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ARTICLE

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Factors limiting the potential range expansion of lodgepole pine in Interior Alaska

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Abstract

Understanding the factors influencing species range limits is increasingly crucial in anticipating migrations due to human-caused climate change. In the boreal biome, ongoing climate change and the associated increases in the rate, size, and severity of disturbances may alter the distributions of boreal tree species. Notably, Interior Alaska lacks native pine, a biogeographical anomaly that carries implications for ecosystem structure and function. The current range of lodgepole pine (*Pinus contorta* var. *latifolia*) in the adjacent Yukon Territory may expand into Interior Alaska, particularly with human assistance. Evaluating the potential for pine expansion in Alaska requires testing constraints on range limits such as dispersal limitations, environmental tolerance limits, and positive or negative biotic interactions. In this study, we used field experiments with pine seeds and transplanted seedlings, complemented by model simulations, to assess the abiotic and biotic factors influencing lodgepole pine seedling establishment and growth after fire in Interior Alaska. We found that pine could successfully recruit, survive, grow, and reproduce across our broadly distributed network of experimental sites. Our results show that both mammalian herbivory and competition from native tree species are unlikely to constrain pine growth and that environmental conditions commonly found in Interior Alaska fall well within the tolerance limits for pine.

Xanthe J. Walker and Jill F. Johnstone contributed equally to the development of this publication.

If dispersal constraints are released, lodgepole pine could have a geographically expansive range in Alaska, and once established, its growth is sufficient to support pine-dominated stands. Given the impacts of lodgepole pine on ecosystem processes such as increases in timber production, carbon sequestration, landscape flammability, and reduced forage quality, natural or human-assisted migration of this species is likely to substantially alter responses of Alaskan forest ecosystems to climate change.

KEYWORDS
boreal forest, climate change, disturbance, experiment, lodgepole pine, *Pinus contorta*, range limits, simulation modeling, species distribution, wildfire

INTRODUCTION

Understanding the controls over species range limits is becoming increasingly important as we anticipate migrations in response to human-caused climate change. Ecological niche theory predicts that species distributions partially reflect environmental tolerance limits, and there is ample evidence that historical and contemporary distributions shift with climate (Chen et al., 2011; MacDonald et al., 2008). However, other factors such as dispersal limitation, life history traits, and biotic interactions often prevent species from occupying all climatically suitable habitats, which leads to migration lags and smaller distributions than determined by environmental requirements (Leibold, 1995). As we seek ways to adapt to and mitigate the effects of human-caused environmental change on ecosystems, it becomes important to understand: (1) the potential for species to occupy and thrive in new locations beyond their current range, (2) the historical legacies of migration lags and implications for current and future migration potential, and (3) the impacts of changing range distributions on extant communities and ecosystems.

The high-latitude boreal biome experiences climate warming at a faster rate than lower latitudes (Brandt et al., 2013; Rantanen et al., 2022). These changing environmental conditions and the associated increases in the rate, size and severity of disturbances may shift boreal tree species distributions (Boulanger et al., 2018; Foster et al., 2019; Stralberg et al., 2020). Boreal forests play a central role in the global carbon (C) cycle, accounting for ~50% of the world's forest C stocks, mostly in their soils (DeLuca & Boisvenue, 2012; Malhi et al., 1999). These forests also provide important ecosystem services, such as primary productivity, water cycling, nutrient cycling, as well as natural and cultural resources (Brandt et al., 2013). Understanding the impacts of climate change on boreal forest structure and function is complicated by the fact that many tree species only occupy a subset of their environmentally suitable range because they are long-lived sessile organisms with relatively short dispersal distances (Seliger et al., 2021; Svenning & Skov, 2007). Furthermore, compositional responses to ongoing climate change and the intensification of disturbances will depend on biogeographic patterns in the pool of regionally available species.

Holocene records show considerable variability in patterns of post-glaciation tree migration into what is now the boreal region of North America (Lloyd et al., 2006). Boreal pines (*Pinus* spp.) migrated more slowly than boreal spruces (*Picea* spp.) and currently have northern range limits that are to the south of spruce range limits (Critchfield, 1985; Payette et al., 2022). Although shore pine (*Pinus contorta* var. *contorta*) has been present in southeast Alaska for more than 10,000 years (Ager, 2019), its distribution is limited to coastal environments, and there is no native pine present in the boreal forest of Interior Alaska. Boreal pines such as lodgepole (*Pinus contorta* var. *latifolia*) and jack pine (*Pinus banksiana*), which thrive in the Canadian boreal forest, are fire-dependent species, with serotinous cones that ensure ample seed to support stand-replacement following fires (Schwilk & Ackerly, 2001). The requirement of fire for seed dispersal likely contributed to a northern migration lag of lodgepole pine and jack pine in comparison to semiserotinous black spruce (*Picea mariana*) and nonserotinous white spruce (*Picea glauca*) during the Holocene (MacDonald & Cwynar, 1986; Payette et al., 2022).

The closest source populations of boreal pines to Interior Alaska are represented by lodgepole pine in south-central Yukon Territory, Canada. The northward migration of lodgepole pine began ~12,000 years BP, near the southern border of Canada (MacDonald & Cwynar, 1986). Lodgepole pine may have reached locations in the southern Yukon Territory as early as the mid-Holocene but remained at low landscape abundances for millennia (Edwards et al., 2015; Strong & Hills, 2013). Landscape spread was likely limited by complex topography that created a patchy habitat mosaic (MacDonald & Cwynar, 1986; Strong & Hills, 2013), as well as Allee effects associated with small founder populations (Edwards et al., 2015). Recent palynological records and current population dynamics suggest ongoing, contemporary spread of lodgepole pine near its Yukon range limits, particularly in association with fire activity (Edwards et al., 2015; Johnstone & Chapin, 2003; MacDonald & Cwynar, 1986). Lodgepole pine from NW Canada also performs well in forestry trials in Interior Alaska (Alden, 2006). The absence of pine in boreal Alaska may represent an idiosyncrasy of biogeography, with consequences for forest structure and ecosystem processes important to society, such as timber production, C sequestration, and landscape flammability.

Evaluating the potential for widespread expansion of pine in Alaska requires testing hypothesized constraints on range limits such as dispersal limitations, environmental tolerance limits, biotic interactions, and historical contingencies or priority effects of which species arrive first (Vannette & Fukami, 2014). In other boreal regions, pines can form mixed stands with fast-growing broadleaf species such as aspen (*Populus tremuloides*) as well as more conservative species such as black spruce. Reconstructed dynamics from the Holocene suggest that once pine arrives, local population expansion may be delayed by unfavorable environmental conditions, disturbance regimes, or priority effects of extant vegetation (Edwards et al., 2015; Payette & Frégeau, 2019). Disentangling the importance of dispersal, environmental constraints, and biotic interactions in setting range limits is important in a modern context as we seek to predict future species distributions and their effects on ecosystem function under a changing climate.

Here we use field experiments with pine seeds and transplanted seedlings extended with model simulations to determine the abiotic and biotic controls over lodgepole pine seedling establishment and growth beyond their current range in Interior Alaska. These experiments were conducted across a range of environmental conditions and in combination with a suite of native tree species likely to represent potential competitors for forest dominance. We followed the fate of experimentally seeded and planted pines over multiple years so that we could assess how climate and soil conditions impact the establishment, growth, and survival of pines during the critical period of post-fire community assembly (Johnstone et al., 2020). We further used simulation modeling to explore the effects of adding pine for long-term patterns of stand dominance, biomass accumulation, and C stocks in Alaska. Our results provide an empirical test of hypothesized constraints on the range expansion of pine in Interior Alaska.

METHODS

Study sites

Extreme fire activity in 2004 produced three large burned areas (total area burned >27,000 km^2) that intersected the road network in Interior Alaska along a broad N–S gradient from the Brooks Range in the north to the Alaska Range in the south. We identified study sites within each of these road-accessible burned areas: the Dalton Complex (DC) along the Dalton Highway north of Livengood, the Boundary Fire (BF) along the Steese Highway east of Fairbanks, and the Taylor Complex (TC) along the Taylor Highway northeast of Tok, Alaska (Johnstone et al., 2010). These roads have infrequent traffic, narrow rights-of-way, and minimal human impact over the last century. We identified 39 intensive study sites (12–13 sites in each burn complex) from a larger sample of 90 sites (Johnstone et al., 2010) for detailed studies of post-fire revegetation (Bernhardt et al., 2011; Brown et al., 2015; Hollingsworth et al., 2013). Sites captured variations in fire severity (biomass fuel consumption) and gradients in site moisture and elevation within each burned area. All sites were dominated by black spruce when they burned, with >95% canopy mortality caused by fire.

Field methods

Each site was represented by a 30 × 30 m sample area, marked with corner stakes to delimit a plot with sides aligned to E–W and N–S compass orientations. We laid out two parallel 30-m transects, spaced 15 m apart, within the site boundaries. Blocks of seedling transplants were designated every 5 m along the transects ($n = 14$ blocks). Additional blocks for seeding ($n = 5$) were assigned randomly to an interval between the transplant blocks. Environmental measurements (see below) at a site were taken at the site center or along transects parallel to the experimental blocks but offset by at least 5 m.

For the seeding experiment, each block contained a set of six 50 × 50 cm seeding plots randomly assigned to seed application of one of five boreal tree species: lodgepole pine, and four species native to the study area: black spruce, white spruce, Alaska paper birch (*Betula neoalaskana*), and trembling aspen. Seedling blocks also included a control plot, in which no seeds were sown. Results for the seeding experiments with native tree species are presented elsewhere (Brown et al., 2015); here we focus specifically on the seeding trials with lodgepole pine. Seeds of pine originated from native pine populations near its range limit west of Whitehorse, Yukon, Canada. Seeds were weighed to obtain approximately 75 viable seeds (mean germination rate in the laboratory of 66%). This sowing rate was selected to provide a reasonable likelihood of obtaining germinants in the majority of plots based on past experiments (Johnstone & Chapin, 2006). Seeds were scattered across the surface of a 50 × 50 cm seeding subplot in late August 2005, on burned soil surfaces that ranged from exposed mineral soil to ~20 cm of residual organic soil. Initial germination of pine seeds occurred during the summer of 2006. Live seedlings were counted in late July of 2006, 2007, 2008, and 2011. All seedlings were removed after counting in 2011, as variable densities and crowding in small plots limited the further utility of monitoring the seeding trials.

