

RESEARCH ARTICLE

Wildfire, salvage logging and warming: Their interactive effects on boreal conifer reforestation

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Abstract

1. In Boreal forests, wildfires are common disturbance agents, important for sustaining forest regeneration and ecosystem processes. However, climate warming has intensified fire activity and severity in recent years, and warmer conditions following fire can alter environmental factors affecting tree seedling survival and growth. Management interventions can potentially counterbalance the effects of fire severity and warming.
2. Using a field experiment, we investigated the main and interactive effects of fire severity, experimental warming, understory shrub presence and salvage logging on the growth of different conifer (*Picea abies* and *Pinus sylvestris*) provenances, to provide insight about how tree seedlings of various species respond to multiple environmental drivers following fire.
3. Our study shows that low fire severity without salvage logging resulted in poorer seedling above-ground growth, whereas experimental warming and ericaceous shrubs removal increased seedling biomass regardless of fire severity or logging treatment.
4. Our results suggest that enhanced light availability and reduced resource competition from the understory supports the growth of conifer seedlings following fire. Post-fire warming further stimulated the growth of conifer seedlings (particularly in high-severity burn areas) potentially due to increased early colonization by fast-growing deciduous trees. Moreover, in warmer conditions, northern provenances of *P. sylvestris* planted in southern locations also showed greater height growth compared to local populations, highlighting the potential for assisted migration under climate change.

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5. *Synthesis and applications.* This study demonstrates that artificial regeneration through planting can support forest recovery following wildfire, especially under high fire severity in sites where natural regeneration is poor. Salvage logging can enhance the growth of *P. sylvestris* seedlings and indirectly benefit *P. abies* on low-severity sites by facilitation by deciduous species that create favourable microhabitats. However, the broader ecological impacts of salvage logging (such as on biodiversity loss and soil and habitat structure) must be considered in management planning. Post-fire vegetation management, including control of competitive ericaceous shrubs, may further improve seedling establishment. Selecting climate-adapted seedling provenances can boost reforestation success under future warming. These findings support an adaptive management framework that integrates fire severity, logging intensity, understory control and assisted migration to foster resilient forest landscapes in a changing climate.

KEYWORDS

assisted migration, boreal forest, climate warming, conifer reforestation, fire severity, open-top chamber, provenances, salvage logging

1 | INTRODUCTION

Wildfires are a natural disturbance in boreal forests that support ecosystem functioning and forest regeneration (Certini, 2005; Johnstone et al., 2004; Kuuluvainen & Rouvinen, 2000). By eliminating fire-intolerant species, wildfires initiate secondary succession and increase light, space and nutrients for fire-tolerant and pioneer species (DeLuca et al., 2002; Schimmel & Granstrom, 1996). In the past decade, Swedish boreal forests have experienced the largest and most intense wildfires in a century, driven by rising summer temperatures and prolonged drought (Aakala et al., 2018; Granström, 2018; Myndigheten för samhällsskydd och beredskap, 2015). These fires often result in high tree mortality and stand-replacing events. Anthropogenic climate warming may lead to greater fire severity, potentially initiating a positive feedback loop, whereby enhanced carbon (C) release to the atmosphere may further enhance global warming (Field et al., 2007; Mack et al., 2011). The extent of this feedback likely depends on how quickly forests regenerate after fire.

Eurasian fires have typically been low-intensity ground fires (Archibald et al., 2013; Rogers et al., 2015). However, due to the accelerating effect of climate change, high-severity fires causing 100% tree mortality are now emerging in Eurasia (Flannigan et al., 2013; Tyukavina et al., 2022). This shift has led to post-fire recruitment failures and an increased risk of ecosystem state change (Baltzer et al., 2021; Burrell et al., 2022; Johnstone et al., 2016; Stevens-Rumann et al., 2018). In addition to global warming indirectly impacting forests via its effect on fire regime, higher temperatures through warming may also directly impact the establishment and growth of boreal forests following fire, with consequences for their capacity to assimilate carbon dioxide, produce biomass and recover carbon stocks (Davis et al., 2023; Goetz et al., 2005;

Johnstone et al., 2016). By the end of the 21st century, temperatures in northern Europe are projected to rise by 2.7°C in summer and 4.3°C in winter (Christensen et al., 2007). Longer growing seasons and warmer springs may boost tree growth and productivity (Bergh et al., 2003; Devi et al., 2020; Kellomäki et al., 2018), partly by triggering earlier bud burst, though this may also increase seedling vulnerability to spring frost (Hänninen, 1991). At the same time, warming may lead to increased drought stress during the post-fire establishment phase, particularly in exposed, severely burned sites where soils retain less moisture (Whitman et al., 2019). Such conditions can limit seedling survival before growth even begins. Further, extreme events like heatwaves, prolonged periods of drought and reduced precipitation may impair biomass accumulation and reduce survival (Jönsson & Lagergren, 2018; Teskey et al., 2015; Venäläinen et al., 2020). Climate warming effects on regeneration may also operate indirectly by altering soil moisture and fertility (Allison & Treseder, 2008), which may counteract some of the direct positive effects of increased temperature (Reich et al., 2018).

The post-fire forest recovery is also influenced by the competition, and the growth of seedlings may depend on the composition of the understory plant community. For example, ericaceous dwarf shrubs are predicted to increase in cover and biomass with climate warming (Bråthen et al., 2018; Hudson & Henry, 2009; Myers-Smith et al., 2011); these associate with ericoid mycorrhizal fungi which impair decomposition and reduce nutrient turnover (Clemmensen et al., 2013, 2015; Fanin et al., 2022) and thereby potentially adversely affect tree seedling regeneration and growth (Jäderlund et al., 1996; Nilsson, 1994; Nilsson & Wardle, 2005). On the other hand, high-severity fires often repress or kill ericaceous vegetation (DeLuca et al., 2002) which may in turn favour forest regrowth in the short term until the ericaceous vegetation recovers. Hence, understanding how climate warming and intensified wildfire affect

understory vegetation is essential for assessing forest regeneration under climate change.

Seedling regeneration is also potentially impacted by management practices initiated following wildfire. In managed forests, wildfire is often followed by salvage logging, which in northern Europe involves the extraction of both dead and live scorched trees (Malvar et al., 2017). After salvage logging, tree seedlings are planted to regenerate the forest. Salvage logging can negatively affect vegetation and soils by reducing moisture retention (Leverkus et al., 2018; Marcolin et al., 2019), disrupting plant–soil–microbe interactions (Pérez-Izquierdo et al., 2021), and impairing decomposition and nutrient cycling (Bowd et al., 2019), which may in turn reduce seedling survival and growth (Leverkus et al., 2020; Lindenmayer & Noss, 2006). However, long-term impacts on soil quality remain uncertain, possibly due to variation in stand conditions and logging intensity (Leverkus et al., 2020; Malvar et al., 2017). It is also unclear how fire severity and climate warming may interact with salvage logging to affect seedlings.

Retaining living trees may support reforestation by enhancing turnover of soil organic nutrients via ectomycorrhizal fungi (Ibáñez, Wardle, et al., 2022; Pérez-Izquierdo et al., 2021). However, these trees can also compete with seedlings for light and nutrients, and thereby reduce seedling growth (Beckage et al., 2008; Gleason et al., 2017). Under climate warming, longer growing seasons may promote seedling growth (Pretzsch et al., 2014), but can also intensify summer drought stress (Marqués et al., 2018). Drought sensitivity may be greatest in high-severity burn areas due to increased runoff and lower soil water storage (Atchley et al., 2018; Phillips et al., 2024). Interactions among fire severity, salvage logging, understory vegetation and warming are therefore critical for seedling survival and forest recovery.

Assisted migration is considered an effective strategy for restoring forest ecosystems after disturbances, including disturbance driven by climate change (MacKenzie & Mahony, 2021; Williams & Dumroese, 2013). It may also help maintain the carbon sink function of forests under warming (Chakraborty et al., 2024). For decades, forest managers have used assisted migration and selection of conifer provenances and seed orchard sources to enhance traits like survival and growth (Hayatgheibi et al., 2020; Stanturf et al., 2024). In northern Europe, this often involves establishing seed orchards and moving provenances latitudinally to improve performance (Persson & Beuker, 1997; White et al., 2007). For *Picea abies*, seedling provenances are often moved from south to north to reduce the risk of spring frost (Lundströmer, 2021). Such provenances also tend to continue growing later into the autumn because their growth cessation is triggered by autumn night length, which are initially shorter in the north than in the south (at least until the autumn equinox). For *Pinus sylvestris*, provenances are often moved southward to promote earlier spring growth and bud set, and thus reduce risk of autumn frost damage (Berlin et al., 2016; Persson & Beuker, 1997). The climate change issue has raised uncertainty about the sustainability of current reforestation practices (Keenan, 2015; Lukac, 2016), though using climate-adapted provenances may improve forest resilience to

fire and warming (Davis et al., 2023; Handler et al., 2018). However, few trials have tested how different provenances respond to such factors as fire severity, warming, understory composition and salvage logging.

