration, and validation

Climate

We constructed a daily contemporary climate (baseline) scenario using gridded climate data from the Global Soil Wetness Project Phase 3 (GSWP3) (Dirmeyer et al. 2006) and the Climate Forecast System Reanalysis (CFSR) datasets (Saha et al., 2010) (Supplement S1). The latter dataset was used as a source for U- and V- wind components, which are not included in the GSWP3 dataset. GSWP3 and CFSR datasets both have a spatial resolution of 57.5 km. Historic climate records for the twenty-first century incorporate recent climate warming, while the record from the early twenty-first century contains little evidence of global climate change (IPCC 2021). We chose to use the contemporary climate (inclusive of existing warming effects) as our baseline climate scenario, so restricted the GSWP3 data to the period, 1980–2014. A complete baseline climate stream was constructed for each landscape by randomly assigning (with replacement) complete years from the 1980–2014 historic record to years in our 2015–2099 simulation period.

Data for our mild, moderate, and extreme climate warming scenarios was obtained from the Coupled Model Intercomparison Project Phase 6 (CMIP6) experiment of the World Climate Research Program (Eyring et al. 2016). We selected three Shared Socioeconomic Pathways (SSP)—SSP2–4.5, SSP3–7.0 and SSP5–8.5—encompassing a range of warming future climates (Supplement S1).

Landscape and vegetation

Individual landscape cells were 2.25 ha in area (150-m cell width), while fire simulation processes in BFOLDS occur in near-continuous time and model outputs were generated at an annual timestep.

Ecoregions were defined and delineated for each study landscape using historic growing season and soil data. Using a cluster analysis (k-means clustering and CLARA (Maechler et al. 2012)) and 1-km gridded monthly temperature and precipitation normals (WorldClim v2.1, Fick & Hijmans 2017), we identified regions of relatively homogenous climate. The optimal number of clusters was evaluated using standardized graphical approaches (e.g., silhouette plots) that depict improvements in model performance from incremental change in the number of clusters. The resultant "climate regions" were overlain with gridded soil texture maps (OpenLandMap, Hengl & MacMillan 2019), to form a series of climate-soil ecoregions for each landscape. This approach produced eight ecoregions for the Southern taiga and Mid-taiga landscapes (average size of 1250 km^2) and seven ecoregions (average size of 1430 km^2) for the Taiga-tundra landscape). Water bodies and areas of human settlement (Schepaschenko et al. 2012, 2015) were designated as "inactive."

Initial species occurrence and biomass in each cell of our study landscapes were reconstructed using large-scale inventory data and model spin-up. The dataset of forest biomass for Eurasia (Schepaschenko et al. 2017) provides consolidated plot- and tree-level data, including species presence and relative dominance, and tree and stand ages, derived from approximately 1200 sets of field measurements conducted between 1930 and 2014. Information from this database was cross-referenced against species and stand age data contained in raster maps of biomass expansion and conversion factors for Russian forests (Schepaschenko et al. 2018), derived from the State (Russia) Forest Register. Maps of species-age cohorts constructed from these datasets were grown forward using the spin-up capabilities of PnET Succession to produce realistic estimates of each cohort's biomass for each cell (Supplement S1, Figure S3), which were then evaluated against the input inventory data, generalized species, structure, distribution, and performance trends across central Siberia (e.g.,Shorohova et al. 2009; Schulze et al. 2012; Loboda & Chen, 2017) and expert opinion (A, Shvidenko; D. Schepaschenko).

Species physiological attributes used to parameterize establishment, growth, mortality, and competition in PnET were obtained from prior simulation of vegetation and forest management in central Siberia using LANDIS-II and the Biomass Succession and PnET-Succession extensions (Gustafson et al. 2010, 2011, 2020a) (Supplement S1). These parameters' values were reviewed and re-calibrated, where required, and additional parameters specific to the latest version of PnET-Succession were calibrated under edaphic and climatic conditions representative of each study area. Simulated biomass growth was validated by comparison with inventory data (Schepaschenko et al. 2017), and parameters were adjusted to maximize agreement between simulated and empirical growth curves for all three study areas (Supplement S1). Calibrations also included adjustment to parameters based on competitive interactions.

To initialize shrubs and herbaceous vegetation (not represented in inventory data), we used a set of landscape-specific, ecologically relevant rules (e.g., species associations, riparian species; see Brussel et al., Assessing Siberia's response to global change through the lens of tipping points, in preparation). Outputs from the implementation of these decision criteria were evaluated using expert opinion (A, Shvidenko; D. Schepaschenko).

The initial calibration of species' demographic parameters (described above) was refined following initial calibration of the fire regime in BFOLDS (below). Adjustments to the initial species' parameterization were made where necessary to ensure that disturbance response (e.g., serotiny in Scots pine) and community-wide relative species dominance was consistent with the ecology of our simulation landscapes (expert opinion: A, Shvidenko; D. Schepaschenko, and generalized sources, e.g., Wirth et al. 1999; Schulze et al. 2005, 2012; Sofronov et al., 2008; Shorohova et al. 2009, 2011).

Fire weather

Fire weather indices used in BFOLDS were calculated using the Climate Library (Lucash & Scheller 2021) and generated for each day of a fixed fire season (the annual period of fire activity) for each year of the simulation period. We used an identical but wide (Julian days 90–320) maximum fire season for all simulation landscapes and climate scenarios to allow seasonal changes in fire occurrence to emerge mechanistically in response to latitude and climatic changes (Kharuk et al. 2021; Talucci et al. 2022), rather than being restricted to current fire season lengths. Maximum fire season length in BFOLDS, controlled by fire season start and end parameters, is the model-constrained period during which fires may occur. The actual fire season length emerges as a result of weather during the simulation period and may be much shorter than this maximum fire season length if climatic conditions are not conducive to fire.

FFMC, DMC, and DC start-of-season values of 85, 6, and 15, respectively, are recommended for application across boreal North America (Lawson & Armitage 2008; Miller 2020), and were applied in our simulations, in the absence of empirically-derived, landscape-specific start-of-season values. We validated fire weather indices produced by the Climate Library through independent recalculation using the same input weather data (R package cffdrs, Wang et al., 2017) and comparison with independent estimates generated using weather inputs from a different climate model (Supplement S1).

Fire ignitions

A daily ignition stream was generated for each year of the simulation period using empirical data and statistical modeling. We used the thermal hotspot archive of the MODIS Collection 6.1 active fire product (Giglio et al. 2020) as our source of observed fire ignitions (2001–2020) (Supplement S1).

Observed fire hotspots were used as a reference point to parameterize statistical distributions of ignitions, which were then sampled repeatedly for each day of the simulation period (Supplement S1). For each study landscape, we visualized annual trends (and their seasonality) in observed fire hotspots and produced histograms of daily ignition numbers. The latter were used to parameterize a zero-inflated negative binomial distribution that characterized the ignitions process for each study landscape under a historic climate. This ignition distribution for each landscape was then adjusted to produce separate distributions for peak fire season and off-peak fire season. Random sampling from these distributions for each day of the fire season in each simulation year produced a daily ignition seed for simulations with the baseline (contemporary) climate. The decadal ignition rate from this ignition seed was validated by comparison with the observed decadal fire hotspot rate.

Ignition seeds for simulations with climate change were produced by adjusting the baseline ignition distributions to account for the expected increase in future circumpolar lightning ignition rates (Chen et al. 2021). For each study landscape and climate change scenario, a target decadal ignitions rate for the 2080–2099 period was calculated using an assumed 24% increase in lightning ignitions per 1 °C in mean annual temperature (Chen et al. 2021), with the projected temperature increase calculated from the CESM2-WACCM climate input data. Parameters of the statistical distribution of ignitions for each landscape and climate scenario were then adjusted iteratively and incrementally, such that the end-of-century decadal ignition rate was within 5% of the target, and the increase to this level was achieved gradually (Supplement S1).

Our approach implicitly assumes that all changes in the rate of ignitions are caused by an increase in the lightning ignitions rate, but we believe this is a reasonable approximation, in the absence of quantitative projections of future human-origin ignitions in Siberia.

Fuels

Fuels types were developed around our classification of tree species into three fire response groups, fire resisters, fire avoiders, and fire endurers (Table 4). For trees, we created separate fuel types for young and mature to old cohorts in each fire response group, reflecting size-based differences in fire tolerance (e.g.,Kukavskaya et al. 2014; Schulze et al. 2012), for a total of six arborescent fuel types. Although trees were the primary focus of this study, we also assigned shrubs and ground-layer vegetation to separate fuel types, created by grouping this vegetation into fire response groups based on life history strategy (Table 4).

Each fuel type was assigned to a CFBP surface fuel type (Forestry Canada, 1992), and a fire intensity-mortality threshold was defined using the best available literature on fire behavior in Siberian forests (Table 4). Controlled fire behavior experiments have been conducted in Scots pine and larch forests in southern Siberia (McRae et al. 2005; Kukavskaya et al. 2014; Ivanova et al. 2020) and were used to identify approximate fire intensity thresholds corresponding to mortality in fuel types dominated by these fire resister species (Table 4). We are not aware of quantitative, empirically-derived accounts of both fire intensity and associated levels of tree and stand mortality in forests dominated by fire avoiders (Siberian fir, Siberian pine, and Siberian spruce) or fire endurers (birch spp. and Eurasian aspen) in Siberia. Consequently, fire intensity-mortality thresholds for fuel types dominated by fire avoider and fire endurer species were developed with reference to qualitative descriptions of species' fire tolerance from Siberia (e.g.,Wirth 2005; Schulze et al. 2012) and quantitative studies on comparable species in North American boreal forests (Table 4). We believe this to be a reasonable simplification given the physiological similarities, levels of fire tolerance, some common adaptative traits (or lack thereof), and fire behavior in constituent forests of Eurasian and North American (*Betula papyrifera* and *Populus tremuloides*) fire endurers, and between common Eurasian (Siberian fir and Siberian spruce, in particular) and North American (specifically *Picea mariana*) fire avoiders (although note that Siberian fire avoiders do not possess the cone serotiny of black spruce) (e.g., Uchytil 1991; Nikolov and Helmisaari 1992; Howard, 1996; Wirth 2005; Fryer 2014; Kharuk et al. 2021).

Fire regime characteristics

Key BFOLDS parameters controlling fire ignition and extinguishment are *IgnitionDMCLimit* and *DMCSpreadLimitMean*, respectively. These parameters were calibrated and validated iteratively, and separately for each landscape. Fire regime calibration occurred following the initial calibration of vegetation demographic parameters and was followed by further calibration simulations aimed at refining vegetation demographic parameters and, where necessary, adjusting fire regime parameters (Supplement S1, Sects. 2 and 3.3). For each landscape, we calculated a series of observed fire regime statistics (e.g., mean annual number of fires and fire return interval), using datasets publicly available at the time of model parameterization (Rogers et al. 2017; Andela et al. 2019) (Table 3). Replicated simulations (four simulations, each 50 years in length) were then conducted for combinations of *IgnitionDMCLimit* and *DMCSpreadLimitMean* values, and simulated fire regime statistics were computed. This process was repeated, tuning these two parameters—plus a third parameter, *DMCSpreadAdjustment*, if required for additional stochasticity—according to their role in simulated fire behavior until the simulated fire regime characteristics converged on the observed fire regime characteristics. Given the many different characteristics of a fire regime (for example, fires per year, fire rotation period, fire intensity, mean annual fire size, fire size distribution), we viewed calibration as successful when a balance of different characteristics approached the observed statistics. Finally, as a generalized check on the reasonableness of both the observed and parameterized fire regime characteristics for our simulation landscapes, we viewed these values alongside regional and Siberia-wide trends in fire regime characteristics from recent publications (e.g., de Groot et al. 2013b; Kharuk & Ponomarev 2017; Kharuk et al. 2021; Ponomarev et al. 2021; Talucci et al. 2022).

Data analysis

Fire

LANDIS outputs were used to calculate simulated fire regime characteristics for each landscape and climate scenario over the 85-year simulation period. We focused on annual area burned, mean and maximum fire size and overall fire size distribution, the number of fires per year, fire intensity (calculated by averaging fire intensity across cells within each fire perimeter and then across all fires occurring during a simulation), and fire rotation period. Annual model output raster maps, in which cells on the simulation landscape that burned are assigned the respective fire event code, were used to delineate individual fire perimeters. Averaging the number of unique fire event codes per year provided the mean annual number of fires, while the number of cells within each fire perimeter was used to calculate fire sizes and mean annual burned area. Fire rotation period was calculated as the number of years in the study interval divided by the proportion of the study area that burned during this time (Miller et al. 2012).

We addressed hypotheses 1 and 2 by constructing linear and generalized linear models for each fire regime characteristic and evaluating pairwise differences between climate scenarios (Table 5). Statistical models were developed separately for each landscape and included climate scenario as the sole categorical explanatory variable. Linear models were employed for annual burned area, mean and maximum fire size, fire intensity, and fire rotation period, while the number of fires per year was modeled using a Poisson generalized linear model (GLM) with a log link. In all models, simulation replicates were treated as samples of the possible fire regime in each landscape. We acknowledge that simulation replicates were not entirely independent, but believe that obtaining some statistical test results outweighs the concerns associated with relaxing this model assumption.

Evidence of non-normality and heteroscedasticity was evaluated through visual examination of diagnostic plots. Violations of the assumption of constant variance were typically relatively minor and were addressed by adopting a weighted least squares linear model, in which the weight assigned to a given observation was proportional to the reciprocal of the error variance for that observation. Overdispersion in GLMs was assessed by calculating the dispersion parameter, Φ, but no corrections for overdispersion were required (Zuur et al. 2009).