Tree seedlings were transplanted into experimental blocks ($n = 14$ seedlings per site) to provide an assessment of potential seedling growth that was independent of seed germination success. We grew seedlings of the five species used in the seed treatments in sterile potting media in a greenhouse for 3 months prior to planting in the field. Seedlings were transplanted to the intensive sites in mid-June 2005. The rapid growth under greenhouse conditions meant that individuals were equivalent in size to approximately a 3-year-old naturally established seedling, with basal diameters and heights of 0.8–2.5 mm and 5–10 cm for pine and spruce, and 1.5–4.5 mm and 15–40 cm for aspen and birch. One seedling of pine and the four native species were planted into 14 blocks, with a distance of 15 cm between the seedlings (Figure 1). Because we had only limited quantities of deciduous seeds, only 10 individuals of aspen were planted at each site, and transplanting of paper birch was limited to 10 individuals at intensive sites in the BF. Given the low sample size and unequal distribution of birch, this species was excluded from the analyses conducted in this paper.

Odd-numbered blocks ($n = 7$) within each site were assigned to protective exclosures designed to prevent mammal herbivory on seedlings during initial seedling establishment. The exclosures encircled the seedlings and were constructed from wire mesh fencing (with 2–3 cm diameter openings) with a diameter of ~60 cm, height of 100 cm, and a closed top. The exclosures were installed

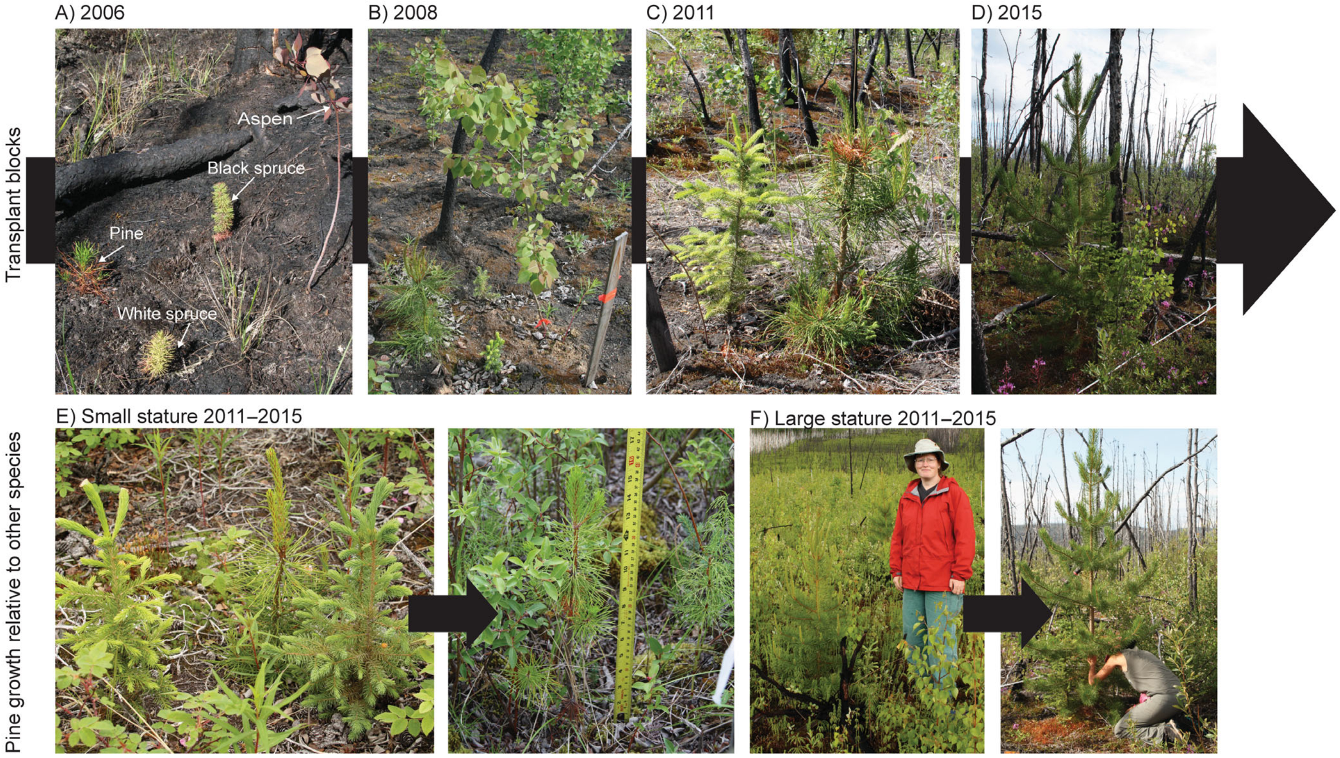

FIGURE 1 Seedling transplants through time. The upper set of images shows individual blocks of transplants (lodgepole pine, black spruce, trembling aspen, and white spruce) pictured in (A) 2006 (1 year after transplanting), (B) 2008, (C) 2011 (the year of the main harvest, at 6 years of growth), and (D) 2015, when all remaining pines were harvested and cone production was measured. Lower images show some of the variation in lodgepole pine sizes at the time of the 2011 and 2015 harvests, for (E) small stature and (F) large stature pine seedlings. Photograph credits: Jill Johnstone.

around the seedlings after planting in 2005 and removed in 2008, when some tree seedlings were beginning to exceed the height of the exclosure.

Transplanted seedlings were measured for apical growth and survival in 2006–2008. In 2011, we harvested half of the transplanted seedlings (blocks 1–7) for aboveground biomass after taking field measurements of seedling basal diameter and stem height in all blocks. Stems of seedlings were cut at ground level and transported in bags to the laboratory, where the live biomass of each individual was dried at 60°C and weighed to obtain total aboveground biomass (g/individual). Allometric relationships between biomass and stem diameter and height were derived from harvested seedlings (Johnstone et al., 2020) and applied to nonharvested seedlings of the same age to provide biomass estimates for all transplanted seedlings in 2011. We used paired plantings of pine, black spruce, white spruce, and aspen (blocks 1–10 at each site) to assess pine relative dominance, or its position in the seedling competitive hierarchy, in each block. Pine relative dominance was estimated as the ratio of pine biomass to the summed total biomass of all four seedlings in a block, using measured or predicted aboveground biomass in 2011. Pine transplants that remained after 2011 were harvested in 2015, by which time several transplants were reaching reproductive maturity. We counted the total number of male and female cones present on pine transplants in 2015.

Environmental conditions at each site were characterized by field measurements collected in 2005–2006 (Boby et al., 2010; Johnstone et al., 2010). Elevation and GPS coordinates at the plot center point were recorded with a handheld GPS. At each site, we dug a soil pit to >50 cm to characterize mineral soil conditions. Samples of mineral soil from the upper 15 cm were collected for laboratory analyses of soil texture and pH. We characterized site moisture using ordinal classes estimated on a six-point scale, ranging from xeric to subhygric, based on a combination of topography-controlled drainage conditions, soil texture, and near-surface permafrost at each site (Johnstone et al., 2008). Site moisture classes were correlated with direct estimates of % soil moisture but showed stronger associations with seedling responses (Johnstone et al., 2020). The depth of post-fire, residual soil organic layers (SOL) was measured at 11 randomly selected points on the transect to characterize the site average post-fire SOL (Boby et al., 2010). We were unable to collect detailed climate data across the network of 39 sites, and instead estimated mean summer temperature (June, July, August) at each site using the gridded daily temperature for the period 1980–2021 from Daymet V. 4, an interpolated product with a spatial resolution of 1 km (Thornton et al., 2021).

At each site we also tracked natural patterns of post-disturbance recovery over the initial two decades after fire (Johnstone et al., 2010, 2020). Monitoring patterns of natural seedling recruitment and growth has allowed us to characterize sites into trajectories leading to spruce dominance, mixtures of spruce and deciduous trees, or deciduous canopy dominance (Johnstone et al., 2020; Mack et al., 2021). We classified sites into post-fire tree species dominance classes based on a deciduous fraction index (DI) calculated from the survey data (DI = relative density plus relative biomass of deciduous tree seedlings divided by two and multiplied by 100). When DI was $\leq$33.33%, sites were classified as black spruce (hereafter Spruce). Sites were classified as mixed black spruce–deciduous (hereafter Mixed) if DI was >33.33% and <66.66%, and as deciduous if DI was $\geq$66.66%. Sites were classified as open if there was less than one tree stem of any species per square meter. Of the 39 experimental sites, 8 were spruce, 16 were deciduous, 9 were mixed, and 6 were open post-fire.

Field data analysis

We examined responses of pine seed germination, survival, and growth to variations in environmental gradients across sites. We were particularly interested in the effects of post-fire seedbed quality, soil moisture and chemistry, and topographic and latitudinal gradients in climate conditions. The nature of our experimental design, with its focus on experimental planting across natural variations in post-fire conditions, meant that environmental gradients were not independent of each other. We relied on a priori biological understanding to identify a potential suite of environmental covariates, which we further reduced to a subset of variables with minimal collinearity. In particular, we expected that soil conditions related to moisture, nutrient availability, and microclimate would be important for seedling emergence and growth, along with the broader effects of topography and latitude on climate severity.

The final environmental covariates tested in our models were: (1) residual SOL depth, because of its direct relationship with seedling germination and initial survival, mediated through controls over soil temperature and availability of moisture and nutrients (Greene et al., 2007; Johnstone & Chapin, 2006); (2) site moisture class, as gradients in soil drainage and moisture availability structure plant communities and natural seedling recruitment in the study area (Johnstone et al., 2010); (3) soil pH, as an indicator of soil chemistry variations that affect nutrient availability and plant communities (Hollingsworth et al., 2006); and (4) summer

(June to August) mean temperature, which represents variations in climate severity occurring with elevation and latitude across our study sites. Summer temperature was selected over annual temperature because it captures growing season conditions and winter temperature is known to have complicated interactions with topographic inversions (Noad et al., 2023). We also recognize that there are linkages between site moisture class and SOL depth, but each provides some unique information due to variations in fire history, severity, and permafrost (Johnstone et al., 2020). Although we considered that environmental covariates may interact in their effects on seedling recruitment, our experimental design and the coarse nature of covariates estimated at the site level meant that modeled interactions were poorly constrained. Consequently, model fit focused solely on the main effects of environmental covariates.