The purpose of this study was to gain insights into how *P. abies* and *P. sylvestris* seedlings of different provenances may respond to environmental conditions following wildfire of varying severities and their interactions with experimental post-fire climate warming, ericaceous shrub removal and salvage logging in a Swedish boreal forest. We aimed to achieve this by addressing these five hypotheses (Figure 1). *First*, we hypothesized that seedlings will grow better in stands subjected to high-severity than low-severity fire, because of the immediate pulse of available soil nutrients after fire (Gundale et al., 2005), and increased light availability from reduced tree canopy cover (Stuiver et al., 2016). *Second*, we hypothesized that experimental warming will enhance seedling growth because higher temperatures may increase soil mineralization rates (Kirschbaum, 1995) which increases nutrient availability for seedlings (Bonan & Cleve, 1992), and that this effect will be most prominent in low fire severity soils that have a greater amount of soil organic matter and therefore greater nutrient capital. Warming is expected to reduce growth by inducing stress-related seedling mortality and growth (Bennett et al., 2015), especially in the presence of understory vegetation (Shovon et al., 2021), and particularly for the less drought-tolerant and temperature-sensitive *P. abies* (Kunert et al., 2022). *Third*, we hypothesized that the presence of ericaceous shrubs will decrease seedling growth post-fire due to resource competition (Kuuluvainen & Rouvinen, 2000; Zackrisson et al., 1997), and that this effect will be more severe in low fire intensity stands because of faster recovery and higher biomass of ericaceous shrubs (DeLuca et al., 2002). *Fourth*, we hypothesized that salvage logging will have a positive effect on seedling regeneration through greater availability of light and soil nutrient resources, and that this effect of logging would be stronger in low-severity fires, due to removal of damaged trees that were still alive and able to compete with the seedlings. *Finally*, we hypothesized that seedling provenances will exhibit different growth rates, and that high-latitude provenances from colder environments will respond more positively to warming than will local or low-latitude provenances (Lukac, 2016; Reich & Oleksyn, 2008), regardless of fire severity. Testing these hypotheses in combination has the potential to provide novel insights about how conifer species used for reforestation respond to multiple interacting factors after fire and provide useful information for developing sustainable management practices in a changing climate.

2 | MATERIALS AND METHODS

2.1 | Selection of stands

In July 2014, the largest forest wildfire in modern Swedish history took place in central Sweden (59°53'51"N; 16°8'19"E) (Gustafsson et al., 2019; Lidskog et al., 2019). The wildfire, named

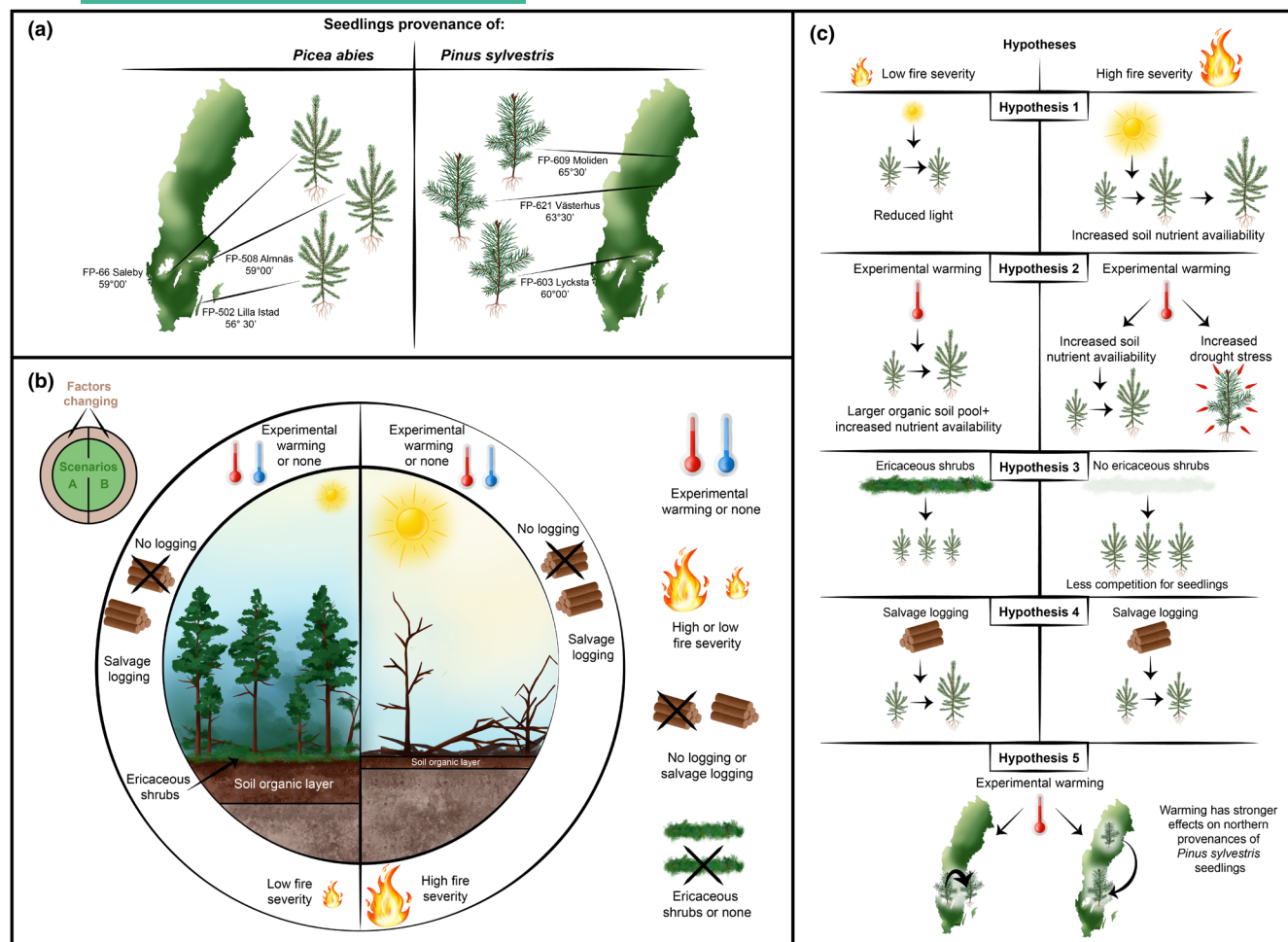


FIGURE 1 Conceptual overview of the experimental design and tested hypotheses. (a) Geographic origin of seedling provenances for *Picea abies* and *Pinus sylvestris* used in the study. (b) Illustration of the factorial experimental design, showing combinations of fire severity (high or low fire severity), salvage logging (salvage logging or no logging), experimental warming (experimental warming or none) and ericaceous shrub removal (ericaceous shrub or none). (c) Summary of five key hypotheses related to the effects of fire severity, warming, shrub removal and salvage logging on seedling growth and survival. Illustration by Daria Chrobok (DC SciArt), designed in collaboration with the authors.

the 'Västmanland burn', covered an area of more than 13,100 ha of land, where 9576 ha of it was managed conifer forest (Nilsson et al., 2014). The intensity of the fire varied across the landscape, leaving some stands with high tree mortality and loss of the organic soil layer, and other stands that were less severely burned. Fieldwork was conducted under permit number Dnr 512-4922-2015, issued by the County Administrative Board of Västmanland, Sweden (Länsstyrelsen i Västmanland, 721 86 Västerås, Sweden). We selected 25 burned forest stands each of which was 0.25 ha, which was dominated (87%) by 40–50-year-old Scots pine (*Pinus sylvestris*) trees. The site productivity, estimated by site index (expected height at 100 years) ranged from 22 to 24 m and stem density of <1000 stems per ha, and with scattered Norway spruce (*Picea abies*) and birch (*Betula* spp.) throughout the area (see Ibáñez, Wardle, et al., 2022 for further details of pre-fire stand characteristics). Each stand had undergone one thinning event prior to the fire. Prior to the fire, understory vegetation was dominated by ericaceous dwarf shrubs (*Vaccinium vitis-idaea*,

V. myrtillus and *Calluna vulgaris*) and mosses (mainly *Pleurozium schreberi*). The stands occurred on podzolized soil and were all situated within an area of 60 km², with a minimum distance of 300 m between stands.

To assess the level of fire severity for each of the 25 stands, in April 2016, data were collected for stem scorch height on the tree, proportion of stem scorched, proportion of crown scorched, tree mortality caused by the fire, depth of the soil organic layer, depth of charred soil and the quantity of charcoal on the soil surface. From these 25 burned stands, we used PCA analysis to identify seven high fire severity and seven low fire severity stands (details presented by Ibáñez, Wardle, et al., 2022). In short, tree mortality, stem scorch height, the proportion of trees with stem and crown scorches were higher in high fire severity stands than in low fire severity stands (Table 1). Before the fire, the high-severity and low-severity stands did not differ with regard to mean tree height, basal area or tree species composition (Ibáñez, Wardle, et al., 2022; Pérez-Izquierdo et al., 2023).