Table 5 Test statistics and model fit for linear or generalized linear models (fires per year) describing the relationship between climate scenario and fire regime characteristics (orange highlight) and vegetation attributes (green highlight) for LANDIS-II simulations in three central Siberian landscape

Landscape	Parameter	F-test ("Climate")		[1] Adjusted R^2
		Test statistic	P-value	
Taiga-tundra	Annual burned area	1416.900	< 0.001	0.99
	Av. fire size	159.760	< 0.001	0.92
	Max. fire size	4.001	0.015	0.19
	Fires per year	679.470	< 0.001	0.79
	Fire rotation period	609.360	< 0.001	0.98
	Fire intensity	211.040	< 0.001	0.94
	Fire resister IV	446.470	< 0.001	0.97
	Fire avoider IV	952.780	< 0.001	0.99
	Fire endurer IV	-	-	-
	Av. cohort age	834.130	< 0.001	0.98
	CV cohort age	755.420	< 0.001	0.98
Mid-taiga	Annual burned area	197.98	< 0.001	0.94
	Av. fire size	58.528	< 0.001	0.82
	Max. fire size	1.264	0.301	0.02
	Fires per year	9408.2	< 0.001	1.00
	Fire rotation period	53.929	< 0.001	0.82
	Fire intensity	126.47	< 0.001	0.91
	Fire resister IV	45.341	< 0.001	0.79
	Fire avoider IV	94.121	< 0.001	0.89
	Fire endurer IV	2239.2	< 0.001	0.99
	Av. cohort age	46.434	< 0.001	0.79
	CV cohort age	76.233	< 0.001	0.86
Southern Taiga	Annual burned area	148.38	< 0.001	0.93
	Av. fire size	14.424	< 0.001	0.55
	Max. fire size	1.8635	0.153	0.13
	Fires per year	270.16	< 0.001	0.53
	Fire rotation period	133.92	< 0.001	0.91
	Fire intensity	30.545	< 0.001	0.72
	Fire resister IV	177.1	< 0.001	0.94
	Fire avoider IV	42.183	< 0.001	0.77
	Fire endurer IV	255.39	< 0.001	0.96
	Av. cohort age	122.43	< 0.001	0.91
	CV cohort age	115.53	< 0.001	0.91

[1] For generalized linear models of fires per year, the test statistic follows a chi-squared distribution, and model fit was assessed using McFadden Pseudo-R^2 values

For each response variable, differences in the mean between climate scenarios were evaluated using pairwise orthogonal contrasts. Multiple comparison 95% confidence intervals around the mean difference were constructed for all pairs of climate scenarios, and confidence intervals that did not include 0 (linear models) or 1 (GLMs) were considered as strong support for a difference in the response variable between climate scenarios.

Differences in fire size distributions for each landscape were evaluated statistically and visually. Two-sample Kolmogorov–Smirnov tests for pairwise differences in the fire size distribution between climate scenario combinations were conducted (Supplement S2 Table S3), but proved to be uninformative. Visual examination of fire size distributions also showed little difference in the distribution shape between climate scenarios for each study landscapes, with the primary difference instead being many more fire events in simulations with climate change than those with the baseline climate. Accordingly, we do not further discuss fire size distributions, but provide visual and statistical data in Supplement S2 (S2 Figure S1, and S2 Table S3).

Vegetation

We addressed Hypotheses 3–5 (fire response groups) using fire response group Importance Values (IV) (Iverson et al. 2008; Peters et al. 2020) for the three (arborescent) fire response groups of primary interest in this study (Table 4): fire resisters (larch spp., Scots pine), fire avoiders (Siberian fir, Siberian pine, Siberian spruce), and fire endurers (birch spp., Eurasian aspen). In this study, we calculated IV of fire response group i in simulation year j as:

$$IV_{\mathrm{ij}} = \frac{biomass_{\mathrm{ij}}}{\sum_i^6 (biomass_{\mathrm{j}})} + \frac{cohorts_{\mathrm{ij}}}{\sum_i^6 (cohorts_{\mathrm{j}})}$$

where IV_{ij} is the importance value of the ith fire response group (i = 1…6) in the jth simulation year (j = 1…85), biomass_{ij} is the landscape-scale biomass of fire response group i in simulation year j, and cohorts_{ij} is the number of cohorts of fire response group i on the landscape in simulation year j. As IV combines abundance and biomass, it is suited for comparisons between species with different growth habits, demographics, and maximum potential biomass.

Changes in fire response group IV during the simulation period were assessed visually, and linear models were constructed for end-of-century IV of each fire response group in each landscape. Linear models employed the same structure as models for fire regime characteristics, and model diagnostics and statistical tests of climate scenarios were conducted as previously described for these fire regime characteristics. In all cases, "end-of-century" IV for each fire response group was computed as the mean of the IV for the final 15 years of the simulation period, i.e., 2085–2099.

We addressed Hypothesis 6 (cohort age) using cohort age class distributions. Cohort ages were binned into 20-year increments and examined graphically for differences in end-of-century cohort age class distribution between climate scenarios for each landscape. Statistical differences in age class distribution were assessed by constructing linear models and using pairwise contrasts for mean end-of-century cohort age and the coefficient of variation in end-of-century cohort age. Although visual examination of cohort age class distributions used stacked bar charts for different fire response groups (Fig. 9), statistical models did not disaggregate cohort age among the different fire response groups.

All data analysis was conducted in R version 4.1.2 (R Core Team, 2022), using the packages ggpubr (Kassambara 2020), goeveg (Goral & Schellenberg 2021), here (Muller, 2020), jtools (Long 2022), multcomp (Hothorn et al. 2008), nlme (Pinheiro and Bates, 2022), sf (Pebesma 2018), terra (Hijmans 2022), tidyverse (Wickham et al., 2019), and VGAM (Yee 2022).

Results

Fire regimes

Simulated changes in fire regime characteristics in our three landscapes were largely consistent with Hypothesis 1—fire activity will progressively increase as the magnitude of climate change increases. Consistent with this hypothesis, we observed a trend toward higher annual burned area and fire intensity, larger fire sizes, more fires per year, and a shorter fire rotation period under climate warming than in our baseline climate scenario (Figs. 2, 3, and 4). However, this generalization obscures more nuanced changes when viewed at the scale of individual study landscapes and for individual fire regime characteristics.

Annual burned area was significantly higher under all three climate change scenarios (SSP2-4.5, SSP3-7.0, and SSP5-8.5) than the baseline (i.e., contemporary) climate. However, while annual burned area peaked under the most extreme (SSP5-8.5) climate change scenario in the southernmost (Southern taiga) study landscape, burned area in our northernmost (Taiga-tundra) study landscape peaked in the moderate (SSP3-7.0) climate change scenario (Figs. 2 and 4).

The relationship between mean fire size and climate was more complex than the annual burned area. Mean fire size peaked under the mild climate change scenario in the Mid-taiga and Southern taiga landscapes, and under the moderate climate change scenario in the

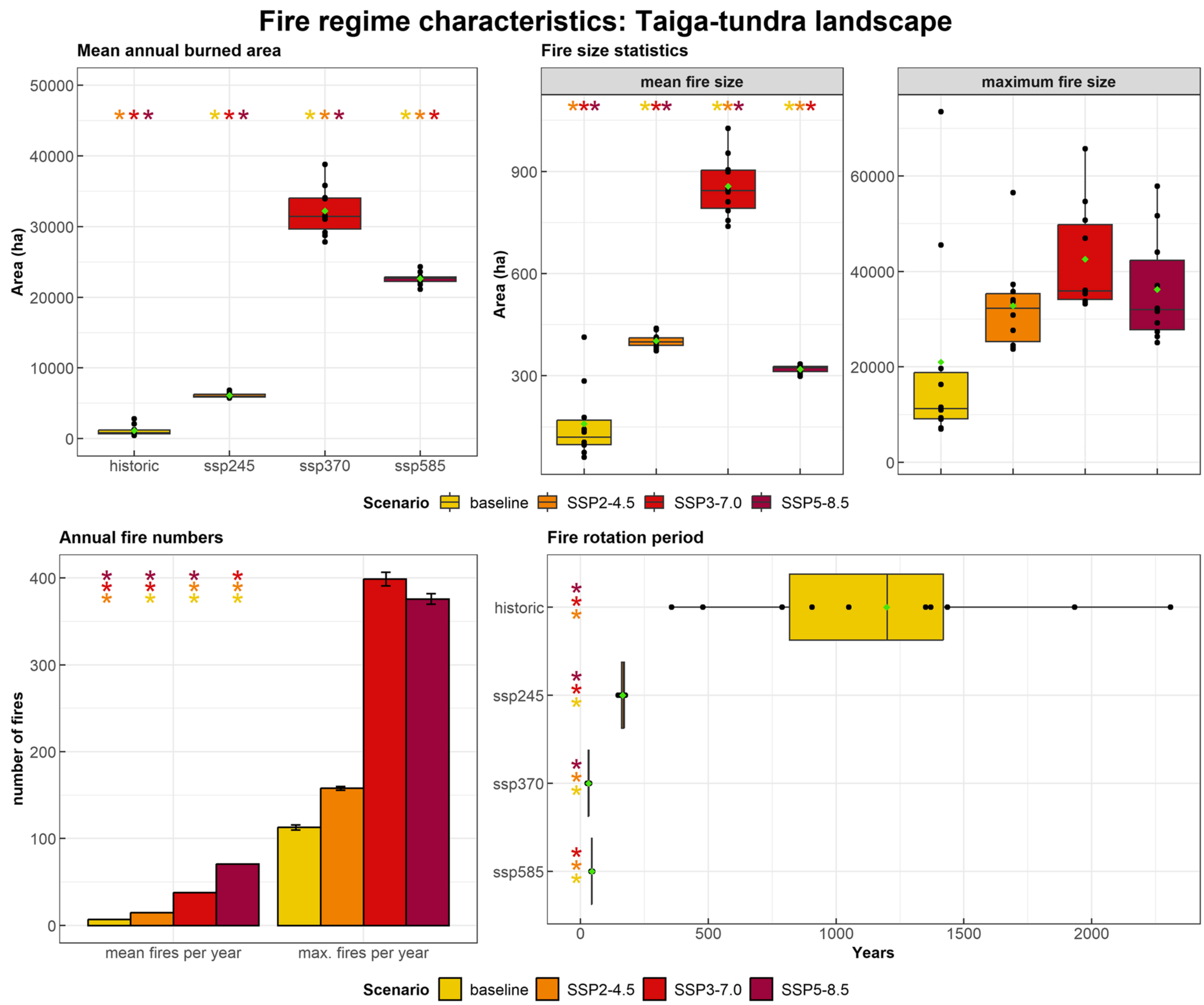

Fig. 2 Fire regime statistics for the Taiga-tundra study landscape for the 2015–2099 study period. For Figs. 2, 3, and 4, colored asterisks over boxplots indicate pairs of climate scenarios for which 95% multiple comparison confidence intervals did not include 0 (of 1, for comparison of the mean number of fires per year), with the color of the asterisk corresponding to the other climate scenario in the pairwise comparison. Note that statistical tests were not conducted for the annual area of stand-replacing fire or the minimum or maximum number of fires per year. Black dots represent individual observations (a single simulation replicate) while green dots indicate the mean value across simulation replicates

Taiga-tundra landscape, based on 95% multiple comparison confidence intervals (Figs. 2, 3, and 4, Supplement S2 Table S2). Maximum fire size was not strongly related to climate scenario. In the Taiga-tundra landscape, maximum fire size was higher under moderate climate change (SSP3-7.0) than the baseline scenario (Fig. 2), but this was the only study landscape in which significant differences were observed.

Differences in the number of fires per year and fire rotation period between climate scenarios were largely consistent with Hypothesis 1. The mean number of fires per year increased with the magnitude of climate change scenario in all landscapes except the Southern taiga, where there was no difference between the baseline and mild climate change scenarios (Figs. 2, 3, and 4, Supplement S2 Table S2). Similarly, our results imply a decrease in fire rotation period, from baseline climate to extreme climate change in the Southern taiga and Mid-taiga landscapes, but fire rotation period was shortest under moderate climate change in the Tundra-taiga landscape (Figs. 2, 3, and 4).

Changes in fire intensity under climate warming were most pronounced in the Taiga-tundra landscape. Mean fire intensity was higher for all climate change scenarios than the baseline climate scenario in each study landscape, but did not differ significantly between climate

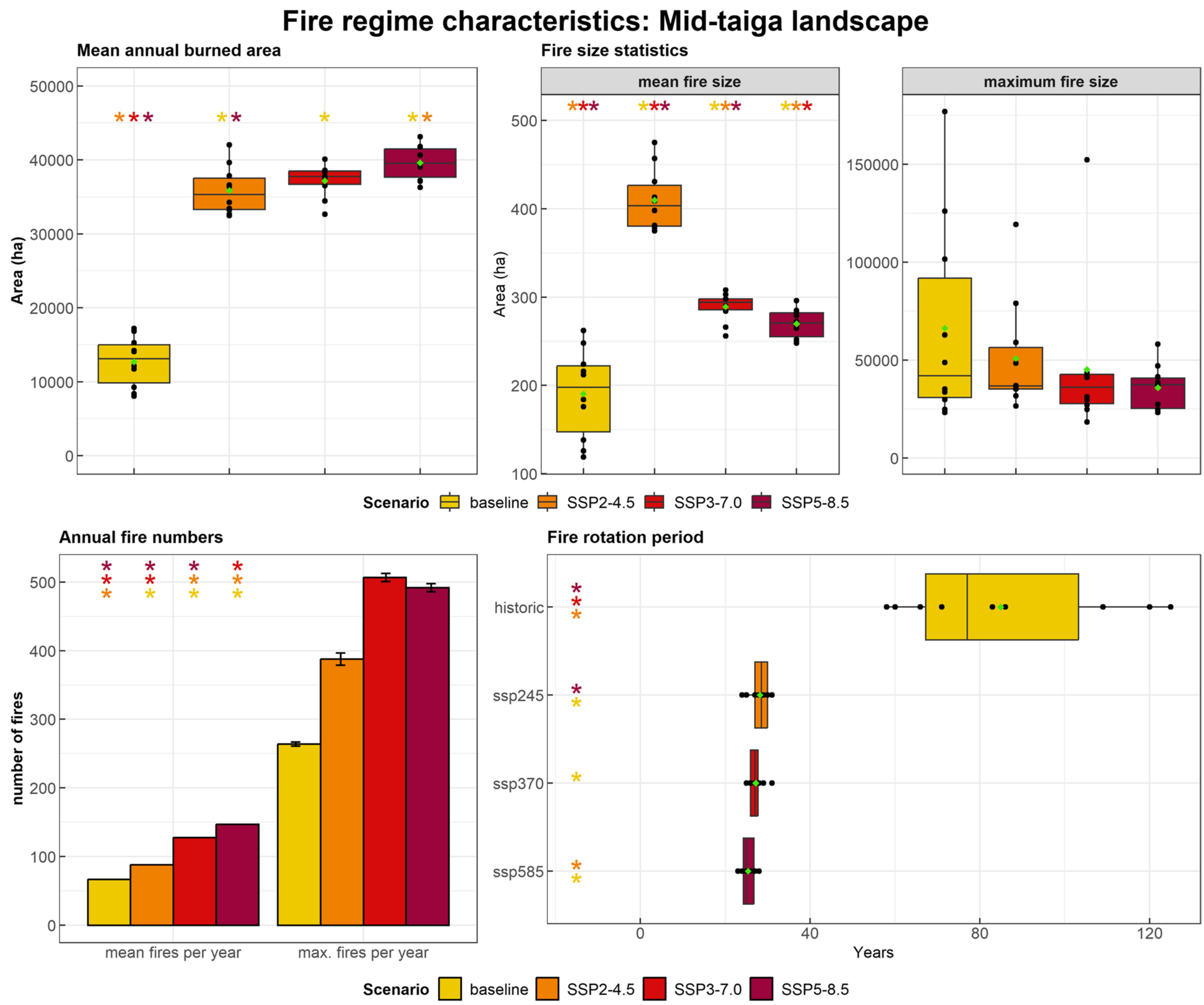

Fig. 3 Fire regime statistics for the Mid-taiga study landscape for the 2015–2099 study period. See Fig. 2 caption for interpretation of symbols

scenarios in any of the study landscapes except the Taiga-tundra (Fig. 5). In the latter, mean fire intensity peaked under the most extreme climate change scenario (SSP5-8.5).