Experimental response variables were modeled using a generalized linear mixed effect modeling approach (GLMM) using the R package *lme4* (Bates et al., 2015) with a random intercept term of site identity to account for the hierarchical structure of our experimental design. All analyses were conducted in the statistical software program R version 4.2 (R Core Team, 2022). For all GLMM that follow, we assessed the significance of fixed effects using the default approach in lme4, Wald-*Z* tests. We verified that statistical assumptions of normality of residuals, normality of random effects, homogeneity of variance, and multicollinearity were not violated using the *DHARMa* package (Hartig, 2020). We centered and scaled all environmental predictor variables. Model results were plotted using the *effects* and *ggplot2* packages (Fox, 2003; Wickham, 2016).

We assessed the influence of environmental conditions (soil pH, SOL depth, moisture class, and summer temperature) on (1) the probability of observing seedling emergence (0 = failure, 1 = success), (2) the number of seedlings (>0) with successful emergence, and (3) the proportion of seedlings that survived to 2011. We constructed separate models for each because we expected that they would be influenced by different environmental drivers (Seidl & Turner, 2022). We modeled the presence of germination within a seeded plot using a GLMM with a binomial error distribution and logit link function. Given the presence of germination, we then modeled the number of seedlings using a GLMM with a negative binomial error distribution (to account for overdispersion). We modeled the probability of seedling survival using a GLMM with a binomial error distribution and logit link function.

We modeled the impact of environmental conditions (soil pH, SOL depth, moisture class, and summer temperature) and herbivore exclosures on lodgepole pine transplants: (1) survival, (2) biomass, and (3) relative dominance in 2011. For the survival model, we also included a fixed effect of biomass in 2008 because we expected that survival would be contingent on seedling size. Survival was modeled using a GLMM with a binomial error distribution and logit link function. To model biomass, we used a GLMM with a Gamma error distribution and log link function. We modeled pine relative dominance within a block using a GLMM with a binomial error distribution and logit link function.

We tested if transplanted pine biomass or survival varied with post-fire successional trajectories of spruce, deciduous, mixed, or open. For the biomass model, we used a GLMM with a Gamma error distribution and log link function. For the pine relative dominance within a block model, we used a GLMM with a binomial error distribution and logit link function.

We tested the relationship between the reproductive maturity of transplanted seedlings and seedling size using data collected on lodgepole pine transplants in 2015. We used the production of female cones as an indicator of reproductive maturity. In contrast with male cones, female cones typically persist on lodgepole pine stems for multiple years and can therefore represent the onset of reproductive maturity during and prior to the year of measurement. The probability of a pine transplant reaching reproductive maturity by 2015 was modeled in relation to $\log_{10}$ transformed biomass using a GLMM with a binomial error distribution and logit link function.

Simulation modeling

We used simulations with the model iLand to estimate centennial growth trajectories of lodgepole pine in Interior Alaska and to estimate the impacts of pine presence on mean tree biomass and stand-level C stocks, given potential competitive interactions with native tree species. iLand is an individual-based forest process model that simulates the growth and mortality of trees in spatially explicit stands and landscapes based on canopy light interception, climate, and nutrients (Seidl, Rammer, et al., 2012; Seidl, Spies, et al., 2012). Individual trees determine light availability at a 2-m spatial resolution within stands. Climate and soil characteristics (% sand, silt, clay, effective depth, and nutrient availability) are considered to be homogenous at the stand scale (1-ha). iLand is forced with daily temperature, precipitation, shortwave radiation, and vapor pressure deficit. iLand also includes a permafrost and surface SOL module that mechanistically simulates daily changes in active layer depth, annual SOL accumulation and decomposition, and their complex ecological effects (Hansen et al., 2023).

We ran the model in stand mode, independent forest stands are simulated in parallel and neighboring stands do not influence one another. The model simulates each stand as if they are "wrapped" where trees on one side of the stand influence trees on the other side, eliminating edge effects. The model has been well tested in landscape and stand modes and applied to forest stands containing lodgepole pine in the western United States (Hansen et al., 2018; Turner et al., 2022) and deciduous and spruce stands in Alaska (Hansen et al., 2021, 2023).

We initialized iLand with data from 90 boreal forest stands in Interior Alaska. This included the 39 stands used in the lodgepole-pine experiment and 51 surveyed stands that were also dominated by black spruce before burning in 2004, but where lodgepole pine seedlings were not experimentally planted (Johnstone et al., 2020). Seedling densities of naturally recruiting tree species (black spruce, trembling aspen, and Alaskan birch) were set using field measurements, and we assumed these seedlings and lodgepole pine seedlings were 1 year old and were between 1 and 4 cm tall at the start of the simulations. We initialized lodgepole pine seedlings at densities consistent with the experimental plantings. Lodgepole pines were simulated using a parameter set from the northern Rocky Mountains of the western United States (Braziunas et al., 2018). While species traits can vary across geographic ranges (Anderegg et al., 2018), our initial benchmarking to field data indicated the parameter set was robust for application to Interior Alaska. Soil information used to initialize iLand was extracted using geographic coordinates of the 90 stands from the global SoilGrids250m database versions 1.0 (for effective soil depth) and 2.0 (for percent sand, silt, and clay) (Hengl et al., 2017). Relative soil fertility, expressed as plant available nitrogen, was set at 45 kg ha^{-1} year^{-1} (Hansen et al., 2021). We used the same interpolated climate data set used in the analysis of the field experiment (Daymet V4) for daily climate data (Thornton et al., 2021).

Simulation experiment

We conducted simulations to extend the field experiment for 89 years. This allowed us to quantify how large lodgepole pine would have grown over a century and how the experimental addition of lodgepole pine may have altered the biomass of other tree species and stand-level C stocks.

Stands were simulated with and without experimentally planted lodgepole pine forced with 2005–2015 daily climate randomly recycled with replacement (i.e., no climate change) for a century. To evaluate correspondence with experimental results, we first compared simulated lodgepole pine height and diameter at breast height (dbh) from model year 11 (corresponding to 2015 in the lodgepole pine transplant experiment) with observations at the 39 experimental sites where lodgepole pine seedlings were transplanted. To quantify the centennial effects of lodgepole pine, we then used outputs from model year 100 with and without lodgepole pine, to calculate the biomass of the naturally occurring tree species, total aboveground live (stem, branch, foliage, regeneration) C stocks, and belowground (SOL, downed wood, coarse roots, fine roots) C stocks. Because parametric statistics are problematic when applied to simulated datasets, where *p*-values can be artificially decreased with increasing sample size, we emphasize ecological rather than statistical differences when interpreting results.

RESULTS

Seeding experiment results

Lodgepole pine seeds successfully germinated in all burn complexes, 85% of sites ($n = 33$), and 61% of the plots ($n = 119$). When seeding plots did have seedlings germinate, the average density was 36.3 seedlings per square meter (standard error of mean, SEM = 4.24). Although most seedlings emerged in the summer of 2006, detection of small seedlings was sometimes delayed and our analysis of total germinants used cumulative emergence up to 2008. Nevertheless, some seedlings that had clearly germinated several seasons before were detected for the first time in 2011 (five individuals at three blocks). This detection error was not large enough to alter our estimates of the seedling to viable seed ratio. Ratios of emerged seedlings to viable seed ranged from 0 to 0.99 (mean = 0.073, SEM = 0.01), slightly higher than seedling to viable seed ratios of black spruce (0.052) from the same experiment. Seedling: seed ratios for lodgepole pine were much above those observed for white spruce (0.014), Alaskan birch (0.015), and trembling aspen (0.0018) in adjacent plots (Brown et al., 2015).

We tested whether environmental factors related to climate and soil conditions affected the emergence (i.e., field observations of germinated seeds) and the survival of lodgepole pine recruiting from seed. Sites with warmer summer temperatures and greater moisture availability generally supported greater initial seedling germination. The probability of pine seedling emergence (i.e., at least one seedling observed in a plot) increased with relative site moisture and mean summer temperature (Figure 2), while soil pH and residual SOL had no significant effects (Table 1). The count of germinated seedlings, given successful germination in a plot, was

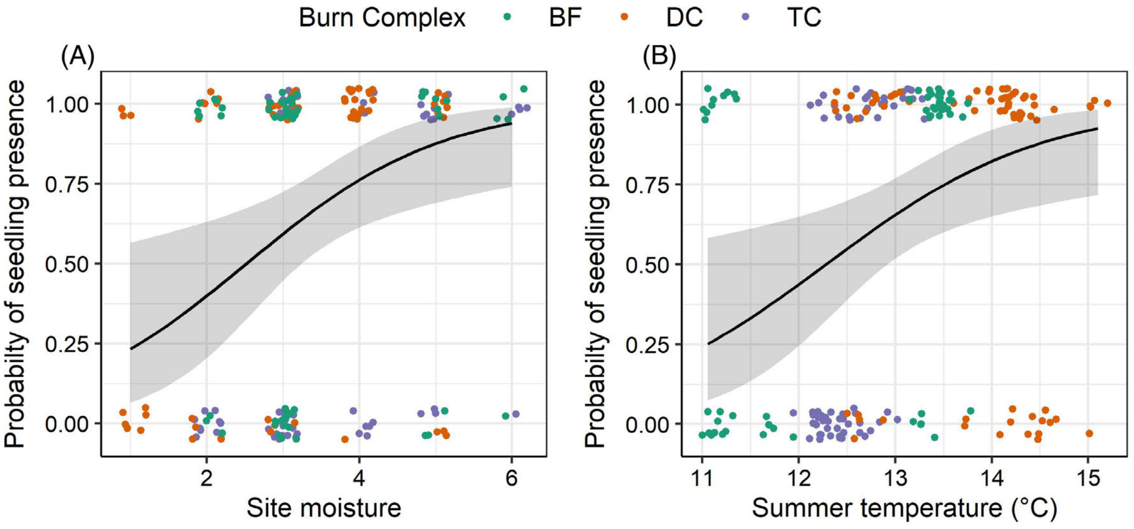

FIGURE 2 Probability of successful pine germination occurring in a seeded plot (0 = no germination, 1 = at least 1 seedling germinated), shown in relation to significant environmental covariates of site moisture (left panel; 1 = xeric and 6 = subhygric) and mean summer (JJA) temperature (average of 2005–2010), both measured at the site level. Lines show the modeled effect of the predictor variable on the response with 95% confidence intervals. Individual points (shown with jittering to reduce overlap) represent seeding plots ($n = 195$) nested within sites ($n = 39$), color-coded by burn complex: BF (Boundary fire) in green, DC (Dalton fire complex) in orange, and TC (Taylor fire complex) in purple.

weakly related to summer temperature, with warmer plots having slightly higher seedling counts (Figure 3, Table 1). Sites located in the TC were generally cooler and did not support any of the high seedling counts found at sites in the DC and BF burn areas. Soil factors became more important in relation to the survival of germinated seedlings, with survival to 2011 decreasing with greater residual SOL depth (Figure 4). Survival was unrelated to other environmental covariates (Table 1). Overall variation in seedling survival was poorly captured by both the fixed and random effects in our model, suggesting that random events or factors unrelated to our model structure govern early seedling survivorship. By 2011, 6 years after the seed sowing treatments, live lodgepole pine seedlings were present in 47% of the seeded plots ($n = 91$) distributed across 82% of sites ($n = 32$).