TABLE 1 Fire severity measures (mean $\pm$ SE) of fire severity characteristics.

	df ^a	High fire severity	Low fire severity	F-value	p-value
Soil organic layer depth (mm) ^b	2, 18	19.8 $\pm$ 1.7	24.0 $\pm$ 1.9	142.42	<0.001
Tree mortality cause during fire	1, 12	100.0 $\pm$ 0.0	32.1 $\pm$ 5.0	186.85	<0.001
Stem scorch height on trees (m)	1, 12	6.8 $\pm$ 1.1	1.0 $\pm$ 0.1	25.62	<0.001
Proportion of stem scorched (%)	1, 12	13.1 $\pm$ 3.6	2.9 $\pm$ 1.9	6.48	0.026
Proportion of crown scorch (%)	1, 12	99.4 $\pm$ 0.4	27.9 $\pm$ 2.4	846.74	<0.001
Depth of charred soil (mm)	1, 12	10.3 $\pm$ 0.8	12.8 $\pm$ 0.8	5.03	0.045
Quantity of charcoal on the soil surface (g/m ^b)	1, 12	120 $\pm$ 25	75 $\pm$ 25	1.50	0.244

Note: With permission from the authors: table modified from Ibáñez, Wardle, et al. (2022) and data sourced from Pérez-Izquierdo et al. (2023). Bold F- and p-values are significant at an alpha value of 0.05.

^aNumerator degrees of freedom, denominator degrees of freedom.

^bThe unburned soil organic layer was 93.9 $\pm$ 5.5 mm, statistically significantly higher than high- and low-burned soils at $p=0.001$ (Bonferroni post hoc test following ANOVA).

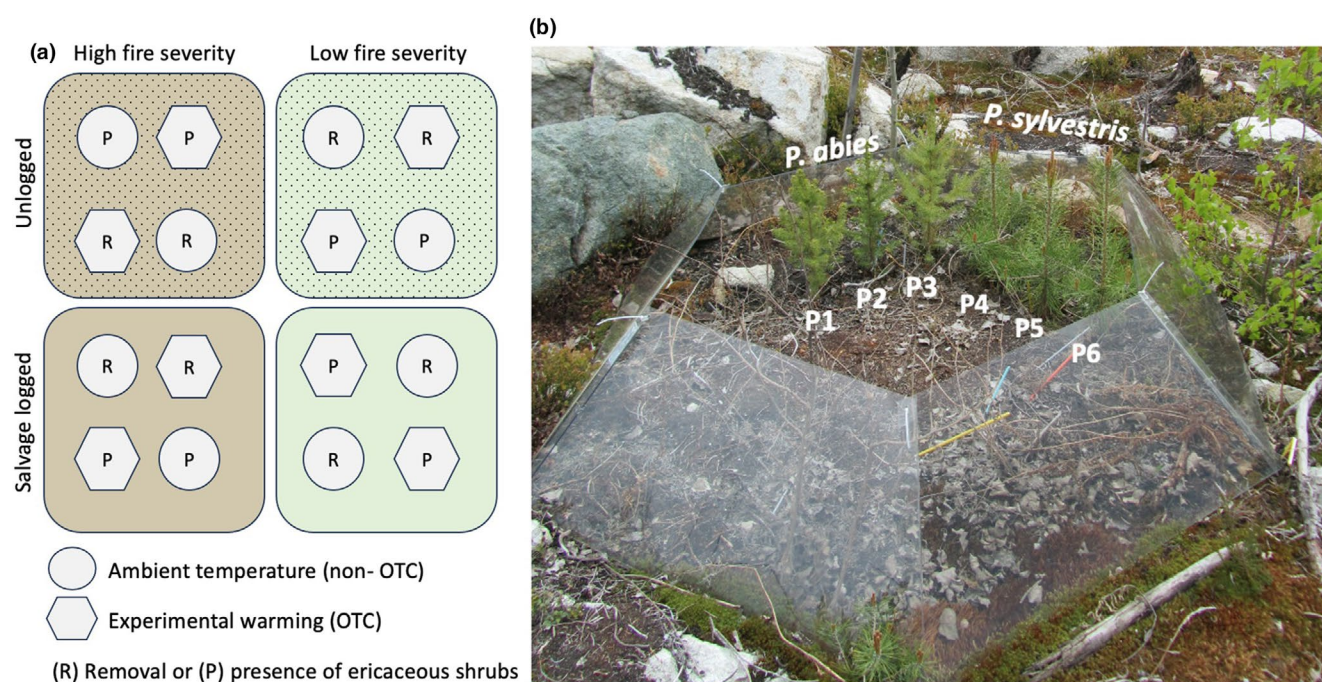


FIGURE 2 (a) Schematic figure over the experimental design. Each of the seven replicates of each high (beige) and low fire severity (green) consisted of one unlogged (patterned) and one logged plot (each approximately 40 $\times$ 40 m). Each plot had four sub-plots (112 sub-plots in total), with a ground surface area of 2.34 m² and top open area of 0.94 m². These were either covered with an open-top chamber (OTC) or left uncovered (non-OTC) to provide experimental warming and ambient temperature, respectively, and within these, ericaceous shrubs were either removed or left intact (present). (b) A photograph of an open-top chamber (OTC) placed in burned salvage-logged sites of high fire severity and planted with randomly assigned conifer seedlings of three different provenances (P1–P3 for *P. abies* and P4–P5 for *P. sylvestris*). The provenances are described in detail in Table 2. Photograph: Theresa S. Ibáñez.

2.2 | Effects of fire severity, salvage logging, warming and shrub removal on tree seedlings

Directly during the first weeks following the fire (August to September 2014), half of each of the 14 stands was salvage logged (i.e. the area was clear-cut, the logs were removed and the branches were left in the area, while no soil scarification took place), so that each stand consisted of a paired logged and unlogged area. On 1–7 June 2016, we set up a climate warming experiment. This consisted of installing four

plots in each of the logged and unlogged portions of each stand, on which we manipulated warming and removed understory ericaceous shrubs (Figure 2a). On two out of four plots, we installed an open-top chamber (OTC) on the burned ground to simulate climate warming (Welshofer et al., 2018), identical to what has been used in other studies (De Long et al., 2016; Dorrepaal et al., 2004). The OTCs were made of transparent Perspex PVC (MacroLife, Arla plast, Sweden) and were hexagonal with 47 cm high (tilted) walls and with a 1 m wide open top (Figure 2b). This open top allowed the inside of the chamber to increase

in temperature without changing natural conditions such as light, precipitation or entry by insects or fungal spores. The remaining two plots were left without an OTC to serve as no-warming controls and had the same dimensions as the OTC. We measured air temperature at 5 cm from ground level with temperature loggers (Tinytag Talk 2, Intab, Stenkullen, Sweden) inside OTCs and in non-OTC plots in salvage-logged and unlogged sites across fire severity during three consecutive days and nights in June 2016. In total, four temperature loggers were installed. The elevated temperature inside the OTC was approximately 2°C warmer compared to non-OTC ambient temperature in salvage-logged sites during daytime (06:00AM to 06:00PM), which created an elevated ambient temperature (see [Figure S1a](#)). However, the OTCs only elevated the temperature in unlogged sites by approximately 0.5°C ([Figure S1b](#)).

The OTCs were placed in the field all year round, potentially reducing snow accumulation inside the chambers and altering winter soil temperature and moisture conditions. In this region, snow typically accumulates from early December to early or mid-March. During the winters of 2016–2019, mean snow depths were 7, 27 and 18 cm, respectively (Swedish Meteorological Institute), which are low compared to many higher latitude ecosystems. OTCs may reduce snow cover slightly, potentially leading to earlier soil exposure (Marion et al., 1997). However, earlier snow melt may simulate natural warming effects, such as extended growing seasons—an effect consistent with projected climate warming (Arft et al., 1999; Henry & Molau, 1997). Although we did not measure snow depth, moisture or CO₂ concentrations inside the OTCs, changes in these factors may reflect realistic warming scenarios (Hollister & Webber, 2000). Despite their limitations, OTCs remain a widely used and established method for simulating warming in field conditions due to their passive function and open design (which allows for continuous air exchange), as well as the fact that they allow proper replication of warming treatments in large experiments (Hollister et al., 2023; Marion et al., 1997).

In each group of four plots in each salvage-logged and unlogged area of each stand, we removed ericaceous shrubs over 1–7 June 2016 for two plots (one with an OTC and one without) by gently pulling out their rhizomes to minimize disturbance in the soil and vegetation layer, while the other two were left intact ([Figure 2a](#)). All above-ground ericaceous shrubs were removed, transported to Umeå, dried in an oven for 48 h at 65°C, and the dry weights per m² were obtained ([Table S1](#)). Any resprouting shrubs were subsequently removed at four occasions during each of the 2017 and 2018 growing seasons, and at three times during the growing season of 2019. These measurements showed that high-severity fires removed 40% more of the shrub layer than low-severity fires did ([Table S1](#)).

Vegetation cover data in a sub-plot of a 50×50 cm quadrat in the centre of each plot was measured on 22–28 July 2019 with a pinpoint quadrat analysis approach (Goodall, 1952 as used by Wardle et al., 2003) to assess post-fire recovery. For each plot, all vegetation including naturally regenerated tree seedlings, herbs, grasses, mosses and lichens intercepted by each of the 100 downward projecting points (in a grid of 10×10 points) was recorded and

identified to species. The total number of intercepts of each species by the 100 points was used to provide a measure of its cover density (Jonasson, 1988).