Fire rotation period is a succinct summary of the total amount of fire on the landscape, and viewed using this metric, our results provide support for Hypothesis 2—changes in fire activity under climate change would be greatest in the northernmost study landscape. Fire rotation period in the Taiga-tundra study landscape decreased from a mean of 1197 years for simulations with a baseline climate to a mean of 32 years for simulations under moderate climate change (Supplement S2, Table S2)—a much greater reduction in fire rotation period than was observed in the other landscapes. Similarly, the greatest proportional increase in fire intensity under climate change was also observed in the Taiga-tundra landscape (~250% increase compared to the baseline scenario).

Vegetation

Our results provided mixed support for Hypothesis 3—the relative importance of fire avoiders (Siberian fir, Siberian pine, and Siberian spruce) will increase in the northernmost study landscape under climate change but decrease in the southernmost landscape. At the end of the twenty-first century, fire avoider importance value (IV) in the Taiga-tundra landscape was higher in the mild climate change scenario than the baseline scenario (Supplement S2 Figure S2, Table S4), but under moderate and extreme climate change scenarios IV was slightly lower than the baseline scenario (Fig. 6, Supplement S2 Figure S2, Table S4). However, consistent with expectations, fire avoider IV in the Southern taiga landscape declined

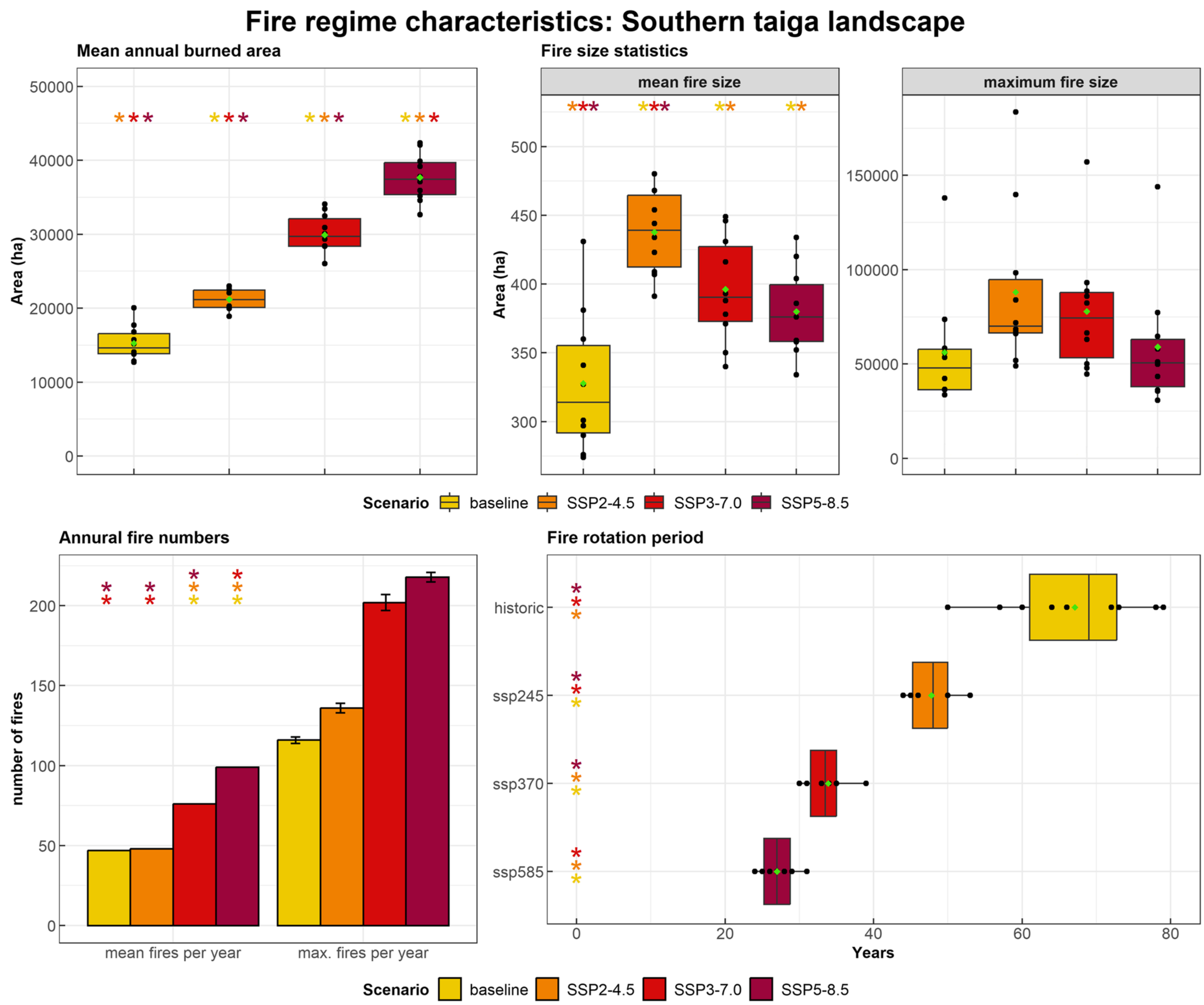

Fig. 4 Fire regime statistics for the Southern taiga study landscape for the 2015–2099 study period. See Fig. 2 caption for the interpretation of symbols

under all climate change scenarios, relative to the baseline scenario (Fig. 8, Supplement S2 Figure S4, Table S4).

Fire resister IV was also lower under all climate change scenarios than the baseline scenario in both the Southern taiga and Mid-taiga study landscapes (Figs. 7 and 8, Supplement S2 Figures S3 and S4)—a finding that is counter to Hypothesis 4. Fire resister IV tended to decline as the magnitude of the climate change increased (Supplement S2, Table S4), such that end-of-century IV was lowest under SSP5-8.5. This pattern was most evident in the Mid-taiga, the study landscape with the highest fire resister IV at the start of simulations.

We hypothesized that the relative importance of fire endurers would decline in the southernmost study landscape (the Southern taiga), but increase or remain constant further north (Hypothesis 5). Instead, our results provide strong support for an increase in fire endurer IV in both the Southern taiga and Mid-taiga in all climate change scenarios, compared to the baseline scenario (Figs. 7 and 8, Supplement S2 Figures S3 and S4 and Table S4). In each of these landscapes, fire endurer IV increased progressively with the magnitude of climate change. This trend is particularly noteworthy for the Mid-taiga landscape, as fire endurers were no longer present on the landscape at the end of the twenty-first century under the baseline climate scenario.

Relative to the baseline scenario, mean cohort age was lower in all climate change scenarios in each study landscape, a finding that is consistent with Hypothesis 6. The climate scenario with the lowest average cohort age differed by study landscape (Supplement S2 Table S4), and in the case of the Mid-taiga landscape, mean age was over 30 years lower under climate warming than

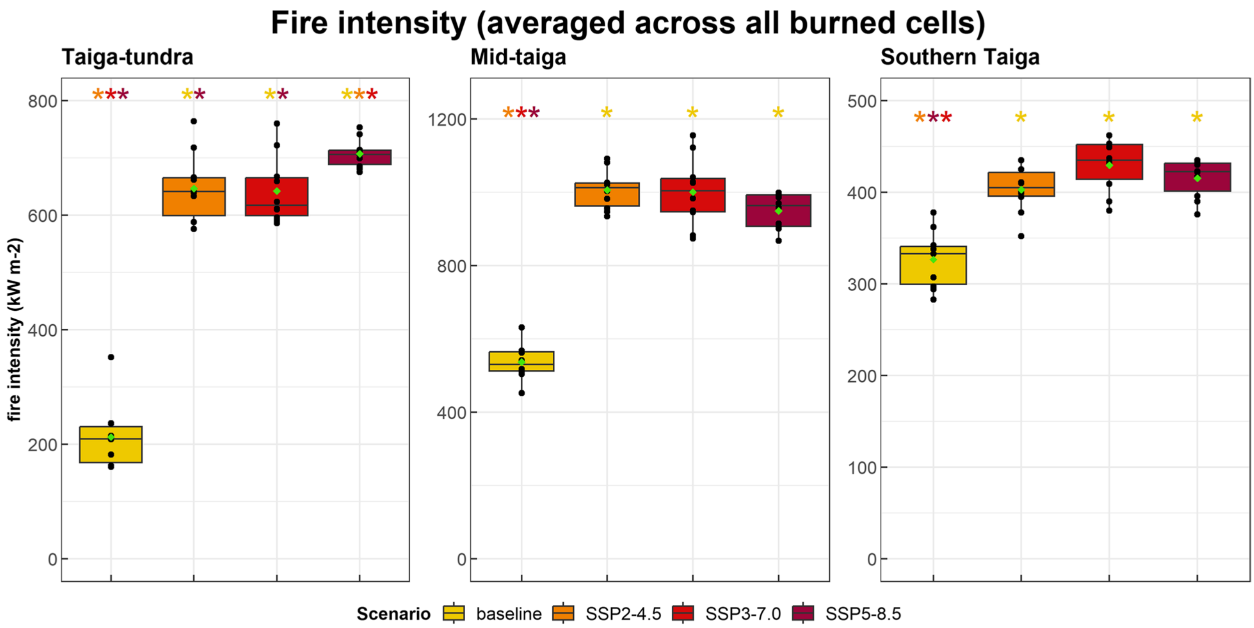

Fig. 5 Differences in fire intensity between climate scenarios for the Taiga-tundra, Mid-taiga, and Southern taiga study landscapes for the 2015–2099 simulation period. See Fig. 2 caption for the interpretation of symbols. Note that fire intensity values for each data point represent the mean value of fire intensity across all fires occurring within a given simulation, and across all cells within each individual fire

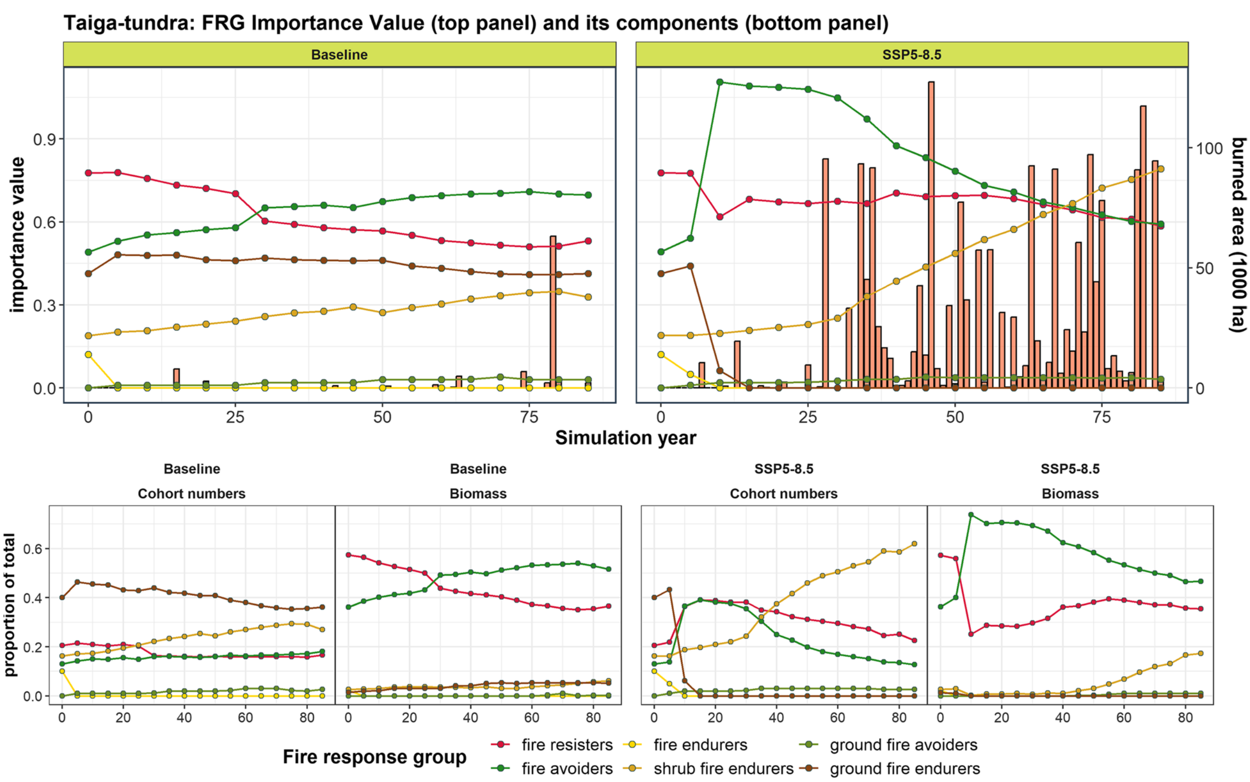

Fig. 6 Main plots: changes in simulated fire response group importance value (top panel) through time (2015–2099 study period depicted as simulation years 0–85 on the *x*-axis) in the Taiga-tundra landscape under baseline (left) and SSP5-8.5 (right) climate scenarios. Lower plots decompose importance value into proportional cohort numbers and proportional biomass by fire response group. The secondary *Y*-axis on the right of the Importance Value represents the annual burned area averaged across all replicates in a given landscape × climate factorial