Transplant experiment results

Lodgepole pine seedlings that were transplanted in 2005 generally exhibited high survival but showed variable growth among sites. Approximately 87% of transplanted seedlings survived to 2008 (475 out of 546 transplants) and 81% to 2011 (442 transplants). Transplant survival from 2008 to 2011 was best predicted by biomass in 2008 (Table 1), indicating that large seedlings had a higher probability of survival.

Measurements of pine biomass based on transplant harvests and allometry in 2011 showed high variability in growth, with biomass of transplants spanning three orders of magnitude after six seasons of growth (Figure 5). Model results indicated that transplanted pine seedlings grew best under conditions of warm summer temperatures, low soil pH, and shallow residual SOL depths, with no strong effects of site moisture (Table 1). The largest pines were observed growing at BF and DC sites, which had the warmest estimates of summer temperatures (BF and DC) and lowest soil pH (DC; Figure 5). In contrast, sites in the TC burned area represented intermediate values of environmental covariates. None of the TC sites produced pines with aboveground biomass in the upper ranges observed in the other burn clusters, an effect that was not well captured by our suite of environmental covariates.

The herbivore exclosures used to protect seedling transplants from mammal herbivory in 2005–2008 had a small but significant effect on pine transplant biomass in 2011 (Table 1). Exclosures had a negative effect on seedling transplants, rather than the expected positive effect: by 2008, when the exclosures were removed, pine seedlings in exclosures were on average 25% smaller (8.2 ± 0.9 g in exclosures vs. 10.3 ± 1.0 g outside) than those without. Although the impact of exclosures carried forward to biomass in 2011, this factor had a relatively small effect on 2011 aboveground biomass (Table 1).

TABLE 1 Estimates, confidence intervals (CI), *p*-values, and Marginal and Conditional R^2 (M-R^2 and C-R^2) from generalized linear mixed effect models of the presence of seedling germination, the number of seedlings per block, given that successful germination occurred, the proportion of seedlings that survived until at least 2011, transplanted lodgepole pine survival to 2011, transplanted lodgepole pine biomass (g/individual) in 2011, relative dominance of lodgepole pine in 2011, calculated as the ratio of pine biomass to total biomass of all transplants in that block (pine, aspen, white spruce, and black spruce), transplanted lodgepole pine biomass in 2011 as a function of successional trajectories, relative dominance of lodgepole pine in 2011 as a function of successional trajectories, and reproductive maturity (production of female cones) observed for seedling transplants during the final surveys in 2015.

Model	Predictors	Estimates[a]	CI	*p*-value	M-R^2 (C-R^2)
Presence of seedling germination[b]					0.214 (0.482)
	(Intercept)	1.93	1.10–3.41	**0.023**	
	Residual organic layer	0.68	0.35–1.33	0.259	
	pH	0.84	0.42–1.68	0.626	
	Soil moisture (2008)	2.6	1.28–5.29	**0.008**	
	Mean summer temperature[e]	2.43	1.23–4.82	**0.011**	
No. seedlings per block, given that successful germination occurred[c]					0.107 (0.605)
	(Intercept)	5.65	4.16–7.67	**<0.001**	
	Residual organic layer	1.02	0.72–1.45	0.903	
	pH	1.09	0.75–1.57	0.651	
	Soil moisture (2008)	1.07	0.74–1.53	0.724	
	Mean summer temperature[e]	1.34	0.95–1.90	0.094	
No. seedlings germinated and survived to 2011[b]					0.070 (0.104)
	(Intercept)	0.52	0.43–0.63	**<0.001**	
	Residual organic layer	0.6	0.48–0.75	**<0.001**	
	pH	0.96	0.75–1.24	0.773	
	Soil moisture (2008)	0.99	0.77–1.27	0.935	
	Mean summer temperature[e]	0.94	0.73–1.20	0.602	
Lodgepole pine survival[b]					0.909 (0.916)
	(Intercept)	249	53.2–1761.6	**<0.001**	
	Residual organic layer	0.68	0.40–1.15	0.147	
	pH	1.11	0.60–2.04	0.74	
	Mean summer temperature[e]	0.49	0.27–0.90	**0.022**	
	Soil moisture (2008)	0.61	0.36–1.02	0.059	
	Exclosure [none]	1	0.46–2.14	0.99	
	Pine Biomass in 2008	307	7.96–11874.57	**0.002**	
Lodgepole pine biomass[d]					0.529 (0.700)
	(Intercept)	47.2	35.81–62.16	**<0.001**	
	Residual organic layer	0.54	0.39–0.73	**<0.001**	
	pH	0.43	0.32–0.58	**<0.001**	
	Mean summer temperature[e]	1.9	1.39–2.61	**<0.001**	
	Soil moisture (2008)	0.74	0.54–1.01	0.082	
	Exclosure [none]	1.39	1.15–1.69	**<0.001**	

(Continues)

TABLE 1 (Continued)

Model	Predictors	Estimates[a]	CI	p-value	M-R^2 (C-R^2)
Relative dominance of lodgepole pine in 2011[b]					0.225 (0.292)
	(Intercept)	0.57	0.39–0.83	**0.003**	
	Residual organic layer	0.72	0.50–1.03	0.071	
	pH	0.39	0.26–0.58	**<0.001**	
	Mean summer temperature[e]	1.61	1.13–2.29	**0.008**	
	Soil moisture (2008)	0.91	0.63–1.32	0.633	
	Exclosure [none]	2.11	1.32–3.36	**<0.001**	
Lodgepole pine biomass[d]					0.141 (0.680)
	Spruce (Intercept)	14.8	5.85–37.66	**<0.001**	
	Mixed	2.76	0.77–9.91	0.118	
	Deciduous	6.45	2.06–20.14	**<0.001**	
	Open	2.93	0.71–12.09	**0.137**	
Relative dominance of lodgepole pine in 2011[b]					0.042 (0.234)
	Spruce (Intercept)	0.36	0.15–0.83	**0.016**	
	Mixed	2.31	0.75–7.14	0.145	
	Deciduous	2.77	1.01–7.64	**0.049**	
	Open	3.7	1.07–12.74	**0.038**	
Reproductive maturity (presence of female cones)[b]					0.716 (0.764)
	(Intercept)	0	0.00–0.00	**<0.001**	
	Pine Biomass in 2015 ($\log_{10}$)	36	7.34–176.80	**<0.001**	

Note: Bolded p-values indicate significance (<0.05). See Appendix S1: Table S1 for the residual variance (σ^2), random intercept variance (τ00 site), intraclass correlation coefficient (ICC), number of sites, and number of observations for each model.

[a] For all models, the estimated coefficients are exponentiated. For all models apart from those of lodgepole pine biomass, the estimates represent odds ratios. For odds ratios, values less than 1 indicate that the odds of the event happening decrease and values greater than 1 indicate that the odds of the event happening increase. For the relative dominance model with a categorical fixed effect, the odds ratio compares the odds of the event occurring for each category of the predictor relative to the reference category of spruce. For the first lodgepole pine biomass model, values less than 1 indicate a negative effect and values greater than 1 indicate a positive effect. For the lodgepole pine biomass model with a categorical fixed effect, values are relative to the reference category of spruce.

[b] Binomial error distribution and logit link.

[c] Negative binomial error distribution and log link.

[d] Gamma error distribution and log link.

[e] 2005–2010.

The co-planting of pine seedlings with black spruce, white spruce, and aspen (Figure 1) across the full set of sites made it possible to evaluate pine performance in relation to other native species. Pine relative dominance was greatest at sites with acidic soils and warmer summer temperatures (Figure 6, Table 1). Although qualitatively similar to the relationships of pine biomass with environmental covariates, we observed stronger responses (effect sizes) of pine relative dominance to soil pH and summer temperatures (see Figure 5 vs. Figure 6 and Table 1). Therefore, response patterns of pine seedling growth to soil acidity and summer temperature led to pine seedlings increasing in competitive dominance under those conditions. Similar to biomass, relative pine dominance was also impacted by the herbivore exclosures present from 2005 to 2008 (Table 1). The presence of exclosures decreased average pine relative dominance within a block from 0.48 ± 0.02 to 0.41 ± 0.02.

When sites were grouped by successional trajectory, we found that pine biomass was significantly lower ($p < 0.001$, GLMM of categorical differences) at sites that were recovering to spruce dominance (Figure 7A). This pattern was weaker but still apparent when examining pine relative dominance, which was significantly lower ($p < 0.05$, GLMM of categorical differences) in sites that remained dominated by spruce after fire (Figure 7B).