Soil samples for obtaining the concentration of carbon (C) and nitrogen (N) of the organic soil layer and mineral soils ([Table S2](#)) were collected in each plot in October 2019. Three soil cores (each 3 cm in diameter) were collected at the centre of each plot, and cores were split into organic layer and mineral layers in the field. At some high fire severity locations, the entire organic layer was consumed by the fire and only the mineral layer was collected. Soil samples were kept under cool temperature conditions until transportation to the laboratory where they were stored at 4°C until further processing. The fresh soil samples were sieved (<2 mm) to remove stones, coarse root and plant debris. Soil cores from the same horizon within each plot were pooled together. Prior to sieving, live plant materials were carefully removed from the top of each organic soil core, while the litter layer was left intact. Soil samples were dried (60°C for 48 h) and homogenized into a fine powder (Unimeg rolling ball, Umeå University Mechanic, 3d) whereafter they were analysed for total C and N content with an EA-IRMS Elemental Analyzer (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany) at the SLU Stable Isotope Laboratory.

2.3 | Conifer seedlings and provenances

On 1–7 September 2016, seedlings of three different provenances of each of two conifer species (*P. abies* and *P. sylvestris*) were planted within each plot (i.e. those with and without OTCs and with and without shrub removal; [Figure 2b](#)) to test for the provenance variation in growth and survival when environmental factors vary. Seedling height and biomass were measured as indicators of early performance, as they reflect how strong and competitive the seedlings are and help evaluate reforestation success. The seedlings were obtained from a nearby forest nursery (Svenska Skogsplantor) and were cultivated in peat-filled nursery containers. Provenances were selected to represent one local provenance and two non-local provenances for each species ([Table 2](#)) while at the same time reflecting seedling transfer practice by Swedish forestry (Hallsby et al., 2013). For *P. sylvestris*, this involves transferring provenances to more southern latitudes, where they will encounter a warmer climate and produce their bud set earlier in autumn so that they are less exposed to autumn frost damage (Berlin et al., 2016). For *P. abies*, this involves moving provenances to more northern latitudes where they experience bud burst later in spring, and therefore avoid the risk of spring frost damage (Lundströmer, 2021), and grow for longer in the autumn. Prior to planting, the total above-ground length and dry weight differed among provenances within species, and *P. abies* seedlings were overall taller than were those of *P. sylvestris* ([Table 2](#)).

During late autumn (after bud set) each year from 2017 to 2019 inclusive, the total height of each live planted seedling was recorded. In November 2019, all seedlings were harvested, and the above-ground part (excluding roots) of each seedling was placed in a

TABLE 2 Information about the *P. abies* and *P. sylvestris* seed and seedling provenances used in this study.

Species	Seed orchard and stand name	Latitude N and altitude (m) of seed orchard	Year of orchard establishment and number of clones	Seed provenance (latitude N of seed collection)	Seedling provenance (latitude N) ^a	Climate transfer distance in mean annual temperature (Δ MAT) units ^b	Mean $\pm$ SE seedling height at planting (cm) ^c	Mean $\pm$ SE seedling dry weight at planting (g) ^d
<i>Picea abies</i>	FP-502 Lilla Istad	56°57'; 10	1986; 140	56°55'	56°30'	-2.1 (-1.6)	19.1 $\pm$ 0.6	1.4 $\pm$ 0.1
	FP-66 Saleby	58°24'; 70	Unknown; 38	59°12'	59°00'	-0.6 (-0.9)	21.4 $\pm$ 0.5	1.0 $\pm$ 0.0
	FP-508 Almnäs ^e	58°15'; 125	1987; 125	59°34'	59°00'	-0.6 (-0.5)	18.7 $\pm$ 0.6	0.9 $\pm$ 0.1
<i>Pinus sylvestris</i>	FP-603 Lycksta ^e	59°41'; 45	1984; 64	60°58'	60°00'	0.6 (-0.2)	10.2 $\pm$ 0.5	1.2 $\pm$ 0.1
	FP-621 Västerhus	63°19'; 15	1991; 28	63°50'	63°30'	2.3 (1.7)	10.4 $\pm$ 0.4	0.8 $\pm$ 0.1
	FP-609 Moliden	63°28'; 20	1984; 192	67°00'	65°30'	4.8 (3.6)	10.5 $\pm$ 0.5	0.6 $\pm$ 0.0

^aSeedling provenance is an estimated mean latitude and based on seed provenance and probability of outcrossing (background pollination) at the seed orchard.

^bCalculated by subtracting the mean annual temperature (MAT) at the planting site from the MAT of the seedling provenance climate. Numbers within parentheses are calculated by subtracting the MAT at the planting site from the MAT at the latitude of the seed orchard. The MAT values are extracted from the closest meteorological station (SMHI) of the latitude and altitude of the seed orchard over the normal periods 1961–1990 and 1991–2020. Source: Svenska skogsplantor AB and Skogsstyrelsen.

^cOne-way ANOVA to detect differences in above-ground seedling height between provenances for *P. abies*: Degrees of freedom (df), denominator df = 2, 27, $F = 7.600$, $p = 0.002$. Pairwise differences among means detected between Saleby–Almnäs and Saleby–Lilla Istad. *P. sylvestris*: Degrees of freedom (df), denominator df = 2, 27, $F = 0.064$, $p = 0.938$.

^dOne-way ANOVA to detect differences in above-ground seedlings biomass between provenances for *P. abies*: Degrees of freedom (df), denominator df = 2, 27, $F = 9.089$, $p < 0.001$. Pairwise differences among means detected between Lilla Istad–Almnäs. *P. sylvestris*: Degrees of freedom (df), denominator df = 2, 27, $F = 17.17$, $p < 0.001$. Pairwise differences among means detected between Moliden–Lycksta and Västerhus–Lycksta.

^eRecommended (local) provenance at the field site.

separate paper bag. The seedlings were oven dried at 65°C for 48 h and were thereafter weighed to obtain the total above-ground biomass, including stem and needles. Tree seedling survival data were obtained in October 2019 by counting surviving tree seedlings per plot.

The experiment was set up with the three provenances of each seedling species planted within each experimental plot; these plots represented a fully factorial design, including two fire severities (high vs. low) $\times$ two logging treatments (salvage logged vs. unlogged) $\times$ two warming treatments (warming vs. ambient) $\times$ ericaceous competition (removal vs. intact) $\times$ seven stand replicates, resulting in 112 plots in total (Figure 2).

2.4 | Statistical analyses

We applied a mixed model with a hierarchical design, where seedling total above-ground biomass served as the dependent variable and fire severity, salvage logging, warming, shrub removal and provenances were fixed factors. Our units of true replication were the individual stands; we used 14 distinct stands in total, that is 7 of high fire severity and 7 of low fire severity. Stand identity (ID) served as a random factor in the model, which effectively paired treatments of fire severity with non-logging or salvage logging operation together at the stand level. Further, to build additional hierarchical levels of the experimental design in the model, we applied random factors, where salvage logging was nested within stand ID, and warming and presence of shrubs were randomized within each combination of

fire severity and salvage logging. Since provenance has the lowest hierarchical level, it was not included as a random factor. The data for the two species (*P. sylvestris* and *P. abies*) were analysed separately. Three-way interactions were included in the analysis, but higher-order interactions were excluded from the model. Main effects were reported alongside interaction terms to aid interpretation and provide context, especially for variables relevant to forest management, while acknowledging that interactions may influence the meaning or strength of the main effects. For total above-ground seedling height, we used the same model as above, but we included year as a fixed factor to account for repeated measurements of individual seedlings across the years, and plant identity (i.e. the identity of each plant that was repeatedly measured every year) as a random factor. We fitted a linear mixed effects model using the 'lme4' R package (Bates et al., 2015). To assess the significance of fixed effects, we conducted analyses analogous to ANOVA using the Type III test implemented in the 'lmerTest' package (Kuznetsova et al., 2017), and pairwise differences between treatment means were evaluated using Tukey's post hoc test implemented in the 'emmeans' package (Lenth et al., 2020). In cases where assumptions of homogeneity of variance were not met, the data were log(x)-transformed. Results are presented on the original scale for visualization and interpretability. The mixed effects models were tested for normality of residuals.

To evaluate the effects of fire severity, salvage logging, temperature and shrub removal, and their interactions, on tree seedling mortality, we used a generalized linear mixed model (GLMM) with a binomial error distribution. The model was appropriate for analysing binary mortality outcomes (dead Δ alive), while accounting for

fixed effects (fire severity, salvage logging, warming, shrub removal and provenances) and a random effect (Stand ID). Each tree species was tested separately. We assessed the significance of each fixed effect using a log-likelihood ratio test with a chi-square distribution, implemented through the ANOVA function in the 'car' package (Fox & Weisberg, 2019).