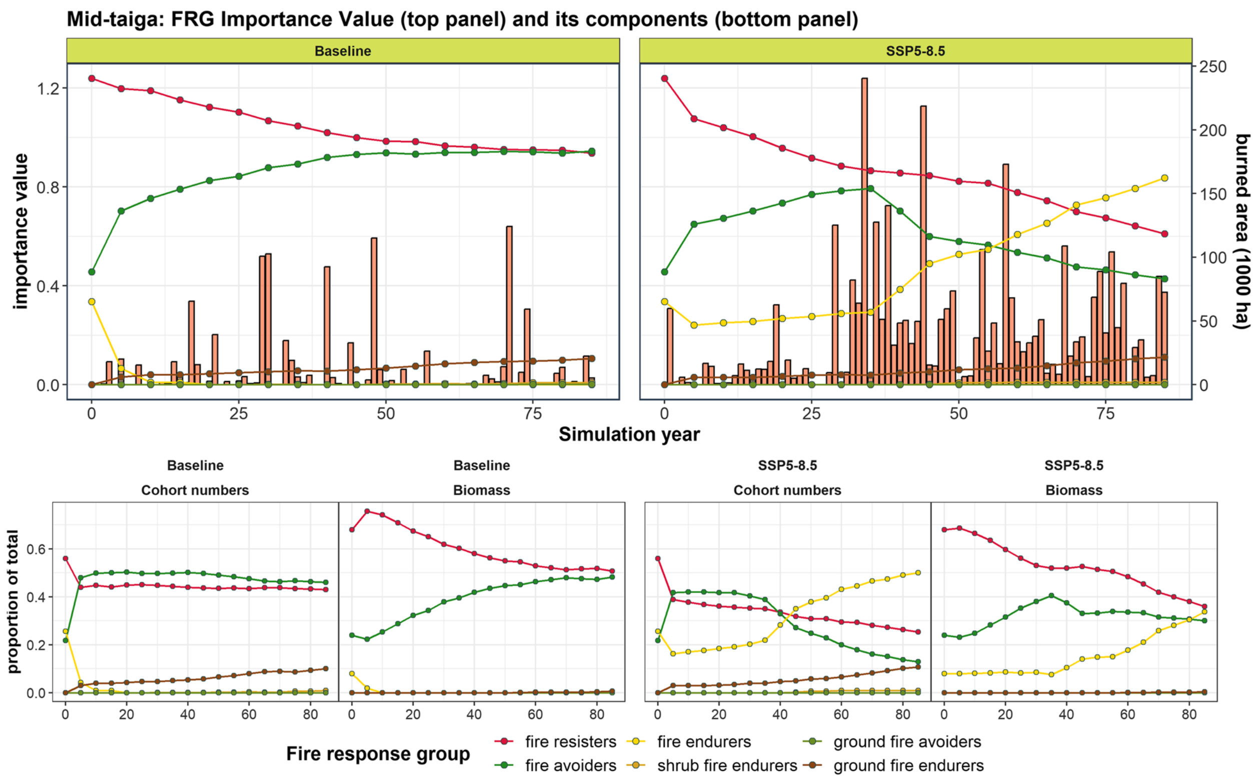

Fig. 7 Main plots: changes in simulated fire response group importance value (top panel) through time (2015–2099 study period depicted as simulation years 0–85 on the *x*-axis) in the Mid-taiga landscape under baseline (left) and SSP5-8.5 (right) climate scenarios. Lower plots decompose importance value into proportional cohort numbers and proportional biomass by fire response group. The secondary *Y*-axis on the right of the Importance Value represents annual burned area averaged across all replicates in a given landscape × climate factorial

under the baseline climate (Supplement S2 Table S4). Age class distributions (Fig. 9) showed a higher coefficient of variation for simulations with climate change than in the baseline scenario (Supplement S2 Table S4).

Discussion

A substantial increase in future fire activity in Siberia could have major ecological, social, and economic consequences at regional to global scales (Rogers et al. 2020; McCarty et al. 2021). Our study provides one of the first process-based, quantitative analyses of potential changes in fire regime characteristics for central Siberia over the twenty-first century and indicates that a major increase in fire activity is probable. Moreover, this conclusion applies even under mild climate warming, and throughout a latitudinal gradient stretching from the southern taiga to the northern forest–tundra ecotone. Fire behavior in Siberia is a product of and a control on the structure and composition of vegetation (Wirth 2005; Flannigan 2015; Rogers et al. 2015), and results from this study suggest future changes in climate and fire activity could be accompanied by widespread shifts in forest type and biomass.

Changing fire regimes

The trends in wildfire activity that we observed suggest recently documented changes in circumboreal fire regimes are likely to be exacerbated under a wide range of future emissions scenarios. Although considerable regional variability exists in rates of annual burned area across boreal Eurasia (e.g., Talucci et al. 2022), recent remote sensing-based estimates suggest Siberia-wide annual burned area increased 2.5-fold, from an average of 6.3 million hectares (Mha) for 2001–2005 to 16.1 Mha for 2016–2020 (Ponomarev et al. 2021). Averaged across the 2015–2099 study period, mean annual burned area in our simulations increased under climate change by 1.4 to 2.4 times in the southernmost (Southern taiga) study landscape, 2.8 to 3.1 times in the Mid-taiga landscape, and 5.4 to 28.3 times in the northernmost (Taiga-tundra) landscape, depending on the climate scenario. These estimates for relatively small (10,000 km^2) landscapes are not directly comparable with Siberia-wide historic fire statistics, but they do provide an important insight into the magnitude of potential climate change effects on fire regimes at

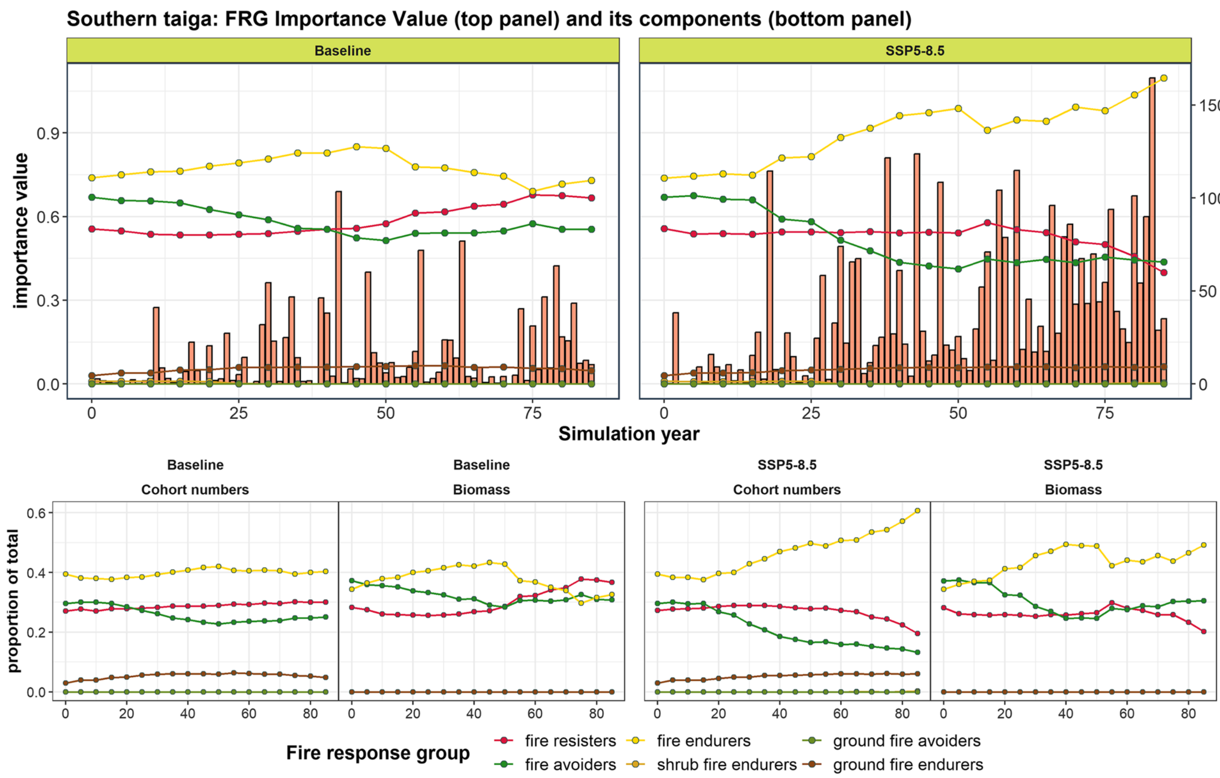

Fig. 8 Main plots: changes in simulated fire response group importance value (top panel) through time (2015–2099 study period depicted as simulation years 0–85 on the *x*-axis) in the Southern taiga landscape under baseline (left) and SSP5-8.5 (right) climate scenarios. Lower plots decompose importance value into proportional cohort numbers and proportional biomass by fire response group. The secondary *Y*-axis on the right of the Importance Value represents the annual burned area averaged across all replicates in a given landscape × climate factorial

ecologically and operationally relevant scales. We are not aware of alternative published estimates of future burned area in Siberia, but in boreal Canada the projected increase in burned area ranged from 1.1 to 3.8 times, depending on the ecozone, under a 3-times historic CO_2 climate scenario (Flannigan et al. 2005). Similarly, Krawchuk et al. (2009) projected a 2.6-fold increase in annual burned area under a 3-times CO_2 climate scenario for a 58,000-km^2 boreal forest landscape in Alberta. Our estimates fall within this range for landscapes of comparable latitude and therefore strengthen the argument that climate change will drive increases in burned area across the boreal zone (Kharuk et al. 2021; McCarty et al. 2021).

Although we documented consistent changes across a range of fire regime attributes, the magnitude of these fire regime shifts waned under extreme climate change. Climate warming is projected to increase the severity of fire weather (Stocks et al. 1998; Malevsky-Malevich et al. 2007; de Groot et al. 2013a) and lightning ignition rates (Chen et al. 2021) across Siberia, reducing the strength of existing climate and ignition limitations to wildfire (Krawchuk & Moritz 2011; Kharuk et al. 2021). These causal factors are incorporated into fire simulation processes in this study, so it is unsurprising that the number of fires per year, mean fire size, and fire intensity were all higher under climate change than simulations with the contemporary climate. Less predictable was that mean fire size peaked under mild climate change in the Southern taiga and Mid-taiga landscapes, and both mean fire size and annual burned area peaked under moderate climate change in the Taiga-tundra landscape. These trends likely reflect feedbacks between vegetation and fire regimes under extreme climate warming.

Dynamic fire-vegetation feedbacks have been posited as part of a long-term adjustment to increasing fire activity (Parks et al. 2016a; Foster et al. 2022) and our results imply that such feedbacks may appear within the twenty-first century in central Siberia. Fuel limitations following fire are implemented in BFOLDS using a minimum threshold on reburn frequency (10 years in this study). Lower mean fire sizes under moderate and extreme warming than mild warming in the Southern taiga and Mid-taiga landscapes occurred despite a concomitant increase in the number of fires per year with increasing climate warming. This implies that recent

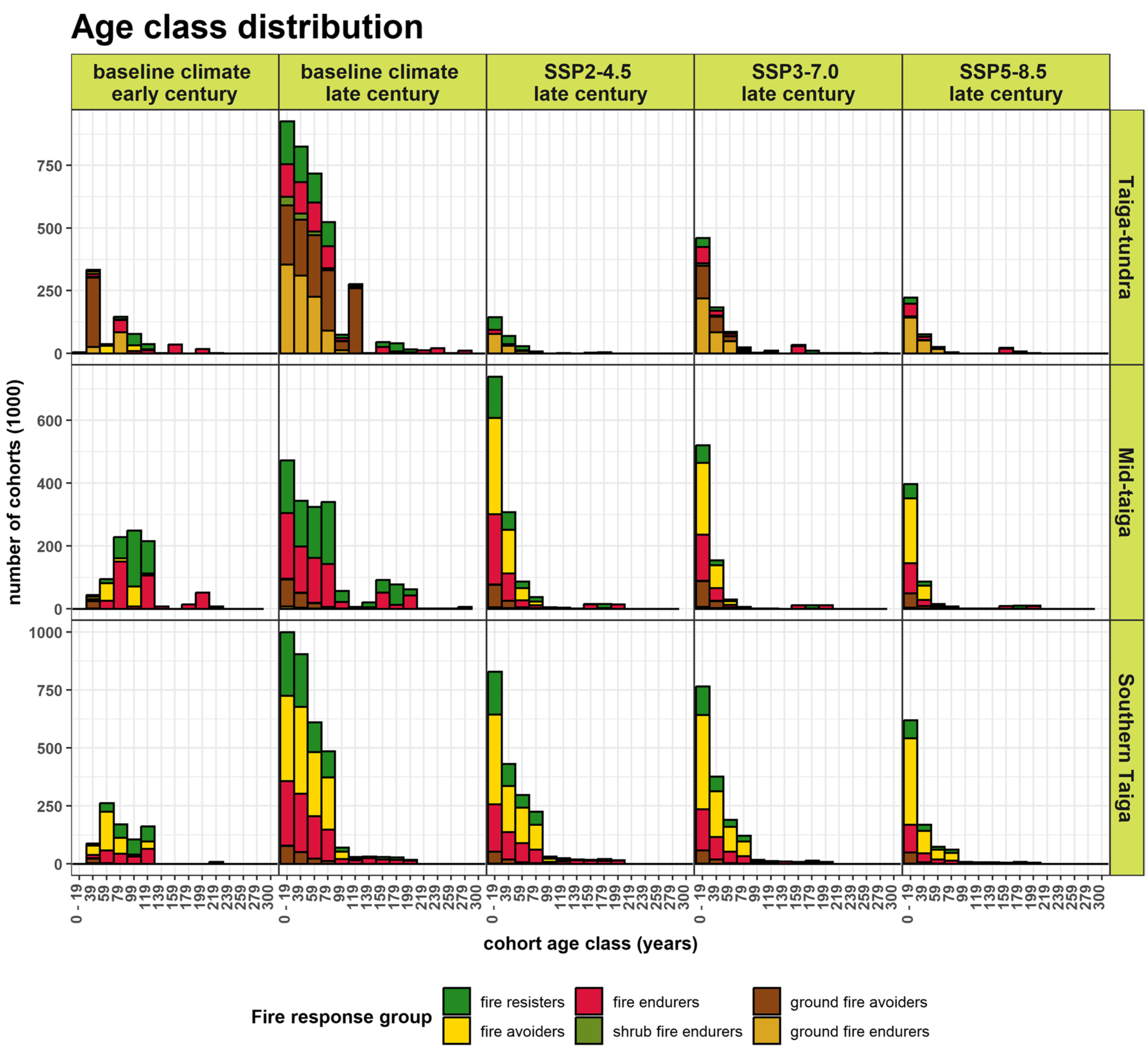

Fig. 9 Age class distributions by fire response group and climate scenario for the Taiga-tundra (top panel), Mid-taiga (middle panel), and Southern taiga (bottom panel) study landscapes. Early-century age class distributions represent the start of simulation, while late-century age class distributions represent the average of the last 15 years of the simulation period (2085–2099), averaged across all simulation replicates. Age classes on the *x*-axis are in 20-year bins from 0 to 300

burn perimeters acted as barriers to fire spread (Parks et al. 2016b; Buma et al. 2020), reducing mean fire size. In the Taiga-tundra landscape, this phenomenon was likely accompanied by fuel limitations imposed by climate-driven mortality events (Fig. 6, right panel) and subsequent regeneration challenges (including light conifers and the moss and herb-dominated vegetation that is a major component of this northern landscape) that collectively reduced fuel availability on the landscape for extended periods (Supplement S2 Figure S6). This rendered large areas of the landscape unable to burn during periods in our simulations, likely reducing the burned area under SSP5-8.5 compared to SSP3-7.0.