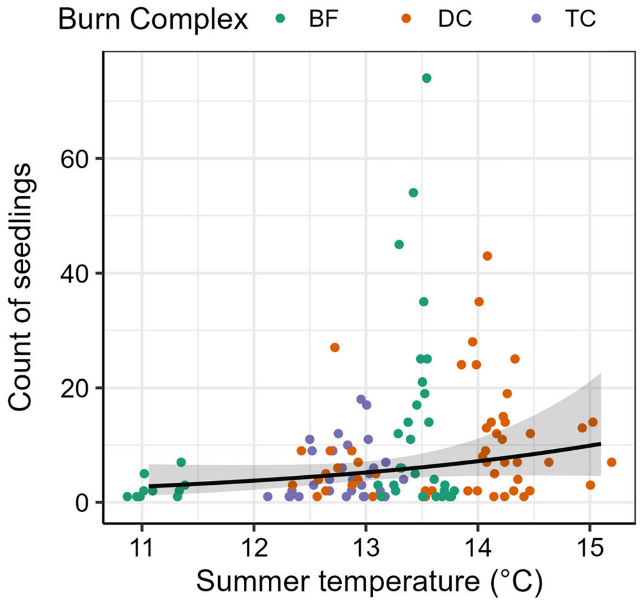

FIGURE 3 The number of seedlings that germinated per seeded plot (0.25 m^2 seeded area) shown in relation to mean summer (JJA) temperature (average of 2005–2010) estimated at the site level. Lines show the fitted relationship with 95% confidence. Individual points (shown with jittering to reduce overlap) represent seeding plots ($n = 195$) nested within sites ($n = 39$), color-coded by burn complex: BF (Boundary fire) in green, DC (Dalton fire complex) in orange, and TC (Taylor fire complex) in purple.

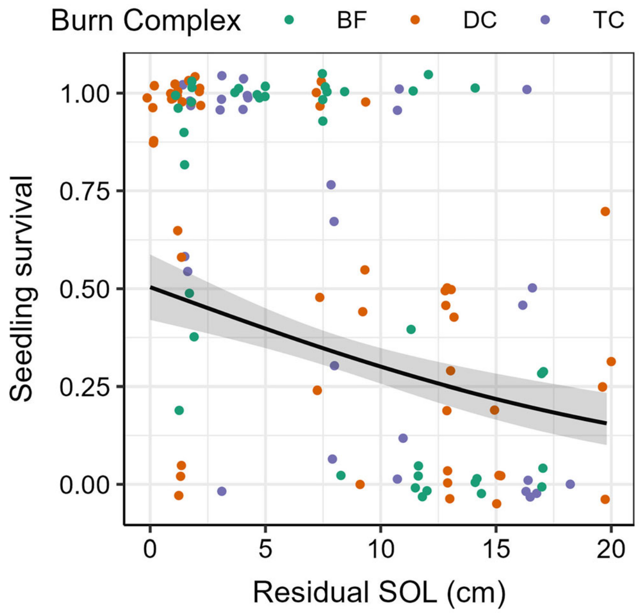

FIGURE 4 The proportion of pine seedlings that survived until 2011 in seeded plots in relation to residual soil organic layer (SOL) depth. Lines show the fitted relationship with gray shading encompassing the 95% confidence interval. Individual points (shown with jittering to reduce overlap) represent seeding plots with at least one successful germinant ($n = 119$), color-coded by burn complex: BF (Boundary fire) in green, DC (Dalton fire complex) in orange, and TC (Taylor fire complex) in purple.

Of the pine transplants that lived until the final harvest in 2015, several had reached reproductive maturity and begun producing female seed cones (31 of 179 total transplants). In contrast, we did not observe female cones on any of the black or white spruce seedlings transplanted at the same sites (data not shown). Female cone production was strongly related to pine transplant size, with the largest transplants in our sample having a higher probability of having cones (Figure 8; Table 1). Based on seedlings being transplanted at a size roughly equivalent to a 3-year-old natural seedling, pine transplants at the time of the 2015 cone surveys had a biological age of 13 years.

Simulation modeling

After a century of simulated growth, lodgepole pine at the 90 sites representing the full sample network (Johnstone et al., 2010) was 19.5 m tall on average with a median dbh of 27 cm. iLand captured the central tendency of lodgepole pine heights and DBHs observed at experimental planting sites in 2015, but did not recreate the stand-to-stand variability in observed lodgepole-pine sizes (Appendix S1: Figure S1). Therefore, model results are likely to represent average tendencies with less variability than may exist in the real world. Simulated stand dynamics with and without pine presence suggest reduced growth for naturally occurring tree species when pine was present (competitive suppression). For the 2004 burned sites, both the model with and without pine estimated the highest accumulation of aboveground biomass for birch and least for black spruce, with trembling aspen at intermediate levels and with the greatest range of variation (Figure 9A). Competition with pine was nevertheless estimated to have greater suppression effects on birch and black spruce compared with trembling aspen. Although the addition of pine suppressed the growth of native trees, increased wood accumulation by pine led to an increase in total simulated ecosystem C stocks in stands with pine after a century of post-fire recovery (Figure 9B).

DISCUSSION

Native boreal populations of lodgepole pine (*P. contorta* var. *latifolia*) are currently found as far north and west as the central Yukon Territory, approximately 100 km from Interior Alaska (Alden & Zasada, 1983). Observations of post-fire expansion of lodgepole pine populations along these geographical boundaries suggest ongoing migration (Johnstone & Chapin, 2003). Furthermore, forestry trials

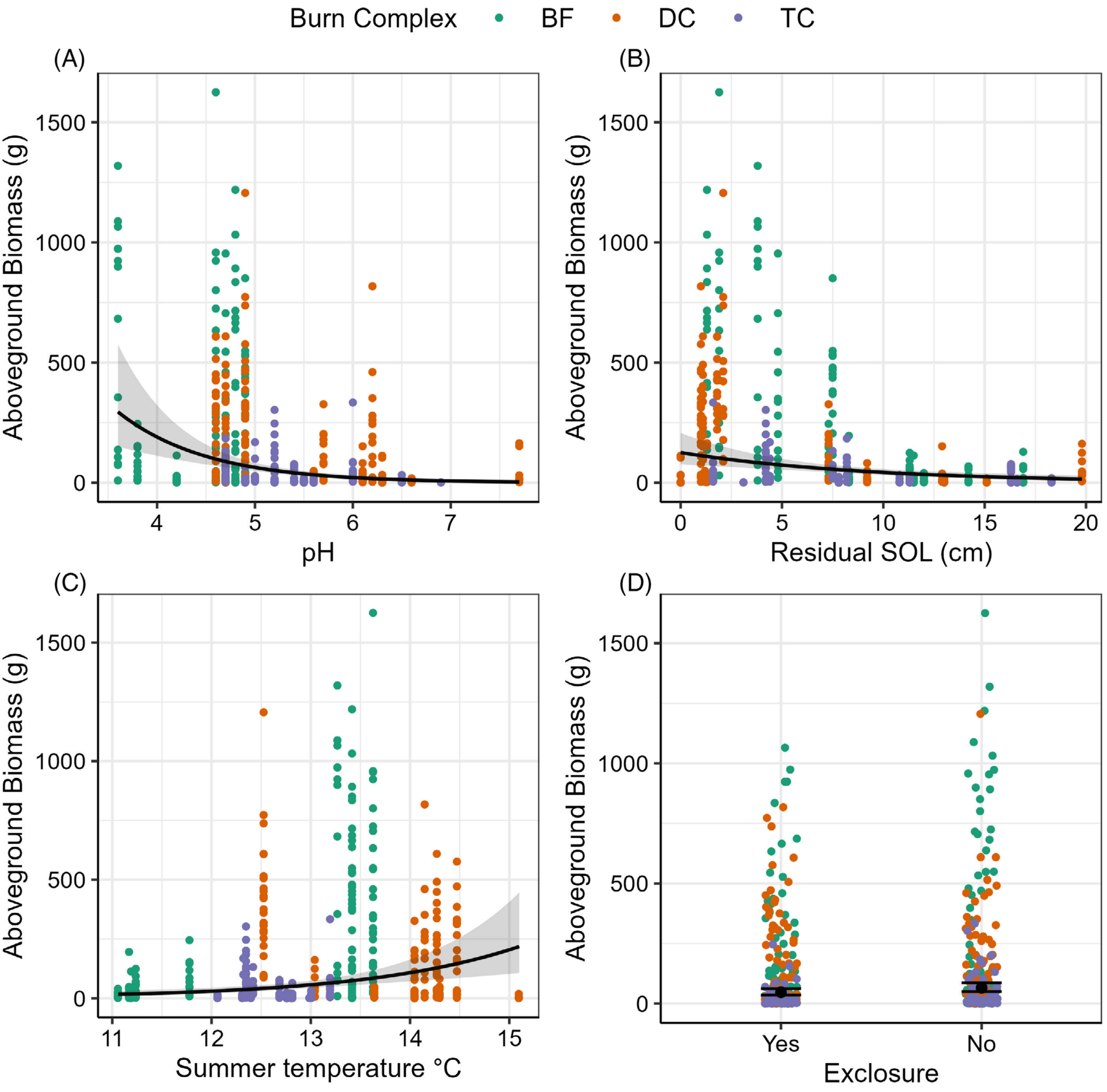

FIGURE 5 Aboveground biomass (g/individual) of transplanted lodgepole pine seedlings measured in 2011, shown in relation to significant environmental covariates of soil pH, residual soil organic layer (SOL) depth (in centimeters), mean summer (JJA) temperature (in degrees Celsius) (average of 2005–2010) measured at the site level, and presence of exclosures. Lines (or black point with error bar for exclosures) show the modeled effect of the predictor variable on the response variable with 95% confidence intervals. Individual points represent transplants ($n = 442$) nested within sites ($n = 39$), color-coded by burn complex: BF (Boundary fire) in green, DC (Dalton fire complex) in orange, and TC (Taylor fire complex) in purple.

indicate that climatic conditions are amenable to productive lodgepole pine growth in plantation settings in Alaska (Alden, 2006). Here we tested the potential for lodgepole pine to become established after fire under natural conditions in habitats previously dominated by black spruce. Our experimental results suggest that, if dispersal constraints are released, the establishment and continued spread of lodgepole pine is likely in the boreal forests of Interior Alaska. Both field observations and model simulations indicate that once established, lodgepole pine exhibits robust growth, and is capable of forming pine-dominated stands. Our empirical evidence underscores that dispersal, rather than environment or biotic interactions, predominantly constrains the northern