The effects of fire severity, salvage logging, temperature and shrub removal on total vegetation cover (i.e. total number of intercepts by 100 points) were evaluated using generalized linear mixed effects models (GLMMs) from the 'lme4' package (Bates et al., 2015). Since the response variable comprised count data and did not conform to normality assumptions, we evaluated multiple GLMMs assuming Poisson error distribution and compared their performance using the 'performance' package (Lüdtke et al., 2021). The final model, a Poisson GLMM without singularity or overdispersion, was selected for further analysis. Fire severity, salvage logging, temperature and shrub removal served as the fixed factors, and site identity (stand ID) was included as a random factor. Statistical significance between treatments was assessed by performing ANOVA on the model package 'car' (Fox & Weisberg, 2019), and pairwise difference between group means was evaluated using Tukey's post hoc test ('emmeans' package (Lenth et al., 2020)). Experimental plots within stands were randomly positioned in the field, and the data were therefore assumed to be randomly distributed. In cases where assumptions of homogeneity of variance were not met for other continuous variables, a log(x) transformation was applied. Results are presented on the original scale to help visualization and interpretability.

We analysed the biomass of removed ericaceous shrubs (response variable) using a one-way ANOVA to test the effect of fire severity. Analyses were conducted separately for unlogged and salvage-logged stands. In the case of significant ANOVA results, Tukey's post hoc test was then applied to detect pairwise differences among means. The above-ground seedlings height and biomass at the time of planting were analysed with one-way ANOVA followed by Tukey's post hoc test.

All statistical analyses were performed in R Core Team (2025), except the statistical analyses in Table 1, where SPSS (SPSS version 24, IBM Corp., Armonk, NY, USA) was applied. The figures were created with GraphPad Prism version 8.4.3 for Macintosh (GraphPad Software, La Jolla California USA).

3 | RESULTS

3.1 | Seedling survival following experimental treatments

Approximately 80% of seedlings survived to the end of the experiment (Table S3). We observed no statistical difference across treatments in seedling mortality (Table S4). However, across all treatment combinations, the mortality was higher in sites with high (23%) than lower (17%) fire severity (Table S3).

3.2 | Above-ground biomass of tree seedlings following experimental treatments

The above-ground tree biomass response differed between tree species. We observed significant main effects of fire severity, salvage logging, warming, presence of shrubs and seedling provenances on the above-ground biomass of *P. sylvestris* seedlings, while only main effects of warming, shrub removal and provenance were significant for *P. abies* seedlings (Table 3). When these main effects occurred, the seedlings grew overall better in sites exposed to high fire severity, salvage logging, elevated temperature and shrub removal. Across all treatments, *Picea abies* had the lowest biomass for the local provenance and the highest biomass for the southernmost provenance (Figure 3h). For *P. sylvestris*, the local provenance had the highest biomass, and the northernmost provenance had the lowest biomass (Figure 3d). We observed a two-way interaction effect of fire severity and salvage logging for both species (Table 3), because both species had lowest biomass in unlogged sites with low fire severity (Figure 3a,e).

3.3 | Seedling height following experimental treatments

We observed significant main effects of fire severity, salvage logging, warming, provenance and year for *P. sylvestris* seedlings, and main effects of warming, shrub removal, provenance and year on *P. abies* seedling height (Table 4). Over time, *P. sylvestris* seedlings grew taller in high fire severity sites and in salvaged logged stands (Figure 4a,b). Both species grew taller in plots with elevated temperature, but only *P. abies* was responsive to ericaceous shrub removal by growing taller when shrubs were removed (Figure 4c,h,i). The northernmost provenance of *P. sylvestris* had a lower total height than did the other two provenances (Figure 4e). For *P. abies*, the southernmost provenance grew taller than the local one (Figure 4j).

Pinus sylvestris showed a two-way interaction effect between warming and provenances, and *P. abies* seedlings had also a two-way interaction effect with fire severity and provenances (Table 4; Figure 5). As such, there were no differences between the provenances of *P. sylvestris* grown in the plots with elevated temperature, but they all increased in height compared to their corresponding provenance grown in ambient temperature (Figure 5a). Also, while the most northern provenance of *P. sylvestris* had the lowest growth overall, it showed the greatest positive response to warming in terms of height increment of all the provenances (Figure 5a). Meanwhile, the local population of *P. abies* had the lowest total seedling height in low fire severity stands than did any provenances in either high or low fire severity stands (Figure 5b).

3.4 | Indirect effects of fire through vegetation responses

Total vegetation cover (presented in Tables S5 and S6; Figure S2) was higher in salvage logged than in unlogged plots, primarily due to

TABLE 3 Result from mixed model analysis of variance comparing main and interactive effects of fire severity (FS), salvage logging (SL), experimental warming (OTC), shrub removal (SRB) and provenances (PR) on total above-ground biomass of *P. abies* and *P. sylvestris* seedlings.

	Total above-ground biomass					
	<i>Pinus sylvestris</i>			<i>Picea abies</i>		
	df ^a	F-value	p-value	df ^a	F-value	p-value
FS	1, 12.0	14.032	0.003	1, 11.9	0.566	0.466
SL	1, 12.0	25.147	<0.001	1, 11.9	3.082	0.105
OTC	1, 68.7	8.001	0.006	1, 64.9	4.457	0.039
SRB	1, 68.4	5.094	0.027	1, 65.8	5.708	0.020
PR	2, 153.0	16.832	<0.001	2, 146.5	9.600	<0.001
FS×OTC	1, 68.9	0.101	0.751	1, 65.0	0.940	0.336
FS×SRB	1, 68.1	2.991	0.088	1, 65.6	3.761	0.057
FS×SL	1, 12.0	11.293	0.006	1, 11.9	8.406	0.013
FS×PR	2, 151.7	1.777	0.173	2, 146.6	2.133	0.122
SL×OTC	1, 68.7	1.431	0.236	1, 64.8	0.477	0.492
SL×SRB	1, 68.6	0.029	0.866	1, 65.9	0.191	0.664
SL×PR	2, 153.3	0.051	0.950	2, 146.1	0.904	0.407
OTC×SRB	1, 68.6	2.169	0.145	1, 66.4	1.376	0.245
OTC×PR	2, 152.9	0.733	0.482	2, 146.5	0.372	0.690
SRB×PR	2, 153.2	0.503	0.605	2, 146.5	0.189	0.828

Note: Three provenances per tree species are included. Corresponding mean values are presented in Figure 3. Bold F- and p-values are significant at an alpha value of 0.05. Three-way interaction effects were all non-significant.

^aNumerator degrees of freedom, denominator degrees of freedom.

an increased abundance of colonizing deciduous trees. Two-way interactions were observed between fire severity × warming and salvage logging × warming, where warming increased vegetation cover under high fire severity, but decreased it under low fire severity. The highest total vegetation cover occurred in salvage-logged plots with high fire severity under warming. Three-way interactions between fire severity × salvage logging × warming and fire severity × warming × presence of shrubs were also detected. Under low fire severity, total vegetation cover was lowest in unlogged ambient temperature plots with shrubs present. When shrubs were removed, warming had no effect on vegetation cover at low fire severity. The highest total vegetation cover was observed in warmed plots with high fire severity, regardless of shrub presence.

4 | DISCUSSION

4.1 | Effects of fire severity on tree seedling growth

We found only partial support for our first hypothesis (i.e. that seedlings will grow better in stands subjected to high-severity than low-severity fire), because high fire severity increased total above-ground biomass and height for *P. sylvestris* while the growth of *P. abies* was unresponsive. *Pinus sylvestris* is a faster growing early successional species that benefits from increased light availability (de Chantal et al., 2003) under high fire severity, that is, extensive tree mortality and tree defoliation. Also, nutrient availability can increase

initially after fire, and elevated nutrient levels shortly after fire have previously been shown to be important for the regeneration of *P. sylvestris* (Ibáñez, Wardle, et al., 2022; Pausas et al., 2002). However, while the depth of the remaining organic layer differed among high and low fire severity sites, fire severity did not affect nutrient availability. Soil total %N (Table S2) and concentrations of inorganic N (i.e. NH_4^+ and NO_3^-) were similar among high and low fire severity sites (Ibáñez, Rütting, et al., 2022). This indicates that, at our sites, the growth response of *P. sylvestris* in relation to fire severity was more dependent on changes in light availability than changes in nutrient availability. However, this appears not to be the case for *P. abies*, which is a late successional shade-tolerant species, and therefore less likely to benefit from increased light availability under high fire severity (de Chantal et al., 2003).