Aggregated across our three landscapes, findings from this study imply that climate change is likely to flatten the existing latitudinal gradient in fire regime characteristics in central Siberia. The contemporary fire rotation period in this region varies from more than 1000 years at the northern forest–tundra boundary to less than 50 years at low elevations in the southern taiga (Soja et al. 2006; Shuman et al. 2017; this study). Simulated fire rotation period in our Taiga-tundra landscape decreased from 1198 years under a contemporary climate to 165 years under mild climate warming and 32 years under moderate climate warming, dramatically reducing the difference in fire rotation period between study landscapes. Trial simulations in the Taiga-tundra landscape indicate changes in climate and lightning ignition numbers were each causal factors in the considerable reduction in fire rotation period (Supplement S2 Figure S5).

Changing vegetation

Although periodic fire contributes to the current dominance of fire resisters in central Siberia (Shorohova et al. 2009; Schulze et al. 2012), our simulations imply that climate warming and the associated increase in fire activity could shift forests in the southern and mid-taiga to dominance by fire endurers. Fire endurers—birch and aspen—are widely distributed in southcentral Siberia (Wirth 2005; Kharuk et al. 2021), often forming early- to mid-seral communities that transition to fire avoider dominance by 80 to 100 years following disturbance (Schulze et al. 2005; Wirth 2005; Shorohova et al. 2009). Based on Importance Values (IV), fire endurers were the dominant fire response group on the Southern taiga landscape at the start of simulations, but a minor component in the Mid-taiga. In both landscapes, fire endurer IV progressively increased with the magnitude of simulated climate change. Decomposing IV into changes in biomass and cohort numbers indicates that increased cohort numbers (and extent on the landscape) of fire endurers, accompanied by a parallel decrease in cohort numbers of fire resisters and fire avoiders, was an important driver of increased fire endurer importance in the Mid-taiga (Fig. 7, Supplement S2 Figure S6). In the Southern taiga, fire endurers maintained cohort numbers and extent under climate warming, while suffering lower reductions in absolute biomass than other fire response groups (Fig. 8, Supplement S2 Figures S6 and S7). This transition to fire endurer dominance under climate warming occurred not because of high resistance to the increasingly frequent fires—in fact, fire-driven cohort mortality was more common for fire endurers than any other fire response group in the mid- to late-twenty-first century (Supplement S2 Figures S9 and S10), likely because of their low tolerance of ground fire (Quintilo et al. 1991). Instead, modeled fire endurer dominance in the Southern and Mid-taiga under climate change appears to stem from strong post-fire recruitment, which may occur via seeding from nearby or residual seed sources or resprouting following top-kill by fire.

Climate change and increasing fire activity may together improve the competitiveness of fire endurers in the Southern and Mid-taiga. Climate warming should improve the competitiveness and survival of birch and aspen by reducing the likelihood of cold-kill events and stimulating temperature-limited physiological processes (Brédoire et al. 2020). On wetter sites, climate warming may also increase fire endurer growth rates by reducing soil moisture levels (Kharuk et al. 2014). It is likely that such improvements in competitive status interacted with the resprouting ability and high seed dispersal distance of birch and aspen (Wirth 2005) to facilitate expansion into new growing space created by increased fire activity. In the previously cold-limited Mid-taiga, the aggregate effect of these changes in climate and fire regime was beneficial under all climate change scenarios, resulting in fire endurer expansion. In the Southern taiga, these changes allowed fire endurers to maintain their presence on the landscape despite high fire-related mortality, except under extreme warming (SSP5-8.5) (and associated fire activity) at the end of the twenty-first century. In the latter situation, sharp reductions in absolute biomass and modest reductions in extent (Supplement S2 Figures S6 and S7) imply that severe changes in climate could act as a hindrance to post-fire regeneration of fire endurers.

Transition to fire endurer dominance in southcentral Siberia under climate warming and increasing fire activity is broadly consistent with observations from other boreal regions. In the absence of fire, simulations under moderate and high greenhouse gas emissions scenarios projected an expansion of broadleaved deciduous-dominated forests into areas of Siberia presently dominated by conifers (Shuman et al. 2015). Future fire-mediated shifts from conifer to broadleaved-dominated forests (including birch and aspen) have also been projected in a warmer climate at the temperate-boreal ecotone in northeastern China using a similar forest landscape model to that applied in our study (Xu et al. 2022). In the boreal forests of interior Alaska and northwestern Canada, transition from black spruce (a fire avoider (Rogers et al. 2015)) to broadleaved deciduous dominance has also been observed as a result of increasing fire frequency and soil burn severity (Johnstone & Chapin 2006; Johnstone et al. 2010b). While the fire regime context of boreal North America is markedly different to that of Siberia (de Groot et al. 2013b; Rogers et al. 2015), our finding that increasing fire activity under climate change may increase the relative importance of deciduous broadleaved tree species (fire endurers) is not unprecedented in the boreal zone.

Fire resisters and avoiders remained present in all simulation landscapes under all climate change scenarios, but with greatly reduced biomass and extent under moderate and extreme warming (Supplement S2 Figures S6 and S7). Although changes in IV of fire resisters and avoiders during the twenty-first century differed between climate scenarios and study landscapes, on aggregate, our results paint a picture of fire-induced mortality and inadequate post-fire regeneration under moderate (SSP3-7.0) and extreme (SSP5-8.5) climate change. Generalized across the landscapes and climate scenarios that we examined, mortality from the mid-twenty-first century onwards was dominantly fire-driven. This implies that inadequate regeneration and/or fire-kill of young trees (i.e., fire kill of young cohorts that survived until model cells with eligible for reburning, 10 years following the previous fire) was unable to replace cohorts killed in the increasing fire activity. Mortality of mature trees and reduced opportunity for younger cohorts to progress through to mature and older ages (because of increasing fire on the landscape) is also evident in the notable shift toward younger age-class distributions in all simulation landscapes under climate change, particularly for fire resisters and fire avoiders. Our observations of increased fire endurer cohort numbers and extent (area of the landscape occupied) in the Southern and Mid-taiga under climate warming suggest that competition for growing space in the post-disturbance environment may also have contributed to the observed forest dynamics in these landscapes. In the Taiga-tundra, a landscape in which forests were primarily confined to a large lowland and riparian zone at the start of simulations, competition from riparian shrubs with a fire endurer habit may have contributed to the low regeneration rates. However, climate-driven permafrost thaw (simulated in PnET-Succession) and other more direct climate effects, such as periods of extreme cold, low photosynthetically active radiation, and soil moisture limitations, are also likely to have influenced post-fire recruitment potential (Velichko & Nechaev 1992; Lawrence & Slater 2005).

These simulated forest dynamics align with some previous modeling conclusions, but depart from others. Northward advance of trees into the tundra has been predicted as the climate warms (e.g., Tchebakova et al. 2011), albeit likely with a lagged response to climate (Kruse et al., 2019). Our results suggest that failing to account for fire in vegetation models substantially underestimates future tree mortality at the forest-tundra ecotone, although studies have suggested that fire may also facilitate forest expansion in some areas (Sizov et al., 2021). In the Southern taiga, significant reductions in total landscape-scale biomass and conversion of fire resister-dominated forests to steppe systems have been described as a potential outcome of climate change and increasing fire activity (Tchebakova et al. 2009; Kukavskaya et al. 2016; Sannikov et al. 2020). Although similar to our own conclusions, these changes were accompanied by conversion to steppe systems, rather than deciduous broadleaved forests, and primarily affected sites at lower latitude than our study landscapes. Further, rather than reducing fire resister importance, modeling by Shuman et al. (2017) indicated that relatively extreme climate warming accompanied by increased fire activity may instead increase larch (a fire resister) dominance across much of central Siberia. The individual-based gap model (UVAFME) applied by Shuman et al. (2017) utilizes historic remotely sensed fire characteristics to implement stochastic fire events of varying fire intensity, with the capacity for species- and size-specific mortality. By contrast, the BFOLDS fire extension to the cohort-based LANDIS-II model used in our study explicitly simulates surface and crown fires of any intensity and enables direct fire-vegetation feedbacks, but species- and size (age)-specific mortality is implemented at the scale of model cells (150 m × 150 m in this study), i.e., based on cellwise average cohort characteristics. These various simulation models have strengths and weaknesses for modeling future vegetation dynamics, and each provides a valuable but incomplete perspective on post-fire succession in Siberia. Neither model explicitly simulates soil burning and associated changes in edaphic conditions, which is relevant to seedling establishment in this region. Although post-fire establishment of larch and Scots pine (fire resisters) benefits from the consumption of ground-layer vegetation (e.g., Kharuk et al. 2008a, b; Ivanova et al. 2020), particularly in the permafrost zone (e.g., Knorre et al., 2018; Kirdyanov et al., 2020), empirical data suggests that higher intensity fires that expose mineral soil may instead favor regeneration of deciduous fire endurers, birch and aspen, as well as non-woody vegetation (Chu et al. 2017). Given the influence of these different seedbed preferences on post-fire succession, incorporating process-based linkages between fire behavior, ground vegetation, edaphic conditions, and seedling establishment will improve simulation of the cumulative effects of changing climate and fire behavior on vegetation dynamics in Siberia.

Limitations

LANDIS-II and BFOLDS together have the capability to simulate spatially dynamic interactions between weather, vegetation, and disturbance processes, but climate change projections from GCMs in the CMIP6 project are currently incomplete and not yet available in downscaled format in most regions. As a consequence, our simulations used coarse-resolution climate data that resulted in a relatively small number of model ecoregions per landscape. As these ecoregions are areas of modeled homogenous climate and soils, the coarse resolution of climate inputs feed into lower variance in growing conditions and weather across our simulation landscapes. This reduces the model ability to translate real-world spatial variation in environmental forcings into finer-scale patterns of vegetation growth and blunts the highly dynamic fire simulation capabilities of BFOLDS. Incomplete data availability for some GCMs, such as the CESM2-WACCM model used in our simulations (Supplement S1), also poses a challenge for comprehensive representation of future climate scenarios in forest modeling.

A further limitation on our ability to model fire effects on fine-scale forest dynamics was BFOLDS' evaluation of species- and size-specific mortality at the scale of model cells, rather than individual cohorts within cells. BFOLDS enables highly sophisticated modeling of a wide range of fire intensities and behaviors, including surface and crown fires in open and closed-canopy stands. However, it was developed with the goal of furnishing estimates of fire intensity in the boreal forests of northern Ontario, Canada, where stand-replacing fire is dominant in many forest types (e.g., de Groot et al. 2013a, b). The majority of fires in Siberian fire resister-dominated forests are not high-severity events. For example, an estimated 42% of fires in light conifer stands between 2002 and 2011 were stand-replacing (Krylov et al. 2014). High-severity ground fires are, however, more typical of larch-dominated forests in the permafrost zone and in fire avoider- and fire endurer-dominated communities (e.g., Shorohova et al., 2011; Krylov et al. 2014; Kharuk et al. 2021). In BFOLDS, species- and age-based mortality thresholds for each fuel type allow fine-tuning of mortality to dominant species and ages present on simulation cells. With cells on our simulation landscape measuring 2.25 ha—considerably less than the average large fire in Siberia (1312 ha) (de Groot et al. 2013a, b) or the scale of typical forest stands—evaluation of mortality in BFOLDS occurs at the patch scale and can account for differences in fuel structure at this scale. While this spatial scale is unsuited to fine-scale investigation of fire effects on tree neighborhood dynamics, it remains appropriate for the landscape-scale analysis that is the focus of this study.

At this landscape scale, the limitations imposed by the lack of individualized cohort-based mortality within cells are as follows: (1) biasing post-fire conditions on individual cells toward those associated with high-severity fire (e.g., light conditions), or closed-canopy forest (produced by fires with 0% overstory mortality on the cell). The former condition would favor regeneration by shade-intolerant species—fire endurers (e.g., birch) and fire resisters (e.g., larch)—while the latter would favor regeneration by shade-tolerant species, such as Siberian fir and Siberian spruce (fire avoiders). As these model behaviors apply at the scale of model cells, our results are not suited to inference on post-fire dynamics at the scale of individual tree neighborhoods or across individual fire perimeters. (ii) Hindering model calibration of fire avoider biomass by preventing fire-driven mortality of young understory fire avoiders in fire resister-dominated communities (Schulze et al. 2012; Kharuk et al. 2021). Low- to moderate-intensity fires in fire resister-dominated communities typically cause mortality among young fire avoiders growing in the understory, without killing all overstory trees. This behavior reduces fire avoider biomass and inhibits long-term replacement of fire resisters by avoiders (Shorohova et al 2009 and 2011; Schulze et al. 2012). In BFOLDS, fuel types are assigned based on the dominant (by cohort numbers and age) characteristics of vegetation on the cell. This means that subordinate fuel types with a lower fire tolerance than the dominant vegetation will not suffer fire mortality until (i) the fire-intensity-mortality threshold of the dominant vegetation is exceeded, or (ii) the subordinate vegetation gains dominance in terms of cohort numbers and age. This behavior increased complexity in simultaneously calibrating fire avoider biomass and fire regime characteristics during model set-up, necessitating a balance between accuracy of expected fire regime characteristics and landscape-scale relative vegetation dominance (Supplement S1, Sect. 3.3). Future modifications of BFOLDS will extend the current fuel type fire intensity-mortality thresholds from individual cells to individual cohorts within cells, enabling differential cohort mortality during fire events. This will improve model flexibility and utility across a wider range of spatial scales in regions or forest types characterized by low-severity fire regimes.