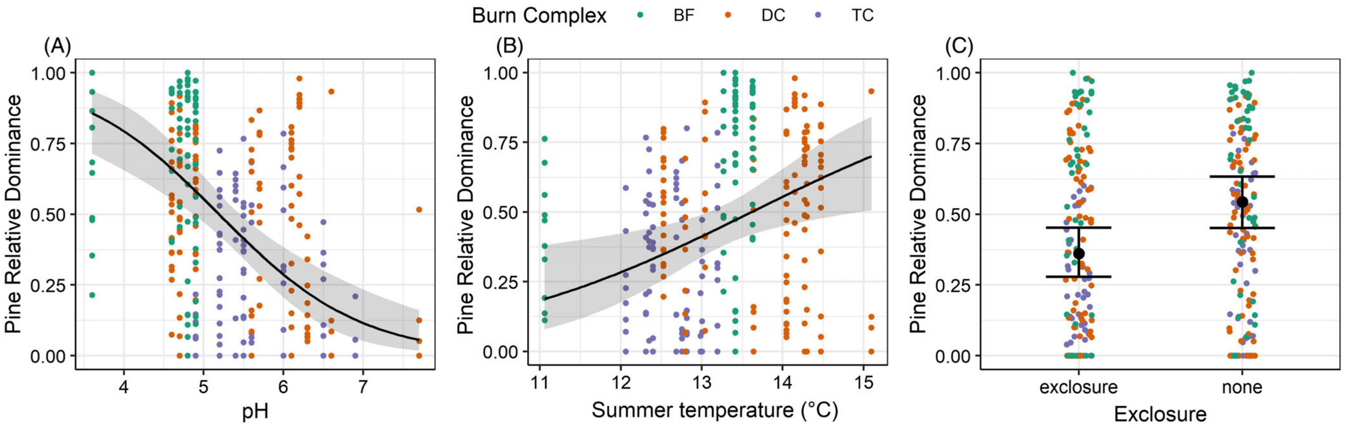

FIGURE 6 Relative dominance of lodgepole pine in 2011, calculated as the ratio of pine biomass (g/individual) to total biomass of all transplants in a block (pine, aspen, white spruce, and black spruce), shown in relation to significant environmental covariates of (A) soil pH, and (B) mean summer (JJA) temperature (in degrees Celsius) (average of 2005–2010) measured at the site level, and (C) presence of exclosures. Values of 0 relative dominance indicate dead pine seedlings that did not contribute to total biomass, while values of 1.0 indicate blocks with pine contributing 100% of total biomass. Lines (or black point with error bars for exclosures) show the modeled effect of the predictor variable on the response variable with 95% confidence intervals. Individual points represent blocks ($n = 376$) nested within sites ($n = 39$), color-coded by burn complex: BF (Boundary fire) in green, DC (Dalton fire complex) in orange, and TC (Taylor fire complex) in purple.

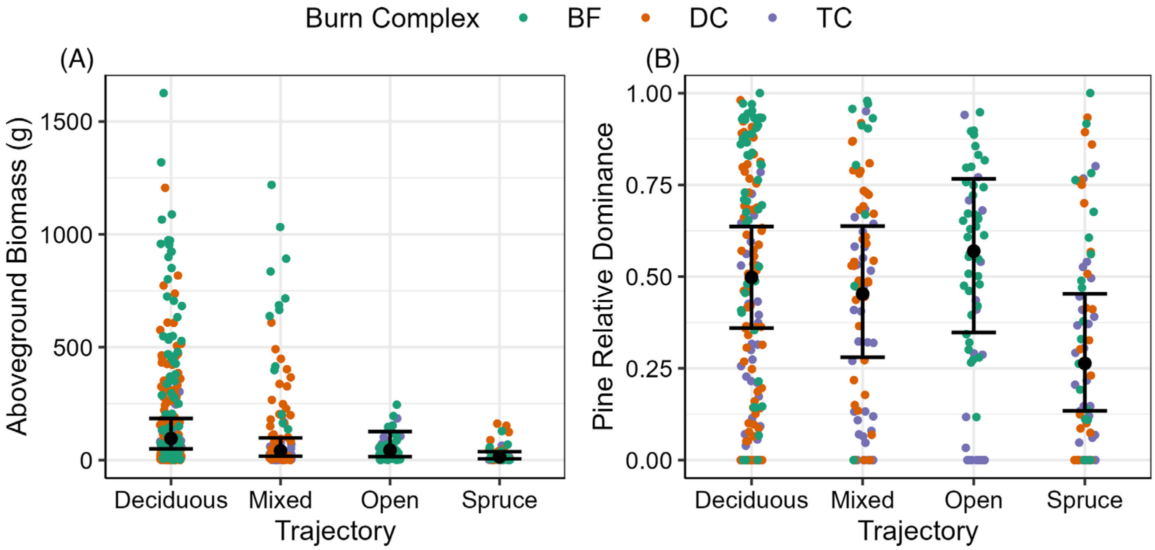

FIGURE 7 Aboveground biomass (g/individual) (A) and relative dominance (B) of lodgepole pine in 2011, grouped according to successional trajectories derived from patterns of natural tree recruitment (Johnstone et al., 2020; Mack et al., 2021). Categories of successional trajectories were defined on the basis of a deciduous fraction index (DI = relative density plus relative biomass of deciduous tree seedlings divided by two and multiplied by 100). Spruce: DI ≤33.33%, Mixed: DI >33.33% and <66.66%, Deciduous: if DI was ≥66.66%. Open: less that one tree stem of any species per sq. m.

range limits of these trees. This finding aligns with large-scale models emphasizing the significance of migration lags in shaping biogeographic responses of tree species to ongoing climate change (Seliger et al., 2021; Svenning et al., 2010). Moreover, the prospect of an extensive lodgepole pine range in Interior Alaska has important implications for considering the impacts of forest plantations or other assisted migration of pine in this region.

Demographically structured field experiments allowed us to distinguish constraints over the different stages required for pine to successfully recruit into burned spruce stands, namely germination, survival, growth, and relative dominance (Seidl & Turner, 2022). The

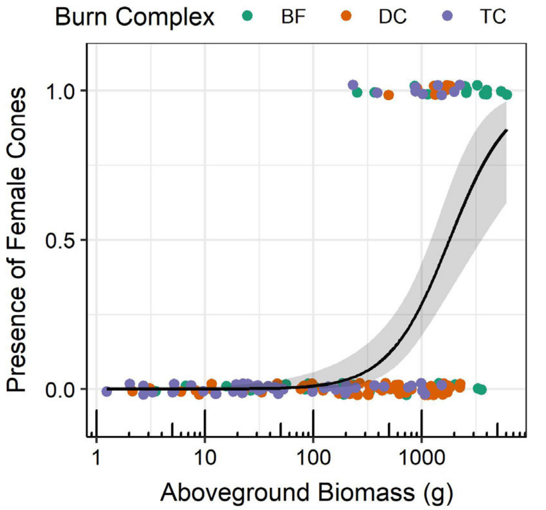

FIGURE 8 Probability of reproductive maturity (production of female cones) in relation to pine aboveground biomass (log 10 (g/individual)) observed for seedling transplants during the final surveys in 2015. Lines show the modeled effect of the predictor variable on the response with 95% confidence intervals. Individual points (shown with jittering to reduce overlap) represent seedling transplants ($n = 179$) nested within sites ($n = 39$), color-coded by burned complex: BF (Boundary fire) in green, DC (Dalton fire complex) in orange, and TC (Taylor fire complex) in purple.

germination success of pine seeds was impacted by multiple environmental factors, but these did not substantially diverge from previously documented effects of environmental factors on seed germination of native tree species already present in Alaska (Brown et al., 2015; Johnstone et al., 2010; Johnstone & Chapin, 2006). It is particularly instructive to compare pine recruitment patterns to those of black spruce, which dominates forests in Interior Alaska and can form co-dominant communities with pine in the boreal forests of northwest Canada (Greene et al., 1999; Johnstone & Chapin, 2003). Both lodgepole pine and black spruce showed an increased likelihood of germination in seeded plots with higher soil moisture in overlapping experiments (Brown et al., 2015). Both species also had reduced recruitment and lower survival on thicker organic soils. Similarly, lodgepole pine and black spruce showed similar positive responses to decreased organic layer depths associated with high fire severity in seedling experiments at sites in Yukon and Alaska, inside and outside the natural pine range (Johnstone & Chapin, 2006). Although lodgepole pine seeds have a larger mass than black spruce seeds (Greene & Johnson, 1993), this does not appear to confer a large advantage for pine recruitment, as average seed requirements to produce an

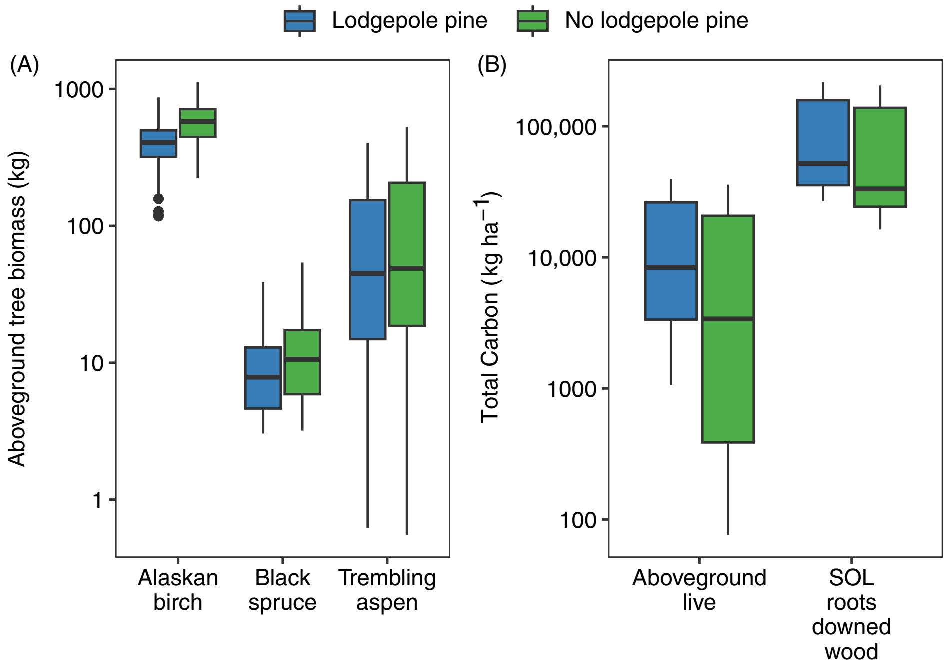

FIGURE 9 Simulated (A) aboveground individual tree (>4 m height) biomass (g) and (B) stand total carbon (C; kg ha^{-1}) after a century of growth at 90 black spruce stands that burned in 2004. Stands were simulated with and without lodgepole pine present, using tree species known to have naturally recruited at the sites (Johnstone et al., 2020). At the stand level, C pools were split into live aboveground C and belowground C pools in the soil organic layer (SOL), roots, and downed woody debris. Boxplots display the median value (central line) within the 25th and 75th quantiles (outer box), with whiskers illustrating the 1.5 Interquartile range. Data from model simulations provide complete samples of populations of interest, without requiring statistical estimates of parameters for interpretation of effect sizes.

established pine seedling were only slightly lower than the requirements for black spruce (Brown et al., 2015).