4.2 | Interactive effects of fire severity and experimental warming on tree seedling growth

For the second hypothesis, we expected experimental warming to increase seedling growth, and for this effect to be greater in low fire severity stands, where parts of the soil organic layer remain. Our alternative hypothesis predicted an increase in seedling mortality and reduced growth of *P. abies*. We found that warming alone stimulated biomass and height growth of both *P. sylvestris* and *P. abies*, which may be driven by enhanced rates of nutrient cycling and supply in the soil (Hartley et al., 1999), or through promoting plant photosynthesis and respiration rates (Kurepin et al., 2018). These findings partly

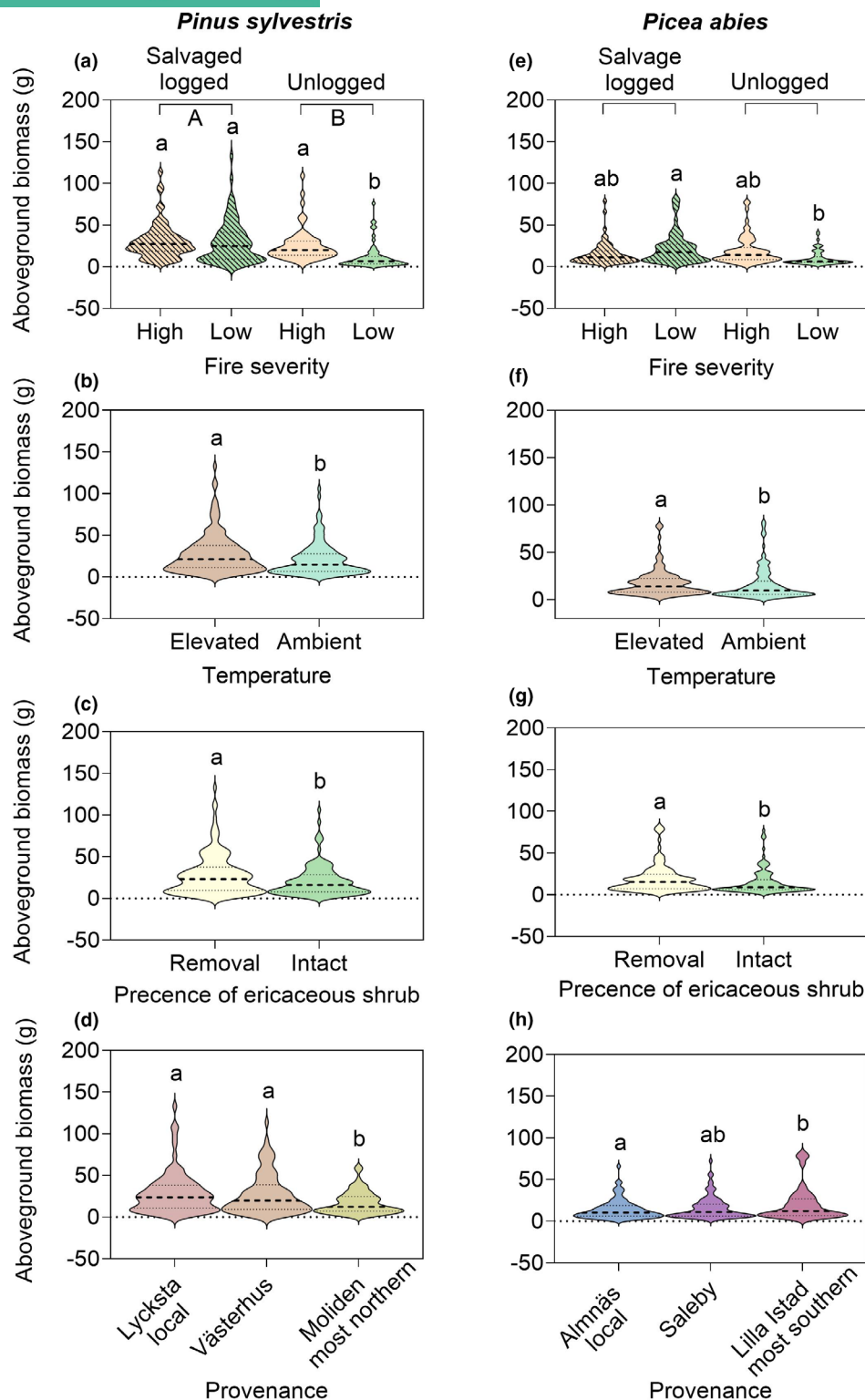


FIGURE 3 Mean $\pm$ SE of total above-ground biomass of *P. sylvestris* and *P. abies* seedlings in response to fire severity and salvage logging (a, e), warming treatment (b, f), shrub removal (c, g) and of each seedling provenance across all treatment combinations (d, h) in November 2019. Capital letters indicate statistical significance among pairs of bars, and lower case letters indicate significance among individual bars, according to Tukey's post hoc test at $p \leq 0.05$. Corresponding ANOVA results (F- and p-values) are reported in Table 3.

contradict the results from a field study by Jessen et al. (2023) which reported neutral responses of *P. abies* to experimental warming regardless of fire successional stage. Similarly, Marty et al. (2020)

did not observe a positive growth response of *P. mariana* seedlings to soil warming. In contrast, our findings align more closely with the work of Okano et al. (2021), who found that *P. glauca* seedlings in

TABLE 4 Result from mixed model analysis of variance comparing main and interactive effects of fire severity (FS), salvage logging (SL), experimental warming (OTC), shrub removal (SRB), provenances (PR) and year (YR) on seedlings total height of *P. abies* and *P. sylvestris* analysed across years.

	Total seedling height					
	<i>Pinus sylvestris</i>			<i>Picea abies</i>		
	df ^a	F-value	p-value	df ^a	F-value	p-value
FS	1, 12.1	20.980	<0.001	1, 12.0	0.091	0.768
SL	1, 12.1	18.684	0.001	1, 12.0	2.756	0.123
OTC	1, 70.5	75.044	<0.001	1, 70.3	44.962	<0.001
SRB	1, 71.5	0.931	0.338	1, 70.3	7.703	0.007
PR	2, 177.7	12.792	<0.001	2, 175.2	4.393	0.014
YR	2, 505.1	1545.109	<0.001	2, 499.0	582.287	<0.001
FS×OTC	1, 70.5	0.002	0.967	1, 70.2	1.734	0.192
FS×SRB	1, 71.2	1.402	0.240	1, 70.3	0.098	0.756
FS×SL	1, 12.1	3.014	0.108	1, 12.0	4.468	0.056
FS×PR	2, 177.5	1.134	0.324	2, 175.4	3.758	0.025
FS×YR	2, 504.1	19.259	<0.001	2, 499.4	6.183	0.002
SL×OTC	1, 70.9	0.268	0.606	1, 70.5	0.005	0.943
SL×SRB	1, 71.2	0.873	0.353	1, 70.5	0.080	0.778
SL×PR	2, 178.4	2.302	0.103	2, 175.0	0.139	0.870
SL×YR	2, 504.8	9.234	0.001	2, 499.1	12.334	<0.001
OTC×SRB	1, 71.1	0.238	0.627	1, 70.1	2.728	0.103
OTC×PR	2, 177.3	3.842	0.023	2, 175.5	1.000	0.370
OTC×YR	2, 505.9	19.539	<0.001	2, 499.6	3.999	0.019
SRB×PR	2, 178.3	0.161	0.851	2, 175.3	0.014	0.986
SRB×YR	2, 505.0	2.151	0.117	2, 499.2	0.297	0.743
PR×YR	4, 505.9	1.957	0.100	4, 500.2	0.158	0.959

Note: Corresponding mean values are presented in [Figures 4](#) and [5](#). Bold *F*- and *p*-values are significant at an alpha value of 0.05. Three-way interactions are in some cases significant as follows for *Picea abies*: (FS×SL×YR; *F*=24.119, *p*<0.001), (FS×SRB×YR; *F*=8.570, *p*<0.001), (OTC×SRB×YR; *F*=6.473, *p*<0.002) and for *Pinus sylvestris*: (FS×SL×OTC; *F*=7.418, *p*=0.008), (FS×OTC×PR; *F*=3.272, *p*=0.040), (FS×SL×YR; *F*=18.862, *p*<0.001).

^aNumerator degrees of freedom, denominator degrees of freedom.

high-altitude forests grew larger following warming. This could in part be due to our warming treatment not causing the temperature to increase to the level needed for induction of thermal stress in *P. abies* (Kunert et al., 2022). Inconsistent with our second hypothesis, we did not detect any interactive effects of warming and fire severity on seedling growth. A likely mechanism is that seedlings of both tree species grew taller in the warming treatment to access light, because the other plants (such as grasses and naturally established fast-growing deciduous trees) also grew taller in the warmed plots and competed with them for light, and that this effect overrides the importance in variation of organic layer depth ([Figure S2](#); [Table S6](#)).

4.3 | Interactive effects of fire severity and presence of ericaceous shrub on tree seedling growth

In support of our third hypothesis, we found impaired seedling biomass for both species in plots where ericaceous shrubs were present,

though only *P. abies* also showed reduced height. Stress-tolerant late successional species are often poorer competitors, and *P. abies* could therefore be expected to be more responsive to treatments that involve varying levels of competition imposed from other plants (Grime, 1977). Further, it is well known that understory ericaceous shrubs can be detrimental for seedling regeneration due to them both being strong resource competitors and producing allelochemicals against other plants (Jäderlund et al., 1996; Nilsson, 1994). Most ericaceous species can survive low-severity fires by resprouting from underlying rhizomes when the organic layer is not fully consumed by the fire (Mallik, 1993; Matlack et al., 1993), and consistent with this, the recovery of ericaceous species in unlogged sites under low fire severity was greater than in unlogged sites under high fire severity ([Table S1](#)). In contrast to our third hypothesis, we did not see any interactive effects between fire severity and shrub removal on seedling growth. This means that shrub impairment of tree seedling growth was relatively constant across fire severity treatments, despite the differences in shrub biomass observed among them.