LANDIS-II has been widely employed in the study of disturbance and succession (https://www.landis-ii.org/projects), but our experiences highlight the challenges of model application in the extremely harsh environments of northern Siberia. Despite extensive model calibration and clear warming trends in all climate change simulations in our Taiga-tundra landscape (Supplement S1), model cohorts still proved sensitive to extreme weather conditions and short-term climatic deviations (e.g., successive years with extremely low growing season temperatures and photosynthetically active radiation) causing sizable mortality events (e.g., early- to mid-century reductions in importance value or absolute cohort numbers/biomass for one or more species in Fig. 6, Supplement S2 Figures S2, S6 and S7). In our simulations, the normal environmental challenges associated with growth, survival, and reproduction in the harsh conditions at the taiga–tundra ecotone (represented in our baseline climate simulations) may have interacted with other challenges associated with climate change (e.g., permafrost thaw and increasing soil moisture limitations) and increased fire activity to drive further mortality and hinder subsequent regeneration. Stochasticity in the timing of mortality events during our simulations produced variation in the relative importance trends of different fire response groups through time and across climate scenarios in the Taiga-tundra landscape. More widespread application of LANDIS-II at high latitudes will help improve model performance in these extreme environments and strengthen understanding of the role of stochastic climate-related events, and their interaction with disturbance and changes in climate to shape succession.

Finally, while this study is among the first to provide quantitative, mechanistically derived projections of changes in fire regimes and vegetation under climate change in Siberia, our results include only one of several important disturbances in Siberian forests. Fire, harvesting, and insect pests are all disturbances of central importance to forest dynamics in Siberia (Shvidenko et al. 2013; Schaphoff et al. 2016; Kharuk et al. 2021). Such disturbances often provide the catalyst for realignment of vegetation with current and future climate (Gustafson et al. 2010, 2020b; Halofsky et al. 2020). Moreover, disturbance interactions may form a complex web that amplify, reinforce, or mitigate the effect of any single disturbance mode, and many of these interactions could be modified by changes in climate (Millar & Stephenson 2015; Lucash et al. 2018; Sturtevant & Fortin 2021). This study helps illuminate one piece of the complex central Siberian disturbance-web, but further studies are required to expand our perspectives on climate change effects on future forest dynamics in central Siberia (e.g., Brussel et al., Assessing Siberia's response to global change through the lens of tipping points, in preparation).

Conclusions

This study provides one of the first quantitative, mechanistically derived accounts of potential changes in Siberian fire regimes and vegetation under multiple GCM-based climate change scenarios, produced using highly dynamic, process-based vegetation and fire behavior models. Our results suggest that a substantial increase in fire activity is likely across a range of future warming scenarios, resulting in increased annual burned area, the number of fires per year and fire intensity, and a reduction in fire rotation period. These changes are projected to occur throughout a latitudinal gradient ranging from the northern forest-tundra ecotone to the southern taiga, and, collectively, indicate that future fire regimes across this space may display much less heterogeneity than presently exists. Our results suggest that moderate and extreme climate warming, combined with significantly more fire activity, may cause a major transition to fire endurer-dominated forests (birch and aspen being important components) in the southern and mid-taiga with a much younger age class structure and lower biomass than at present. Such changes, if they occur, would have implications for the Eurasian boreal forest carbon cycle, including carbon storage in woody vegetation and emission during fires, as well as the susceptibility of regional forests to emerging and unpredictable climate and disturbance stressors, both natural and anthropogenic in origin.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-023-00188-1.

Additional file 1: Supplement S1.

Additional file 2: Supplement S2.

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Authors' contributions

NGW: study design, model calibration and implementation, data analysis, manuscript preparation; MLS, TB, EJG: study design, model calibration and implementation, manuscript review and editing; MRO: model development and calibration, manuscript review and editing; SAW: model development and calibration, manuscript review and editing; BRS: study design, manuscript review and editing; DCS, AZS: study design, supply of data, provision of expert opinions, manuscript review and editing. The authors read and approved the final manuscript.

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Availability of data and materials

Supplementary material S1 (methods) and S2 (results) will be published online with this manuscript. Data generated during this study and used in the data analysis in this manuscript will be made publicly available on acceptance of this manuscript. Complete LANDIS-II input files for use in our simulations will be uploaded to the LANDIS-II Foundation Github site.

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

Author details

[1]University of Oregon, 1585 E 13Th Avenue, Eugene, Oregon 97403, USA. [2]Present Address: USDA Forest Service, Rocky Mountain Research Station, Oak Ridge Institute for Science and Education, P.O. Box 117, Oak Ridge, TN 37831, USA. [3]Ontario Forest Research Institute, Ministry of Northern Development, Mines, Natural Resources and Forestry, 1235 Queen Street. E, Sault Ste. Marie, ON P6A 2E5, Canada. [4]US Department of Agriculture Forest Service Northern Research Station, 5985 Highway K, Rhinelander, WI 54501-9128, USA. [5]International Institute for Applied Systems Analysis, Schlossplatz 1 - A-2361, Laxenburg, Austria.

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References

Aber, J.D., and C.A. Federer. 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia* 92 (4): 463–474.

Aber, J.D., J.M. Melillo, C.A. McClaugherty, and K.N. Eshleman. 1983. Potential sinks for mineralized nitrogen following disturbance in forest ecosystems. *Environmental Biogeochemistry* 35: 179–192.

Agee, J. 1993. *Fire ecology of Pacific Northwest forests*. Washington, D.C.: Island Press.

Alexander, M.E., B.J. Stocks, and B.D. Lawson. 1991. Fire behavior in black spruce-lichen woodland: the Porter Lake project. In*Forestry Canada Northern Forestry Centre Information Report NOR-X-310*.

Andela, N., D.C. Morton, L. Giglio, R. Paugam, Y. Chen, S. Hantson, G.R. van der Werf, and J.T. Anderson. 2019. The Global Fire Atlas of individual fire size, duration, speed and direction. *Earth System Science Data* 11 (2): 529–552. https://doi.org/10.5194/ESSD-11-529-2019.

Barrett, K., R. Baxter, E. Kukavskaya, H. Balzter, E. Shvetsov, and L. Buryak. 2020. Postfire recruitment failure in Scots pine forests of southern Siberia. *Remote Sensing of Environment* 237: 111539. https://doi.org/10.1016/J.RSE.2019.111539.

Brédoire, F., Z.E. Kayler, J.L. Dupouey, D. Derrien, B. Zeller, P.A. Barsukov, O. Rusalimova, P. Nikitich, M.R. Bakker, and A. Legout. 2020. Limiting factors of aspen radial growth along a climatic and soil water budget gradient in south-western Siberia. *Agricultural and Forest Meteorology* 282–283 (November 2019): 107870. https://doi.org/10.1016/j.agrformet.2019.107870.

Buma, B., Weiss, S., Hayes, K., and M. Lucash. 2020. Wildland fire reburning trends across the US West suggest only short-term negative feedback and differing climatic effects. *Environmental Research Letters*, *15*(3). https://doi.org/10.1088/1748-9326/ab6c70

Chen, Y., D.M. Romps, J.T. Seeley, S. Veraverbeke, W.J. Riley, Z.A. Mekonnen, and J.T. Randerson. 2021. Future increases in Arctic lightning and fire risk for permafrost carbon. *Nature Climate Change* 11 (5): 404–410. https://doi.org/10.1038/s41558-021-01011-y.

Chu, T., Guo, X., and K. Takeda. 2017. Effects of burn severity and environmental conditions on post-fire regeneration in Siberian larch forest. *Forests*;*8*(76). https://doi.org/10.3390/f8030076.

de Groot, W.J. 1998. Interpreting the Canadian Forest Fire Weather Index (FWI) System. In *Proceedings of the Fourth Central Region Fire Weather Committee Scientific and Technical Seminar*, 1–9.

de Groot, W.J., M.D. Flannigan, and A.S. Cantin. 2013a. Climate change impacts on future boreal fire regimes. *Forest Ecology and Management* 294: 35–44. https://doi.org/10.1016/j.foreco.2012.09.027.

de Groot, W.J., A.S. Cantin, M.D. Flannigan, A.J. Soja, L.M. Gowman, and A. Newbery. 2013b. A comparison of Canadian and Russian boreal forest fire regimes. *Forest Ecology and Management* 294: 23–34. https://doi.org/10.1016/j.foreco.2012.07.033.

Dirmeyer, P.A., X. Gao, M. Zhao, Z. Guo, T. Oki, and N. Hanasaki. 2006. GSWP-2: Multimodel analysis and implications for our perception of the land surface. *Bulletin of the American Meteorological Society* 87 (10): 1381–1398. https://doi.org/10.1175/BAMS-87-10-1381.

Eyring, V., S. Bony, G.A. Meehl, C.A. Senior, B. Stevens, R.J. Stouffer, and K.E. Taylor. 2016. Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization. *Geoscientific Model Development* 9 (5): 1937–1958. https://doi.org/10.5194/gmd-9-1937-2016.

Fick, S.E., and R.J. Hijmans. 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37 (12): 4302–4315. https://doi.org/10.1002/joc.5086.

Flannigan, M. 2015. Fire evolution split by continent. *Nature Geoscience* 8 (3): 167–168. https://doi.org/10.1038/ngeo2360.

Flannigan, M.D., K.A. Logan, B.D. Amiro, W.R. Skinner, and B.J. Stocks. 2005. Future area burned in Canada. *Climatic Change* 72: 1–16. https://doi.org/10.1007/s10584-005-5935-y.

Forestry Canada. 1992. *Development and Structure of the Canadian Forest Fire Behavior Prediction System*. Forestry Canada Fire Danger Group Information Report ST-X-3.

Foster, A.C., J.K. Shuman, B.M. Rogers, X.J. Walker, M.C. Mack, L.L. Bourgeau-Chavez, S. Veraverbeke, and S.J. Goetz. 2022. Bottom-up drivers of future fire regimes in western boreal North America. *Environmental Research Letters* 17 (2): 025006.

Fryer, J. L. 2014. *Picea mariana*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: https://www.fs.usda.gov/database/feis/plants/tree/picmar/all.html

Giglio, L., L. Boschetti, D. Roy, A.A. Hoffmann, M. Humber, and J.V. Hall. 2020. *Collection 6 MODIS Burned Area Product User's Guide Version 1.3*. Sioux Falls, SD, USA: NASA EOSDIS Land Processes DAAC.

Goral, F., and J. Schellenberg. 2021. *_goeveg: Functions for Community Data and Ordinations_*. *R package version 0.5.1*.https://CRAN.R-project.org/package=goeveg.

Groisman, P.Y., B.G. Sherstyukov, V.N. Razuvaev, R.W. Knight, J.G. Enloe, N.S. Stroumentova, P.H. Whitfield, E. Førland, I. Hannsen-Bauer, H. Tuomenvirta, H. Aleksandersson, Av. Mescherskaya, and T.R. Karl. 2007. Potential forest fire danger over Northern Eurasia: Changes during the 20th century. *Global and Planetary Change* 56 (3–4): 371–386. https://doi.org/10.1016/J.GLOPLACHA.2006.07.029.

Gustafson, E.J. 2013. When relationships estimated in the past cannot be used to predict the future: using mechanistic models to predict landscape ecological dynamics in a changing world. *Landscape Ecology.* 28: 1429–1437. https://doi.org/10.1007/s10980-013-9927-4.

Gustafson, E.J., and B.R. Miranda. 2022. *PnET-Succession v5.0 Extension User Guide*.

Gustafson, E. J., Kern, C. C., Miranda, B. R., Sturtevant, B. R., Bronson, D. R., & Kabrick, J. M. (2020b). Climate adaptive silviculture strategies: How do they impact growth, yield, diversity and value in forested landscapes? *Forest Ecology and Management*, *470–471*(February), 118208. https://doi.org/10.1016/j.foreco.2020.118208

Gustafson, E. J., Miranda, B. R., Shvidenko, A. Z., and B. R. Sturtevant. 2020a. Simulating growth and competition on wet and waterlogged soils in a forest landscape model. Frontiers in Ecology and Evolution, 8.;https://doi.org/10.3389/fevo.2020.598775.

Gustafson, E. J. Shvidenko, A. Z., and ;R. M. Scheller. 2011. Effectiveness of forest management strategies to mitigate effects of global change in south-central Siberia. *Canadian Journal of Forest Research* ;:1405–1421. https://doi.org/10.1139/x11-065. ;

Gustafson, E.J., A.Z. Shvidenko, B.R. Sturtevant, and R.M. Scheller. 2010. Predicting global change effects on forest biomass and composition in south-central Siberia. *In Ecological Applications* 20 (3): 700–715. https://doi.org/10.1890/08-1693.1.

Halofsky, J. E., Peterson, D. L., and B. J. Harvey. 2020. Changing wildfire, changing forests: The effects of climate change on fire regimes and vegetation in the Pacific Northwest, USA. *Fire Ecology* ;*16*(1). https://doi.org/10.1186/s42408-019-0062-8.

Hengl, T., and R.A. MacMillan. 2019. *Predictive Soil Mapping with R*, 370. Wageningen, the Netherlands: OpenGeoHub foundation. www.soilmapper.org, ISBN: 978–0–359–30635–0.

Hijmans, R. 2022. *_terra: Spatial Data Analysis_*. *R package version 1.5–21*.https://CRAN.R-project.org/package=terra.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50 (3): 346–363. https://doi.org/10.1002/bimj.200810425.

Howard, J. L. 1996. *Populus tremuloides*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: https://www.fs.usda.gov/database/feis/plants/tree/poptre/all.html.

IPCC. 2021. *limate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*https://doi.org/10.3724/sp.j.7103161536.

Ivanova, G.A., V.A. Ivanov, N.M. Kovaleva, S.G. Conard, S.V. Zhila, and P.A. Tarasov. 2017. Succession of vegetation after a high-intensity fire in a pine forest with lichens. *Contemporary Problems of Ecology* 10 (1): 52–61. https://doi.org/10.1134/S1995425517010061.

Ivanova, G. A., Ivanov, V. A., Kukavskaya, E. A., and , A. J. Soja. 2010. The frequency of forest fires in Scots pine stands of Tuva, Russia. *Environmental Research Letters* ;*5*(1). https://doi.org/10.1088/1748-9326/5/1/015002.