As with germination, aboveground biomass and the survival of transplanted pine seedlings showed responses to environmental factors that are qualitatively similar to those exhibited by naturally recruiting black spruce following the 2004 burns (Johnstone et al., 2020). We observed high rates of transplant survival, with mortality primarily occurring among small individuals, suggesting favorable environmental conditions. Water limitation is likely to constrain seedling survival in warmer, drier portions of the range (Coops & Waring, 2011; Hansen & Turner, 2019; Monserud et al., 2008) but does not appear to play a large role in the more northerly setting of this study, where warmer summer climate had a positive effect on growth. Pine biomass was also higher on the more acidic soils in this experiment, consistent with a general tendency for lodgepole pine to specialize in lower fertility soils (Lotan & Perry, 1983). Pine seedlings showed reduced growth on deeper organic layers, similar to native tree responses to post-fire organic layer depth (Greene et al., 2007; Johnstone et al., 2020; Johnstone & Chapin, 2006). Differential responses of pine to soil acidity and temperature were the most important factors in predicting the conditions under which lodgepole pine out-grew co-planted native trees.

Biotic interactions do not appear to significantly constrain the potential for pine range expansion in Alaska. Frequent competitive dominance of pine seedlings in our experiments and model simulations indicates that pine is unlikely to be outcompeted by other native tree species during expected disturbance-free intervals of <150 years (Johnstone et al., 2010). Fungal communities associated with the planted pine seedlings broadly overlapped with mycorrhizal communities present on native spruce seedlings, suggesting that pine expansion in Alaska could be facilitated by local fungal taxa (DeVan et al., 2023). However, pine seedlings were associated with a unique set of host-specific *Suillus* fungi that are likely to favor the competitive dominance of pine (DeVan et al., 2023).

We found no evidence that mammalian herbivory is likely to constrain pine growth across diverse sites, which is consistent with our estimate of weak to no effect of moose or hare herbivory on natural tree recruitment in the same burn areas (Johnstone et al., 2020). Exclosures designed to protect transplanted seedlings from herbivory by moose and hare instead had a weak negative effect on pine transplants. Although the exclosures were removed 3 years after the transplant experiment began, pine seedlings at the most productive sites were already rapidly outgrowing the wire cages. This crowding effect is likely to have been the mechanism underlying the negative exclosure effect. Although we observed occasional signs of snowshoe hare herbivory on pine seedlings, particularly the removal of stem leaders, pine seedlings were resilient to these events and transferred apical growth to lateral meristem growth. Therefore, although herbivores were present and active in removing biomass from some seedlings, mammalian herbivory did not act as a strong filter on early pine survival and growth in this study.

The onset of reproductive maturity of transplanted pine seedlings was strongly linked to seedling biomass, suggesting that this onset is affected by the same environmental factors that impact growth. Early production of nonserotinous cones by lodgepole pine creates opportunities for infilling while stands are still young (Kashian et al., 2005). Our findings indicate that close to one out of five transplanted pine seedlings reach reproductive maturity by the equivalent of 13 years of growth. This aligns with observations of pine reproduction in plantations in Interior Alaska, where the average age to reproductive maturity was 17 years and the earliest onset was 11 years (Alden, 2006). In southerly locations, where pine growth is faster, cone production may begin for naturally recruited seedlings as early as 9 years after fire and is similarly linked to tree size (Turner et al., 2007). In contrast, none of the black spruce transplants in our experiment were producing cones by 2015, when the experiment concluded. The ability of pine to produce cones at an early age, combined with high growth in areas with thin SOLs and high cone serotiny, could confer a competitive advantage over the semiserotinous black spruce. This advantage may facilitate pine expansion, particularly as wildfire increases and fire return intervals decrease in the region.

Natural tree recruitment in pre-fire black spruce-dominated sites is sensitive to variations in post-fire organic layer depth (Johnstone et al., 2020). Previous research shows that thick organic layers inhibit the germination and survival of small-seeded deciduous species (Greene et al., 2007; Johnstone et al., 2020; Johnstone & Chapin, 2006), therefore favoring a return to spruce dominance. Patterns of pine biomass and relative dominance in relation to natural patterns of post-fire recovery suggested that the same factors that constrain deciduous tree colonization and favor post-fire spruce resilience (Johnstone et al., 2010) are likely to constrain the potential dominance of lodgepole pine. Therefore, if pine seed were available for post-fire colonization in Interior Alaska, we predict that it would colonize sites with a high potential for shifting to deciduous tree dominance after fire. The presence of a boreal pine species with similar recruitment tolerance and competitive ability as deciduous trees could reduce the potential for severe fires to initiate shifts from conifer to deciduous tree dominance, altering the indirect effects of severe fires on boreal C balance (Mack et al., 2021).

Pine migration and dominance in Interior Alaska could significantly impact C storage, forest products, wildlife habitat, and future fire hazards. Our iLand simulations suggest that the expansion of pine in this region would alter successional trajectories, shift ecosystem C stocks from belowground to aboveground pools, and affect forest harvest yields. While the rapid growth of pine trees could increase forest productivity, it could also lead to changes in canopy closure and litter production, impacting understory vegetation and reducing forage availability for wildlife. The potential implications of pine expansion for disturbance dynamics within Interior Alaska are largely unknown but crucial. Adaptations of lodgepole pine for post-disturbance spread indicate that, if seed were available, increased fire activity and warmer summer temperatures could facilitate pulses of pine expansion, as observed in Yukon, Canada (Johnstone & Chapin, 2006). Holocene pine spread has also tended to occur in association with increasing fire activity (Carcaillet et al., 2001; Edwards et al., 2015; Payette et al., 2022). The rapid growth of pine may cause fuel accumulation that supports crown fire spread more rapidly than other conifers and certainly deciduous broadleaf species (Cumming, 2001; Nelson et al., 2017). Existing plantations of pines in boreal Alaska (Alden, 2006) could set the stage for rapid shifts in forest composition, especially where fires intersect with pine seed sources. Pine expansion may exacerbate increases in fire activity due to high flammability. However, the high resilience of pine to wildfire may also aid in maintaining forest cover in the face of warming-induced increases in fire (Hart et al., 2019; Héon et al., 2014).

Successful recruitment, survival, growth, and reproductive maturity of lodgepole pine across our broadly distributed network of experimental sites indicates that environmental conditions commonly found in Interior Alaska fall well within the tolerance limits for pine. Relative biomass dominance in the first decade after the fire suggests that pine is a strong competitor under current conditions at many sites previously dominated by black spruce, even in the presence of alternative competitive species such as trembling aspen and white spruce. Pine does not uniformly outperform the other native species, but there is a broad set of site conditions where it does well. Evidence of rapid development of reproductive maturity, before that of white or black spruce in the same environment, indicates that lodgepole pines have the reproductive potential to persist across generations even under short fire return intervals in Alaska. In sum, our experimental results provide evidence that lodgepole pine has a geographically expansive potential range in Alaska, with a current distribution constrained by seed dispersal. Simulated projections of future lodgepole pine colonization in Alaskan landscapes could help determine consequences for forest reorganization and the boreal C cycle. Such studies are particularly valuable in the context of understanding how migration lags caused by dispersal limitation may shape forest structure and function (Seliger et al., 2021; Svenning et al., 2010). Furthermore, a better understanding of factors constraining range expansion and the potential effects on landscape processes has implications for policy decisions related to assisted migration and species conservation in a changing climate.

AUTHOR CONTRIBUTIONS

Jill F. Johnstone, Michelle C. Mack, F. Stuart Chapin, Teresa N. Hollingsworth conceived and implemented the study. Jill F. Johnstone, F. Stuart Chapin, Carissa D. Brown, Mélanie Jean, and Xanthe J. Walker collected the data. Jill F. Johnstone curated the data. Xanthe J. Walker, Sarah Hart, Mélanie Jean, Rebecca Hewitt, and Winslow D. Hansen analyzed the results. Winslow D. Hansen performed the model simulations. All authors contributed to writing and editing the paper.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Tree seedling data (Johnstone, Walker, Mack, et al., 2024) and seedling count data (Johnstone, Walker, Chapin, & Bonanza Creek, 2024) are available in the Environmental Data Initiative's EDI Data Portal at https://doi.org/10.6073/pasta/01234afb1948f79908bf1892208accd6 and https://doi.org/10.6073/pasta/d9c252935c8037e1edfca65d10905e43, respectively. Model data (Hansen et al., 2024) are available in the Cary Institute repository at https://doi.org/10.25390/caryinstitute.25499848.

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REFERENCES

Ager, T. A. 2019. "Late Quaternary Vegetation Development Following Deglaciation of Northwestern Alexander Archipelago, Alaska." *Frontiers in Earth Science* 7: 104.

Alden, J. N. 2006. "Field Survey of Growth and Colonization of Nonnative Trees on Mainland Alaska." US Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Alden, J. N., and J. Zasada. 1983. "Potential of Lodgepole Pine as a Commercial Forest Tree Species on an Upland Site in Interior Alaska." In *Lodgepole Pine: Regeneration and Management. Proceedings of a Fourth International Workshop*. General Technical Reports PNW-157 42–48. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station.

Anderegg, L. D. L., L. T. Berner, G. Badgley, M. L. Sethi, B. E. Law, and J. HilleRisLambers. 2018. "Within-Species Patterns Challenge our Understanding of the Leaf Economics Spectrum." *Ecology Letters* 21: 734–744.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 48.

Bernhardt, E. L., T. N. Hollingsworth, and F. S. Chapin, III. 2011. "Fire Severity Mediates Climate-Driven Shifts in Understorey Community Composition of Black Spruce Stands of Interior Alaska: Effects of Fire Severity on Understorey Composition." *Journal of Vegetation Science* 22: 32–44.