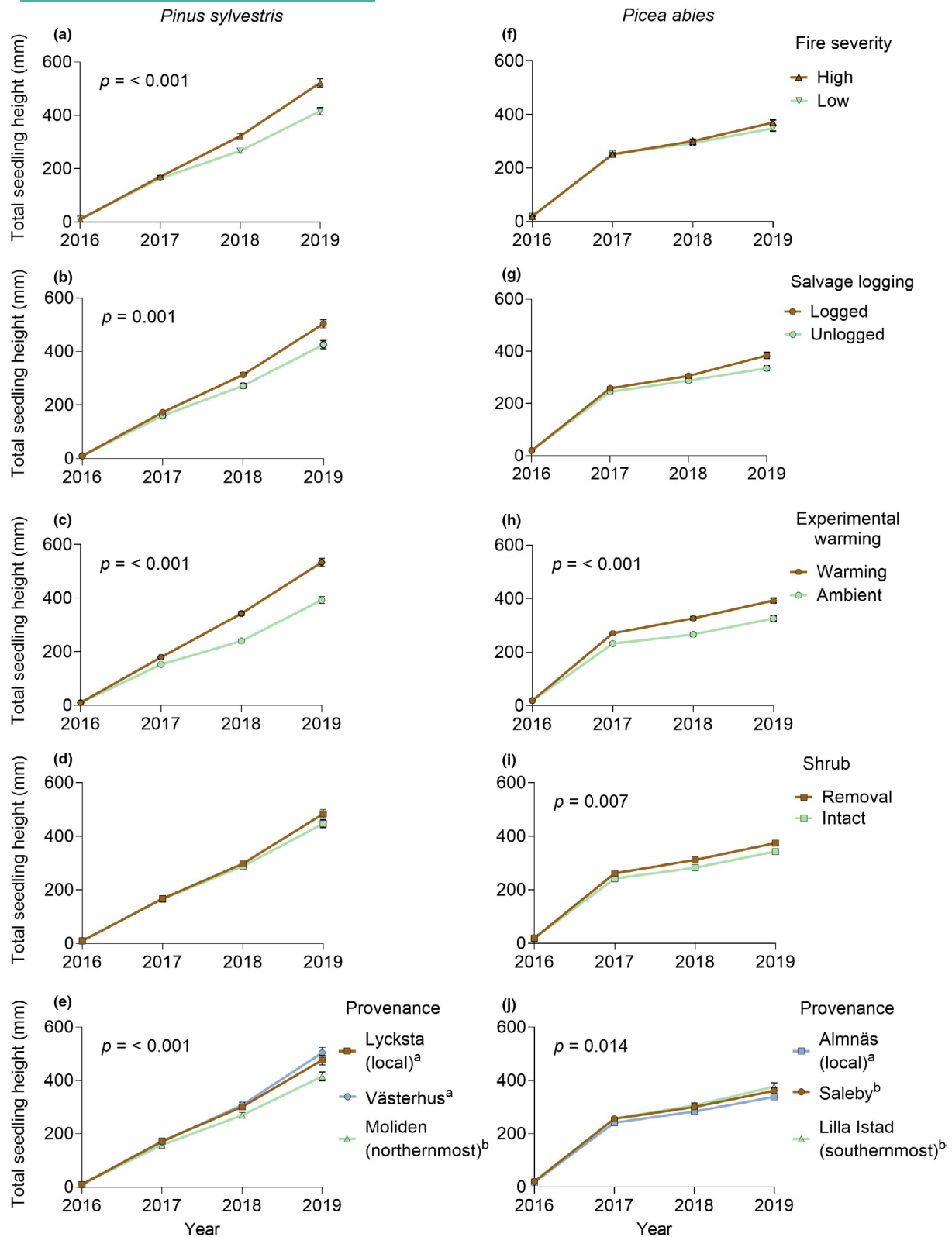
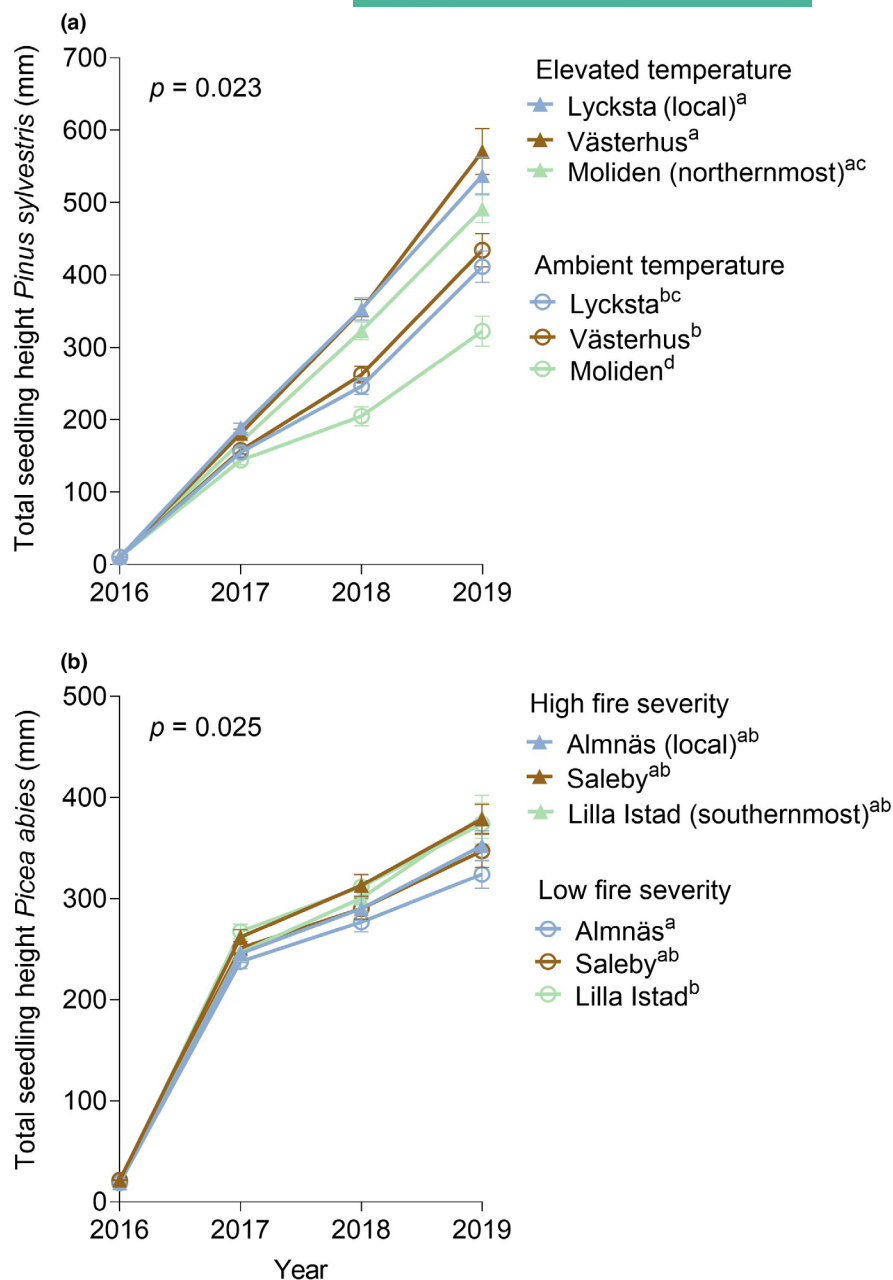


FIGURE 4 Mean $\pm$ SE of seedling height of *P. sylvestris* and *P. abies* seedlings measured in October/November each year from 2016 to 2019, in response to the main effects of (a, f) fire severity, (b, g) salvage logging, (c, h) warming, (d, i) shrub removal and (e, j) seedling provenance. The standard error (SE) bars are not visible when they are smaller than the symbol representing the mean value. The p -values shown refer to statistically significant ANOVA results at $p \leq 0.05$. All ANOVA results are reported in Table 4. Lower case letters indicate statistical significance over all three measurement years according to Tukey's post hoc test $p \leq 0.05$.

FIGURE 5 Mean $\pm$ SE of seedling height of *P. sylvestris* and *P. abies* measured in October/November each year from 2016 to 2019, in response to (a) warming $\times$ provenance for *P. sylvestris* and (b) interaction effects of fire severity $\times$ provenance for *P. abies*. The standard error (SE) bars are not visible when they are smaller than the symbol representing the mean value. The p -values shown refer to statistically significant ANOVA results at $p \leq 0.05$. All ANOVA results are reported in Table 4. Provenance names followed by different letters are statistically significantly different overall according to Tukey's post hoc test $p \leq 0.05$.



4.4 | Interactive effects of fire severity and salvage logging on tree seedling growth

In partial support of our fourth hypothesis, we found that on average across fire severity levels salvage logging enhanced biomass growth of *P. sylvestris* (but not *P. abies*) seedlings, and that salvage logging enhanced seedling growth of both species only in the low fire severity stands (Figure 3a,e). This effect of logging is likely due to the reduction of shading and competition resulting from the removal of scorched standing but still living trees. Further, the occurrence of this effect of logging for only low-severity fire stands is likely because low fire severity sites had a larger proportion of living trees with green foliage, and salvage logging of these stands (and thus removed damaged live trees) would have therefore resulted in these positive effects being greater.