Ivanova, G.A., E.A. Kukavskaya, V.A. Ivanov, S.G. Conard, and D.J. McRae. 2020. Fuel characteristics, loads and consumption in Scots pine forests of central Siberia. *Journal of Forestry Research* 31 (6): 2507–2524. https://doi.org/10.1007/s11676-019-01038-0.

Iverson, L.R., A.M. Prasad, S.N. Matthews, and M. Peters. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management* 254 (3): 390–406. https://doi.org/10.1016/j.foreco.2007.07.023.
Johnstone, J.F., and F.S. Chapin. 2006. Fire interval effects on successional trajectory in boreal forests of northwest Canada. *Ecosystems* 9 (2): 268–277. https://doi.org/10.1007/s10021-005-0061-2268.
Johnstone, J.F., F.S. Chapin, T.N. Hollingsworth, M.C. Mack, V. Romanovsky, and M. Turetsky. 2010a. Fire, climate change, and forest resilience in interior Alaska. *Canadian Journal of Forest Research* 40 (7): 1302–1312. https://doi.org/10.1139/X10-061/ASSET/IMAGES/LARGE/X10-061F6.JPEG.
Johnstone, J.F., T.N. Hollingsworth, F.S. Chapin, and M.C. Mack. 2010b. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology* 16 (4): 1281–1295. https://doi.org/10.1111/j.1365-2486.2009.02051.x.
Kassambara, A. 2020. *_ggpubr: 'ggplot2' Based Publication Ready Plots_. R package version 0.4.0.*https://CRAN.R-project.org/package=ggpubr.
Kharuk, V.I., and E.I. Ponomarev. 2017. Spatiotemporal characteristics of wildfire frequency and relative area burned in larch-dominated forests of Central Siberia. *Russian Journal of Ecology* 48 (6): 507–512. https://doi.org/10.1134/S1067413617060042.
Kharuk, V.I., M.L. Dvinskaya, K.J. Ranson, and S.T. Im. 2005. Expansion of evergreen conifers to the larch-dominated zone and climatic trends. *Russian Journal of Ecology* 36 (3): 186–193.
Kharuk, V.I., M.L. Dvinskaya, S.T. Im, and K.J. Ranson. 2008b. Tree vegetation of the forest-tundra ecotone in the Western Sayan mountains and climatic trends. *Russian Journal of Ecology* 39 (1): 8–13. https://doi.org/10.1134/S1067413608010025.
Kharuk, V.I., K.J. Ranson, S.T. Im, and M.L. Dvinskaya. 2009. Response of *Pinus sibirica* and *Larix sibirica* to climate change in southern Siberian alpine forest-tundra ecotone. *Scandinavian Journal of Forest Research* 24 (2): 130–139. https://doi.org/10.1080/02827580902845823.
Kharuk, V. I., Ranson, K. J., and M. L. Dvinskaya. 2008a. Wildfires dynamic in the larch dominance zone. *Geophysical Research Letters* ;*35*(1). https://doi.org/10.1029/2007GL032291.
Kharuk, V.I., V.V. Kuzmichev, S.T. Im, and K.J. Ranson. 2014. Birch stands growth increase in Western Siberia Birch stands growth increase in Western Siberia. *Scandinavian Journal of Forest Research*. https://doi.org/10.1080/02827581.2014.912345.
Kharuk, V.I., E.I. Ponomarev, G.A. Ivanova, M.L. Dvinskaya, S.C.P. Coogan, and M.D. Flannigan. 2021. Wildfires in the Siberian taiga. *Ambio*. https://doi.org/10.1007/s13280.
Kidnie, S.M., B.M. Wotton, and W.N. Droog. 2010. *Field guide for predicting fire behaviour in Ontario's Tallgrass Prairie*.
Kirdyanov A.V., M. Saurer, S. Rolf, A.K. Knorre, A.S. Prokushkin, O.V. Churakova, V.F. Marina, and B. Ulf. 2020. Long-term ecological consequences of forest fires in the continuous permafrost zone of Siberia. *Environmental Research Letters* 15(3) 034061-10.1088/1748-9326/ab7469
Kirillina, K., E.G. Shvetsov, V.v. Protopopova, L. Thiesmeyer, and W. Yan. 2020. Consideration of anthropogenic factors in boreal forest fire regime changes during rapid socio-economic development: case study of forestry districts with increasing burnt area in the Sakha Republic, Russia. *Environmental Research Letters* 15 (3): 035009. https://doi.org/10.1088/1748-9326/AB6C6E.
Knorre, A.A., A.V. Kirdyanov, A.S. Prokushkin, P.J. Krusic, and U. Büntgen. 2018. Tree ring-based reconstruction of the long-term influence of wildfires on permafrost active layer dynamics in Central Siberia. *Science of the Total Environment* 652: 314–319. https://doi.org/10.1016/j.scitotenv.2018.10.124.
Krawchuk, M.A., and M.A. Moritz. 2011. Constraints on global fire activity vary across a resource gradient. *Ecology* 92 (1): 121–132. https://doi.org/10.1890/09-1843.1.
Krawchuk, M.A., S.G. Cumming, and M.D. Flannigan. 2009. Predicted changes in fire weather suggest increases in lightning fire initiation and future area burned in the mixedwood boreal forest. *Climatic Change* 92 (1): 83–97. https://doi.org/10.1007/s10584-008-9460-7.
Kruse, S., A. Gerdes, N.J. Kath, L.S., Epp, K.R. Stoof-Leichsenring, L.A. Pestryakova, and U. Herzschuh. 2019. Dispersal distances and migration rates at the arctic treeline in Siberia – a genetic and simulation-based study. *Biogeosciences* 16 (6): 1211-1224. https://doi.org/10.5194/bg-16-1211-2019
Krylov, A., J.L. McCarty, P. Potapov, T. Loboda, A. Tyukavina, S. Turubanova, and M.C. Hansen. 2014. Remote sensing estimates of stand-replacement fires in Russia, 2002–2011. *Environmental Research Letters* 9 (10): 105007.
Kukavskaya, E. A., Buryak, L. V., Ivanova, G. A., Conard, S. G., Kalenskaya, O. P., Zhila, S. V., and D. J. McRae. 2013. Influence of logging on the effects of wildfire in Siberia. *Environmental Research Letters*, *8*. https://doi.org/10.1088/1748-9326/8/4/045034.
Kukavskaya, E.A., G.A. Ivanova, S.G. Conard, D.J. McRae, and V.A. Ivanov. 2014. Biomass dynamics of central Siberian Scots pine forests following surface fires of varying severity. *International Journal of Wildland Fire* 23 (6): 872–886. https://doi.org/10.1071/WF13043.
Kukavskaya, E.A., L.V. Buryak, E.G. Shvetsov, S.G. Conard, O.P. Kalenskaya, and V.N. Sukachev. 2016. The impact of increasing fire frequency on forest transformations in southern Siberia. *Forest Ecology and Management* 382: 225–235. https://doi.org/10.1016/j.foreco.2016.10.015.
Lawrence, D. M., and A. G. Slater. 2005. A projection of severe near-surface permafrost degradation during the 21st century. *Geophysical Research Letters* ;32(24). https://doi.org/10.1029/2005GL025080.
Lawson, B.D., and O.B. Armitage. 2008. *Weather Guide for the Canadian Forest Fire Danger Rating System*.
Lawson, B.D., ; Armitage, O.B., and W.D. Hoskins. 1996. Diurnal variation in the Fine Fuel Moisture Code: tables and computer source code. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre and B.C. Ministry of Forest Resources, Branch, Victoria, BC. FRDA Rep. 245. 20 p.
Loboda, T.V., and D. Chen. 2017. Spatial distribution of young forests and carbon fluxes within recent disturbances in Russia. *Global Change Biology* 23 (1): 138-153. https://doi.org/10.1111/gcb.13349
Long, J.A. 2022. *_jtools: Analysis and Presentation of Social Scientific Data_. R package version 2.2.0.*https://cran.r-project.org/package=jtools.
Lucash, M.S., and R.M. Scheller. 2021. *LANDIS-II Climate Library v4.2 User Guide*.
Lucash, M. S., Scheller, R. M., Sturtevant, B. R., Gustafson, E. J., Kretchun, A. M., and J. R. Foster. 2018. More than the sum of its parts: how disturbance interactions shape forest dynamics under climate change. *Ecosphere* ;*9*(6). https://doi.org/10.1002/ecs2.2293.
Mack, M.C., X.J. Walker, J.F. Johnstone, H.D. Alexander, A.M. Melvin, M. Jean, and S.N. Miller. 2021. Increased dominance of deciduous trees. *Science* 372 (6539): 280–283. https://doi.org/10.1126/science.abf3903.
Maechler, M., P. Rousseeuw, A. Struyf, M. Hubert, and K. Hornik. 2012. Cluster: Cluster analysis basics and extensions. *R Package Version* 1 (2): 56.
Malevsky-Malevich, S.P., E.K. Molkentin, E.D. Nadyozhina, and O.B. Shklyarevich. 2007. An assessment of potential change in wildfire activity in the Russian boreal forest zone induced by climate warming during the twenty-first century. *Climatic Change* 86: 463–474. https://doi.org/10.1007/s10584-007-9295-7.
McCarty, J.L., J. Aalto, V.V. Paunu, S.R. Arnold, S. Eckhardt, Z. Klimont, J.J. Fain, N. Evangeliou, A. Venäläinen, N.M. Tchebakova, E.I. Parfenova, K. Kupiainen, A.J. Soja, L. Huang, and S. Wilson. 2021. Reviews and syntheses: Arctic fire regimes and emissions in the 21st century. *Biogeosciences* 18 (18): 5053–5083. https://doi.org/10.5194/BG-18-5053-2021.
McRae, D.J., J.-Z. Jin, S.G. Conard, A.I. Sukhinin, G.A. Ivanova, and T.W. Blake. 2005. Infrared characterization of fine-scale variability in behavior of boreal forest fires 1. *Canadian Journal of Forest Research* 35: 2194–2206. https://doi.org/10.1139/X05-096.
McRae, D.J., S.G. Conard, G.A. Ivanova, A.I. Sukhinin, S.P. Baker, Y.N. Samsonov, et al. 2006. Variability of fire behavior, fire effects, and emissions in Scotch pine forests of Central Siberia. *Mitigation and Adaptation Strategies for Global Change* 11 (1): 45–74.
Millar, C.I., and N.L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. *Science* 349 (6250): 823–826. https://doi.org/10.1126/science.aaa9933.
Miller, E.A. 2020. A conceptual interpretation of the drought code of the Canadian forest fire weather index system. *Fire* 3 (2): 1–8. https://doi.org/10.3390/fire3020023.
Miller, J.D., C.N. Skinner, H.D. Safford, E.E. Knapp, and C.M. Ramirez. 2012. Trends and causes of severity, size, and number of fires in northwestern California, USA. *Ecological Applications* 22 (1): 184–203. https://doi.org/10.1890/10-2108.1.
Miquelajauregui, Y., S.G. Cumming, and S. Gauthier. 2016. Modelling variable fire severity in boreal forests: Effects of fire intensity and stand structure.