4.5 | Interactive effects of provenances and experimental warming on tree seedling growth

Consistent with our fifth hypothesis, we found several differences in growth rates between provenances. The local provenance of *P. abies* had a lower biomass production than did the most southern provenance, whereas the local provenance for *P. sylvestris* obtained a higher biomass than did the most northern provenance; however, this did not impact seedling survival (Figure 3). This indicates that northern movement of seedlings to cooler conditions is beneficial for *P. abies* seedling growth, whereas southern movement of *P. sylvestris* to warmer conditions is detrimental. We note that the farthest north provenance of *Pinus sylvestris*, which showed the poorest performance, was transplanted beyond its tolerable latitudinal range. Forest managers are aware of these constraints

and generally avoid transferring provenances beyond their adaptive range to minimize risks of poor performance. As such, *P. sylvestris* seedlings moved too far south may be sensitive to the increase in temperature and day length because bud burst would occur earlier in spring, making seedlings more vulnerable to spring frost (Hänninen, 1991). In partial support of our fifth hypothesis, we did observe a significant interactive effect between provenance and climate warming on the height growth of *P. sylvestris*, though not of *P. abies* (Table 4). Specifically, the northernmost provenance of *P. sylvestris*, which was subjected to the greatest climate transfer distance, showed the greatest growth response to warming, and the local provenance the least. One explanation could be that while *P. sylvestris* seedlings moved south would be exposed to a longer growing season because they are more adapted to start growing at lower temperatures earlier in spring, they would also be less likely to encounter spring frost (and thus frost damage) in the warming treatment relative to the un-warmed control. The climate transfer distance for all *P. abies* provenances was negative (all were moved northwards), and the warming effect of the OTC might not have been strong enough to induce differences in responses among the *P. abies* provenances.

4.6 | Management implications

Our findings provide important guidance for forest managers aiming to promote post-fire recovery in coniferous forests under changing climatic conditions. We demonstrate that artificial regeneration through planting, commonly used after conventional clear-cut harvesting (Örlander et al., 1990), is also an effective strategy for restoring *P. sylvestris* and *P. abies* following wildfire, particularly where natural regeneration is insufficient, which is a situation that is expected to become more common with increasing frequency and severity of fires driven by climate change (Baltzer et al., 2021; Burrell et al., 2022; Stevens-Rumann et al., 2018). Salvage logging, often debated because of the ecological trade-offs (Lindenmayer & Noss, 2006; Thorn et al., 2018), was able to support seedling growth under certain conditions. As such, on sites with high fire severity, salvage logging can be strategically applied to create open, low-competition environments that are favourable for the establishment and growth of *P. sylvestris*, a pioneer species that is likely, at least in the short term, to benefit from warmer post-fire conditions (Saravesi et al., 2019; Zhao et al., 2024). On sites with low fire severity, salvage logging may facilitate the development of fast-growing deciduous species (Gustafsson et al., 2019), which in turn can create favourable microhabitats which then support the regeneration of the shade-tolerant *P. abies* (Valkonen & Valsta, 2001). However, it is important to acknowledge that this study focused on tree seedling responses and did not evaluate broader ecosystem-level impacts of salvage logging. Documented negative effects, such as reductions in biodiversity, alterations of soil properties and microclimates, and loss of deadwood habitat, should be carefully weighed when planning post-fire interventions (Bowd et al., 2019; Lindenmayer & Noss, 2006;

Marcolin et al., 2019; Thorn et al., 2018). Adaptive management approaches that balance timber recovery with ecological integrity are therefore recommended.

In addition to logging practices, our results underscore the need to manage competing understory vegetation (Nilsson & Wardle, 2005). The presence of ericaceous shrubs negatively affected seedling growth, and their expected increase under climate change may pose a growing challenge to tree regeneration efforts (Jessen et al., 2023). However, shrub cover was similar in warmed and ambient plots. Mechanical or manual removal of such vegetation could enhance planting success, especially in areas of dense shrub cover. We also found that warming itself had a direct positive effect on seedling growth, suggesting that post-fire recovery rates may improve in some regions despite harsher fire regimes. Finally, our study highlights the potential of assisted migration as a viable tool for improving seedling performance under future climate conditions (Chakraborty et al., 2024). Northward movement of *P. abies* and southward movement of *P. sylvestris* provenances led to improved growth, indicating that selection of climate-adapted genetic material should be considered in reforestation planning.

Ultimately, effective post-fire forest management in boreal systems may benefit from an integrated approach that considers fire severity, salvage logging impacts, vegetation dynamics, warming effects and genetic adaptation. Such strategies can improve resilience and ensure sustainable forest recovery in a rapidly changing climate.

AUTHOR CONTRIBUTIONS

Theresa S. Ibáñez: Conceptualization (equal); data curation (lead); formal analysis (equal); investigation (equal); methodology (equal); visualization (equal); writing original draft and editing (equal). Michael J. Gundale: Conceptualization (equal); investigation (equal); methodology (equal); supervision (equal); visualization (equal); writing original draft; review and editing (equal). David A. Wardle: Conceptualization (equal); investigation (equal); methodology (equal); supervision (equal); visualization (equal); writing original draft; review and editing (equal). Hélène Barthelemy: Data curation (equal); investigation (equal); writing review and editing (supporting). Joachim Strengbom: Methodology (equal); writing review and editing (supporting). Gustaf Granath: Methodology (equal); writing review and editing (supporting). Kishore Vishwanathan: Data curation (equal); formal analysis (equal); visualization (equal); writing review and editing (supporting). Marie-Charlotte Nilsson: Conceptualization (equal); data curation (lead); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); supervision (lead); visualization (equal); writing original draft and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Swedish National Data Service <https://doi.org/10.5878/xnw1-4y91> (Ibáñez & Nilsson, 2025).

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SUPPORTING INFORMATION

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

Table S1. Mean $\pm$ SE aboveground biomass (g/m^2) of ericaceous shrubs removed from plots during the experimental start up in 2016 in low fire and high fire severity forest stands, in both unlogged and salvage logged sites.

Table S2. Soil nutrients (mean $\pm$ SE) in response to fire severity (high or low fire severity), logging (salvage logged or unlogged), experimental warming (ambient or elevated) and presence (P) or removal (R) of ericaceous shrubs in 2019. No statistical differences between treatments were observed except from a weak three-way interaction between fire severity $\times$ experimental warming $\times$ presence of shrub on N (df: 1, 37.4, F -value: 5.1631, p -value: 0.0281) and C:N ratio (df: 1, 37.6, F -value: 4.9947, p -value: 0.0315) in the organic soil layer. However, no pairwise differences among means were obtained by post hoc tests.

Table S3. Tree seedling mortality in 2019 (total number and % out of all seedlings planted) in each experimental treatment combination, for all seven logged and unlogged stands. Abbreviations: presence of shrub (P), removal of shrubs (R) Ambient (non-OTC) and Warming (OTC).

Table S4. Results of a generalized linear mixed model (GLMM) analyzing binomial mortality data for tree seedlings of varying provenances (PR) of *P. abies* and *P. sylvestris* planted in stands of fire severity (FS; high or low fire severity), logging (SL; salvage logged or unlogged), experimental warming (OTC; ambient or elevated) and shrub removal (SRB; presence or removal of ericaceous shrubs) in 2019.

Table S5. Mean vegetation cover (%) of plant species in response to fire severity (high or low fire severity), salvage logging (salvage logged or unlogged), experimental warming (ambient or elevated) and presence (P) or removal (R) of ericaceous shrubs in 2019.

Table S6. Main and interactive effects of fire severity (FS), salvage logging (SL), experimental warming (OTC) and shrub removal (SRB) on total vegetation cover in 2019. A generalized linear mixed effects model was fitted with site (stand number with corresponding level of fire severity) as the random factor, to study these effects. Results were obtained by performing type III ANOVA on the fitted model. Corresponding mean values are presented in Figure S2.

Figure S1. Temperature ($^{\circ}\text{C}$) recorded every 2 min, 5 cm above ground, in each of four experimental treatment combinations for (a) salvage logged and (b) unlogged stands during June 1–3, 2016. Yellow = open top chamber (warming treatment) with shrubs present; Grey = open top chamber with shrubs removed; Blue = ambient temperature with shrubs removed; Orange = ambient temperature with shrubs present.

Figure S2. Mean $\pm$ SE of total vegetation cover (%) in response to (a) salvage logging, (b) fire severity + warming, (c) fire severity $\times$ salvage logging $\times$ warming, (d) salvage logging $\times$ warming, (e) shrub removal $\times$ warming and (f) fire severity $\times$ shrub removal $\times$ warming. Lower case letters indicate significant difference and empty error bars denote non-significance between groups at $p \leq 0.05$, using ANOVA for the general linear mixed effects model and subsequent post hoc analysis using Tukey's test. Corresponding ANOVA results are reported in Table S6.

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