PLoS one 11 (2): e0150073. https://doi.org/10.1371/journal.pone.0150073.
Müller, K. 2020. *_here: A Simpler Way to Find Your Files_. R package version 1.0.1*https://CRAN.R-project.org/package=here.
Nikolov, N., and H. Helmisaari. 1992. Silvics of the circumpolar boreal forest tree species. In *A systems analysis of the global boreal forest (pp. 13–84)*, ed. H. Shugart, R. Leemans, and G. Bonan, 565. Cambridge: Cambridge University Press.
Parks, S. A., Miller, C., Abatzoglou, J. T., Holsinger, L. M., Parisien, M. A., and S. Z. Dobrowski. 2016a. How will climate change affect wildland fire severity in the western US? *Environmental Research Letters* ;*11*(3). https://doi.org/10.1088/1748-9326/11/3/035002.
Parks, S.A., C. Miller, L.M. Holsinger, L.S. Baggett, B.A. Bird, and B. J., & Leopold, A. 2016b. Wildland fire limits subsequent fire occurrence. *International Journal of Wildland Fire* 25: 182–190. https://doi.org/10.1071/WF15107.
Pebesma, E. 2018. Simple features for R: Standardized support for spatial vector data. *The R Journal* 10 (1): 439–446. https://doi.org/10.32614/RJ-2018-009.
Perera, A.H., M.R. Ouellette, and D. Boychuk. 2014. *BFOLDS Fire Regime Module v2 .0 User Guide for LANDIS-II Extension*.
Peters, M.P., A.M. Prasad, S.N. Matthews, and R. Iverson. 2020. *Climate change tree atlas, Version 4*. Delaware, OH: U.S. Forest Service, Northern Research Station and Northern Institute of Applied Climate Science https://www.nrs.fs.fed.us/atlas.
Petrov, I.A., A.S. Shushpanov, A.S. Golyukov, and V.I. Kharuk. 2019. *Pinus sibirica* Du Tour response to climate change in the forests of the Kuznetsk Alatau Mountains. *Сибирский Лесной Журнал* 5: 43–53. https://doi.org/10.15372/sjfs20190506.
Pinheiro, J., D. Bates. 2022. *_nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3.1–157*https://CRAN.R-project.org/package=nlme.
Ponomarev, E., A. Zabrodin, and T. Ponomareva. 2022. Classification of fire damage to boreal forests of Siberia in 2021 based on the dNBR index. *Fire* 5 (1): p.19.
Ponomarev, E. I., Kharuk, V. I., Ranson, K. J., Bergeron, Y., and ;S. Gauthier. 2016. Wildfires dynamics in Siberian larch forests. *Forests* ;*7*(125). https://doi.org/10.3390/f7060125.
Ponomarev, E., N. Yakimov, T. Ponomareva, O. Yakubailik, and S.G. Conard. 2021. Current trend of carbon emissions from wildfires in Siberia. *Atmosphere* 12 (5): 1–15. https://doi.org/10.3390/atmos12050559.
Puettmann, K. J. 2021. Extreme events: Managing forests when expecting the unexpected. *Journal of Forestry*:422–431. https://doi.org/10.1093/jofore/fvab014
Puettmann, K.J. 2011. Silvicultural challenges and options in the context of global change: "Simple" fixes and opportunities for new management approaches.*Journal of Forestry* 109 (6): 321–311 https://academic.oup.com/jof/article/109/6/321/4734860.
Quintilo, D., M.E. Alexander, and R.L. Ponto. 1991. *Spring fires in a semimature trembling aspen stand in central Alberta.* Forestry Canada Northern Forestry Centre, NOR-X-323.
R Core Team. 2022. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing https://www.R-project.org/.
Rogers, B.M., A.J. Soja, M.L. Goulden, and J.T. Randerson. 2015. Influence of tree species on continental differences in boreal fires and climate feedbacks. *Nature Geoscience* 8 (3): 228–234. https://doi.org/10.1038/NGEO2352.
Rogers, B.M., A.J. Soja, M.L. Goulden, and J.T. Randerson. 2017. *Fire intensity and burn severity metrics for circumpolar boreal forests, 2001–2013*. Tennessee, USA: ORNL DAAC, Oak Ridge. https://doi.org/10.3334/ORNLDAAC/1520.
Rogers, B.M., J.K. Balch, S.J. Goetz, C.E.R. Lehmann, and M. Turetsky. 2020. Focus on changing fire regimes: Interactions with climate, ecosystems, and society. *Environmental Research Letters* 15 (3): 030201. https://doi.org/10.1088/1748-9326/AB6D3A.
Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. In *The role of fire in northern circumpolar ecosystems*, ed. R.W. Wein and D.A. McLean, 135–154. Chichester: Wiley.
Saha, S., et al. 2010. NCEP Climate Forecast System Reanalysis (CFSR) Selected Hourly Time-Series Products, January 1979 to December 2010. In *Research Data Archive at the National Center for Atmospheric Research, Computational and Information Systems Laboratory*. https://doi.org/10.5065/D6513W89. Accessed Sept 2021.
Sannikov, S.N., N.S. Sannikova, I. Petrova, and v, & Cherepanova, O. E. 2020. The forecast of fire impact on *Pinus sylvestris* renewal in southwestern Siberia. *Journal of Forestry Research*. https://doi.org/10.1007/s11676-020-01260-1.
Schaphoff, S., C.P. Reyer, D. Schepaschenko, D. Gerten, and A. Shvidenko. 2016. Tamm Review: Observed and projected climate change impacts on Russia's forests and its carbon balance. *Forest Ecology and Management* 361: 432–444. https://doi.org/10.1016/j.foreco.2015.11.043.
Scheller, R.M. 2020. *LANDIS-II Biomass Community Output v2.0 Extension User Guide*, 0–4.
Scheller, R.M., and J.B. Domingo. 2020. *LANDIS-II Age Reclass Output v3.0 Extension User Guide*.
Scheller, R.M., J.B. Domingo, B.R. Sturtevant, J.S. Williams, A. Rudy, E.J. Gustafson, and D.J. Mladenoff. 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling* 201 (3–4): 409–419. https://doi.org/10.1016/j.ecolmodel.2006.10.009.
Schepaschenko, D., L. See, S. Fritz, I. McCallum, C. Schill, C. Perger, A. Baccini, H. Gallaun, G. Kindermann, F. Kraxner, S. Saatchi, M. Obersteiner, M. Santoro, C. Schmullius, A. Shvidenko, and M. Schepaschenko. 2012. *Observing Forest Biomass Globally*. Earthzine.
Schepaschenko, D., E. Moltchanova, A. Shvidenko, V. Blyshchyk, E. Dmitriev, O. Martynenko, L. See, and F. Kraxner. 2018. Improved estimates of biomass expansion factors for Russian forests. *Forests* 9 (6): 312. https://doi.org/10.3390/f9060312.
Schepaschenko, D., See, L., Lesiv, M., McCallum, I., Fritz, S., Salk, C., Moltchanova, E., Perger, C., Shchepashchenko, M., Shvidenko, A., Kovalevskyi, S., Gilitukha, D., Albrecht, F., Kraxner, F., Bun, A., Maksyutov, S., Sokolov, A., Dürauer, M., Obersteiner, M., …, and P. Ontikov. 2015. Development of a global hybrid forest mask through the synergy of remote sensing, crowdsourcing and FAO statistics. *Remote Sensing of Environment* ;162:208–220. https://doi.org/10.1016/j.rse.2015.02.011.
Schepaschenko, D., Shvidenko, A., Usoltsev, V., Lakyda, P., Luo, Y., Vasylyshyn, R., ... and ;M. Obersteiner. 2017. A dataset of forest biomass structure for Eurasia. *Scientific Data* ;4(1):1–11. https://doi.org/10.1038/sdata.2017.70.
Schulze, ED., C. Wirth, D. Mollicone, and W. Ziegler. 2005. Succession after stand replacing disturbances by fire, wind throw, and insects in the dark Taiga of Central Siberia. *Oecologia* 146: 77–88. https://doi.org/10.1007/s00442-005-0173-6.
Schulze, ED., C. Wirth, D. Mollicone, N. von Lupke, W. Ziegler, F. Achard, M. Mund, A. Prokushkin, and S. Scherbina. 2012. Factors promoting larch dominance in central Siberia: Fire versus growth performance and implications for carbon dynamics at the boundary of evergreen and deciduous conifers. *Biogeosciences* 9: 1405–1421. https://doi.org/10.5194/bg-9-1405-2012.
Serra-Diaz, J. M., Maxwell, C., Lucash, M. S., Scheller, R. M., Laflower, D. M., Miller, A. D., Tepley, A. J., Epstein, H. E., Anderson-Teixeira, K. J., and ; J. R. Thompson. 2018. Disequilibrium of fire-prone forests sets the stage for a rapid decline in conifer dominance during the 21st century. *Scientific Reports* ;*8*(1). https://doi.org/10.1038/s41598-018-24642-2.
Shorohova, E., D. Kneeshaw, T. Kuuluvainen, and S. Gauthier. 2011. Variability and dynamics of old-growth forests in the circumboreal zone: implications for conservation restoration and management. *Silva Fennica* 45 (5). https://doi.org/10.14214/sf.72
Shvetsov, E. G., Kukavskaya, E. A., Buryak, L. V., and K. Barrett. 2019. Assessment of post-fire vegetation recovery in Southern Siberia using remote sensing observations. *Environmental Research Letters* ;*14*(5). https://doi.org/10.1088/1748-9326/ab083d.
Shorohova, E., T. Kuuluvainen, A. Kangur, and K. Jõgiste. 2009. Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: A review with special reference to Russian studies. *Annals of Forest Science* 66 (2): 201–201. https://doi.org/10.1051/forest/2008083.
Shuman, J.K., N.M. Tchebakova, E.I. Parfenova, A.J. Soja, H.H. Shugart, D. Ershov, and K. Holcomb. 2015. Forest forecasting with vegetation models across Russia. *Canadian Journal of Forest Research* 45 (2): 175–184.
Shuman, J. K., Foster, A. C., Shugart, H. H., Hoffman-Hall, A., Krylov, A., Loboda, T., Ershov, D., and E. Sochilova. 2017. Fire disturbance and climate change: Implications for Russian forests. *Environmental Research Letters* ;*12*(3). https://doi.org/10.1088/1748-9326/aa5eed.

Shvidenko, A.Z., and S. Nilsson. 2000. Extent, distribution, and ecological role of fire in Russian forests. In *Fire, climate change, and carbon cycling in the boreal forest*, ed. E.S. Kasischke and B.J. Stocks, 132–150. New York, NY: Springer.
Shvidenko, A., and S. Nilsson. 2002. Dynamics of Russian forests and the carbon budget in 1961–1998: An assessment based on long-term forest inventory data. *Climatic Change* 55 (1): 5–37.
Shvidenko, A.Z., and D.G. Schepaschenko. 2013. Climate change and wildfires in Russia. *Contemporary Problems of Ecology* 6 (7): 683–692. https://doi.org/10.1134/S199542551307010X.
Shvidenko, A.Z., E. Gustafson, A.D. McGuire, V.I. Kharuk, D.G. Schepaschenko, H.H. Shugart, et al. 2013. Terrestrial ecosystems and their change. In *Regional Environmental Changes in Siberia and their Global Consequences*, ed. P.Y. Groisman and G. Gutman, 171–249. Springer.
Sizov, O., E. Ezhova, P. Tsymbarovich, A. Soromoti, N. Prihod'ko, T. Petäjä, S. Zilitinkevich, M. Kulmala, J. Bäck, and K. Köster. 2021. Fire and vegetation dynamics in northwest Siberia during the last 60 years based on high-resolution remote sensing. *Biogeosciences* 18 (1): 207-228. https://doi.org/10.5194/bg-18-207-2021
Sofronov, M.A., and A.V. Volokitina. 2010. Wildfire ecology in continuous permafrost zone. In *Permafrost ecosystems, Siberian larch forests*, ed. A. Osawa, O. Zyryanova, Y. Matsuura, T. Kajimoto, and R. Wein, 59–82. Dordrecht: Springer.
Sofronov, M.A., A. V. Volokitina, and T. M. Sofronova. 2008. Fires and pyrogenic successions in the forests of the south Baikal region. *Contemporary Problems of Ecology* 1 (3): 304-309. https://doi.org/10.1134/S199542550803003X
Soja, A.J., H.H. Shugart, A. Sukhinin, S. Conard, and P.W. Stackhouse. 2006. Satellite-derived mean fire return intervals as indicators of change in Siberia (1995–2002). *Mitigation and Adaptation Strategies for Global Change* 11 (1): 75–96.
Stocks, B.J., M.A. Fosberg, T.J. Lynham, L. Mearns, B.M. Wotton, Q. Yang, J.-Z. Jin, K. Lawrence, G.R. Hartley, J.A. Mason, and D.W. Mckenney. 1998. Climate change and forest fire potential in Russian and Canadian boreal forests. *Climatic Change* 38: 1–13.
Sturtevant, B.R., and M.J. Fortin. 2021. Understanding and modeling forest disturbance interactions at the landscape level. *Frontiers in Ecology and Evolution* 9: 636. https://doi.org/10.3389/FEVO.2021.653647/BIBTEX.
Sturtevant, B.R., R.M. Scheller, B.R. Miranda, D. Shinneman, and A. Syphard. 2009. Simulating dynamic and mixed-severity fire regimes: A process-based fire extension for LANDIS-II. *Ecological Modelling* 220 (23): 3380–3393. https://doi.org/10.1016/j.ecolmodel.2009.07.030.
Talucci, A.C., M.M. Loranty, and H.D. Alexander. 2022. Siberian taiga and tundra fire regimes from 2001–2020. *Environmental Research Letters* 17 (2): 025001. https://doi.org/10.1088/1748-9326/AC3F07.
Tchebakova, N.M., E. Parfenova, and A.J. Soja. 2009. The effects of climate, permafrost and fire on vegetation change in Siberia in a changing climate. *Environmental Research Letters* 4 (4): 045013. https://doi.org/10.1088/1748-9326/4/4/045013.
Tchebakova, N.M., E.I. Parfenova, and A.J. Soja. 2011. Climate change and climate-induced hot spots in forest shifts in central Siberia from observed data. *Regional Environmental Change* 11 (4): 817–827. https://doi.org/10.1007/s10113-011-0210-4.
Tchebakova, N.M., E.I. Parfenova, M.A. Korets, and S.G. Conard. 2016. Potential change in forest types and stand heights in central Siberia in a warming climate. *Environmental Research Letters* 11 (3): 035016. https://doi.org/10.1088/1748-9326/11/3/035016.
Tollefson, J.E., 2007. *Betula nana*. IN: Fischer, W.C. (compiler). The fire effects information system. United States Department of Agriculture, Forest Service, Intermountain Research Station, Intermountain Fire Sciences Laboratory, Missoula, Montana. http://www.fs.fed.us/database/feis/plants/shrub/betnan/introductory.html.
Uchytil, R.J. 1991. Betula papyrifera. In Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: https://www.fs.usda.gov/database/feis/plants/tree/betpap/all.html.
van Wagner, C.E., and T.L. Pickett. 1985. Equations and FORTRAN program for the Canadian Forest Fire Weather Index System. *Canadian Forest Service. Forestry Technical Report*, 33 https://cfs.nrcan.gc.ca/publications?id=19973.
Velichko, A.A., and V.P. Nechaev. 1992. Evaluation of the permafrost zone dynamics in Northern Eurasia under global climate warming. *Transactions of the Russian Academy of Sciences, Geography Series.* 324: 667–671.
Volokitina, A., A. Kalachev, M. Korets, and T. Sofronova. 2021. Fire behavior prediction in larch forests of the Kazakhstan Altai. *Symmetry* 13 (4): 578–590. https://doi.org/10.3390/sym13040578.
Wang, X., B.M. Wotton, A. Cantin, M.A. Parisien, K. Anderson, B. Moore, and M.D. Flannigan. 2017. cffdrs: An R package for the Canadian Forest Fire Danger Rating System. *Ecological Processes* 6 (1): 5. https://doi.org/10.1186/s13717-017-0070-z.
Wickham, et al. 2019. Welcome to the tidyverse. *Journal of Open Source Software* 4 (43): 1686. https://doi.org/10.21105/joss.01686.
Wirth, C. 2005. *Fire Regime and Tree Diversity in Boreal Forests ;: Implications for the Carbon Cycle* (M. Scherer-Lorenzen & E. D. Schulze, Eds.; Forest Diversity, Issue January 2005). Springer Berlin Heidelberg. ; https://doi.org/10.1007/3-540-26599-6.
Wirth, C., E.-D. Schulze, W. Schulze, D. von Stunzner-Karbe, W. Ziegler, I.M. Miljukova, A. Sogatchev, A.B. Varlagin, M. Panvyorov, S. Grigoriev, W. Kusnetzova, M. Siry, G. Hardes, R. Zimmermann, and N.N. Vygodskaya. 1999. Above-ground biomass and structure of pristine Siberian Scots pine forests as controlled by competition and fire. *Oecologia* 121: 66–80.
Xu, W., He, H. S., Huang, C., Duan, S., Hawbaker, T. J., Henne, P. D., ... ; and Z. Zhu. 2022. Large fires or small fires, will they differ in affecting shifts in species composition and distributions under climate change? *Forest Ecology and Management* ;510:120131. https://doi.org/10.1016/j.foreco.2022.120131
Yee, T.W. 2022. *VGAM: Vector generalized linear and additive models. R package version 1*, 1–6. ;https://CRAN.R-project.org/package=VGAM.
Yevdokimenko, M.D. 2011. Forest-ecological consequences of fires in light conifer forests of Transbaikalia. *Russian Journal of Ecology* 42 (3): 205–210. https://doi.org/10.1134/S1067413611030052.
Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev, and G.M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*, vol. 574. New York: Springer.

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