Boby, L. A., E. A. G. Schuur, M. C. Mack, D. Verbyla, and J. F. Johnstone. 2010. "Quantifying Fire Severity, Carbon, and Nitrogen Emissions in Alaska's Boreal Forest: The Adventitious Root Method." *Ecological Applications* 20: 1633–47.

Boulanger, Y., A. R. Taylor, D. T. Price, D. Cyr, and G. Sainte-Marie. 2018. "Stand-Level Drivers Most Important in Determining Boreal Forest Response to Climate Change." *Journal of Ecology* 106(3): 977–990.

Brandt, J. P., M. D. Flannigan, D. G. Maynard, I. D. Thompson, and W. J. A. Volney. 2013. "An Introduction to Canada's Boreal Zone: Ecosystem Processes, Health, Sustainability, and Environmental Issues." *Environmental Reviews* 21: 207–226.

Braziunas, K. H., W. D. Hansen, R. Seidl, W. Rammer, and M. G. Turner. 2018. "Looking Beyond the Mean: Drivers of Variability in Postfire Stand Development of Conifers in Greater Yellowstone." *Forest Ecology and Management* 430: 460–471.

Brown, C. D., J. Liu, G. Yan, and J. F. Johnstone. 2015. "Disentangling Legacy Effects from Environmental Filters of Post-Fire Assembly of Boreal Tree Assemblages." *Ecology* 96: 3023–32.

Carcaillet, C., Y. Bergeron, P. J. H. Richard, B. Frechette, S. Gauthier, and Y. T. Prairie. 2001. "Change of Fire Frequency in the Eastern Canadian Boreal Forests during the Holocene: Does Vegetation Composition or Climate Trigger the Fire Regime?" *Journal of Ecology* 89: 930–946.

Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. "Rapid Range Shifts of Species Associated with High Levels of Climate Warming." *Science* 333: 1024–26.

Coops, N. C., and R. H. Waring. 2011. "A Process-Based Approach to Estimate Lodgepole Pine (*Pinus contorta* Dougl.) Distribution in the Pacific Northwest under Climate Change." *Climatic Change* 105: 313–328.

Critchfield, W. B. 1985. "The Late Quaternary History of Lodgepole and Jack Pines." *Canadian Journal of Forest Research* 15: 749–772.

Cumming, S. G. 2001. "Forest Type and Wildfire in the Alberta Boreal Mixedwood: What Do Fires Burn?" *Ecological Applications* 11: 97–110.

DeLuca, T. H., and C. Boisvenue. 2012. "Boreal Forest Soil Carbon: Distribution, Function and Modelling." *Forestry* 85: 161–184.

DeVan, M. R., J. F. Johnstone, M. C. Mack, T. N. Hollingsworth, and D. L. Taylor. 2023. "Host Identity Affects the Response of Mycorrhizal Fungal Communities to High Severity Fires in Alaskan Boreal Forests." *Fungal Ecology* 62: 101222.

Edwards, M., L. Franklin-Smith, C. Clarke, J. Baker, S. Hill, and K. Gallagher. 2015. "The Role of Fire in the Mid-Holocene Arrival and Expansion of Lodgepole Pine (*Pinus contorta* var. *Latifolia* Engelm. Ex S. Watson) in Yukon, Canada." *The Holocene* 25: 64–78.

Foster, A. C., A. H. Armstrong, J. K. Shuman, H. H. Shugart, B. M. Rogers, M. C. Mack, S. J. Goetz, and K. J. Ranson. 2019. "Importance of Tree-and Species-Level Interactions with wildfire, Climate, and Soils in Interior Alaska: Implications for Forest Change Under a Warming Climate." *Ecological Modelling* 409: 108765.

Fox, J. 2003. "Effect Displays in *R* for Generalised Linear Models." *Journal of Statistical Software* 8: 1–27.

Greene, D. F., J. C. Zasada, L. Sirois, D. Kneeshaw, H. Morin, and I. Charron. 1999. "A Review of the Regeneration Dynamics of North American Boreal Forest Tree Species." *Canadian Journal of Forest Research* 29(6): 824–839.

Greene, D. F., S. E. Macdonald, S. Haeussler, S. Domenicano, J. Noël, K. Jayen, I. Charron, et al. 2007. "The Reduction of Organic-Layer Depth by Wildfire in the North American Boreal Forest and its Effect on Tree Recruitment by Seed." *Canadian Journal of Forest Research* 37: 1012–23.

Greene, D. F., and E. A. Johnson. 1993. "Seed Mass and Dispersal Capacity in Wind-Dispersed Diaspores." *Oikos* 67: 69.

Héon, J., D. Arseneault, and M. A. Parisien. 2014. "Resistance of the Boreal Forest to High Burn Rates." *Proceedings of the National Academy of Sciences of the United States of America* 111(38): 13888–93.

Hansen, W. D., A. Foster, B. Gaglioti, R. Seidl, and W. Rammer. 2023. "The Permafrost and Organic LayEr Module for Forest Models (POLE-FM) 1.0." *Geoscientific Model Development* 16: 2011–36.

Hansen, W. D., K. H. Braziunas, W. Rammer, R. Seidl, and M. G. Turner. 2018. "It Takes a Few to Tango: Changing Climate and Fire Regimes Can Cause Regeneration Failure of Two Subalpine Conifers." *Ecology* 99: 966–977.

Hansen, W. D., R. Fitzsimmons, J. Olnes, and A. P. Williams. 2021. "An Alternate Vegetation Type Proves Resilient and Persists for Decades Following Forest Conversion in the

North American Boreal Biome." *Journal of Ecology* 109: 85–98.

Hansen, W. D., X. J. Walker, S. Hart, M. Jean, C. Brown, F. S. Chapin, R. Hewitt, T. N. Hollingsworth, M. C. Mack, and J. F. Johnstone. 2024. *Model Data for Factors Limiting the Potential Range Expansion of Lodgepole Pine in Interior Alaska*. Millbrook, NY: Cary Institute. https://doi.org/10.25390/caryinstitute.25499848.

Hansen, W. D., and M. G. Turner. 2019. "Origins of Abrupt Change? Postfire Subalpine Conifer Regeneration Declines Nonlinearly with Warming and Drying." *Ecological Monographs* 89: e01340.

Hart, S. J., J. Henkelman, P. D. McLoughlin, S. E. Nielsen, A. Truchon-Savard, and J. F. Johnstone. 2019. "Estimating Forest Resilience to Changing Fire Frequency in a Fire-Prone Region of Boreal Forest." *Global Change Biology* 25: 869–884.

Hartig, F. 2020. "DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models." R Package Version 0.3.3.0. https://CRAN.R-project.org/package=DHARMa.

Hengl, T., J. Mendes De Jesus, G. B. M. Heuvelink, M. Ruiperez Gonzalez, M. Kilibarda, A. Blagotić, W. Shangguan, et al. 2017. "SoilGrids250m: Global Gridded Soil Information Based on Machine Learning." *PLoS One* 12: e0169748.

Hollingsworth, T. N., J. F. Johnstone, E. L. Bernhardt, and F. S. Chapin, III. 2013. "Fire Severity Filters Regeneration Traits to Shape Community Assembly in Alaska's Boreal Forest." *PLoS One* 8: e56033.

Hollingsworth, T. N., M. D. Walker, F. S. Chapin, III, and A. L. Parsons. 2006. "Scale-Dependent Environmental Controls over Species Composition in Alaskan Black Spruce Communities." *Canadian Journal of Forest Research* 36: 1781–96.

Johnstone, J. F., G. Celis, F. S. Chapin, III, T. N. Hollingsworth, M. Jean, and M. C. Mack. 2020. "Factors Shaping Alternate Successional Trajectories in Burned Black Spruce Forests of Alaska." *Ecosphere* 11: e03129.

Johnstone, J. F., T. N. Hollingsworth, F. S. I. Chapin, and M. C. Mack. 2010. "Changes in Fire Regime Break the Legacy Lock on Successional Trajectories in Alaskan Boreal Forest." *Global Change Biology* 16: 1281–95.

Johnstone, J. F., T. N. Hollingsworth, and F. S. Chapin, III. 2008. *A Key for Predicting Postfire Successional Trajectories in Black Spruce Stands of Interior Alaska*. General Technical Report PNW-GTR-767. 1–44. Portland: USDA Forest Service, Pacific Northwest Research Station.

Johnstone, J. F., X. J. Walker, F. S. Chapin, and L. T. E. R. Bonanza Creek. 2024. "Alaska 2004 Burns: Counts of Live and Dead Seedlings of Lodgepole Pine in a Post-Fire Seeding Experiment at 39 Sites ver 2." Environmental Data Initiative. https://doi.org/10.6073/pasta/d9c252935c8037e1edfca65d10905e43.

Johnstone, J. F., X. J. Walker, M. C. Mack, F. S. Chapin, T. N. Hollingsworth, G. Celis, and L. T. E. R. Bonanza Creek. 2024. "Alaska 2004 Burns: Growth and Survival of Tree Seedlings in Post-Fire Experimental Transplant Study across 39 Sites ver 2." Environmental Data Initiative. https://doi.org/10.6073/pasta/01234afb1948f79908bf1892208accd6.

Johnstone, J. F., and F. S. Chapin. 2003. "Non-equilibrium Succession Dynamics Indicate Continued Northern Migration of Lodgepole Pine." *Global Change Biology* 9: 1401–9.

Johnstone, J. F., and F. S. Chapin. 2006. "Effects of Soil Burn Severity on Post-Fire Tree Recruitment in Boreal Forests." *Ecosystems* 9: 14–31.

Kashian, D. M., M. G. Turner, W. H. Romme, and C. G. Lorimer. 2005. "Variability and Convergence in Stand Structural Development on a Fire-Dominated Subalpine Landscape." *Ecology* 86: 643–654.

Leibold, M. A. 1995. "The Niche Concept Revisited: Mechanistic Models and Community Context." *Ecology* 76: 1371–82.

Lloyd, A. H., M. E. Edwards, B. P. Finney, J. A. Lynch, V. A. Barber, and N. H. Bigelow. 2006. "Holocene Development of the Alaskan Boreal Forest." In *Alaska's Changing Boreal Forest*, edited by I. F. S. Chapin, M. Oswood, K. van Cleve, L. A. Viereck, and D. L. Verbyla, 62–78. Oxford: Oxford University Press.

Lotan, J. E., and D. A. Perry. 1983. *Ecology and Regeneration of Lodgepole Pine* 51. Washington: USDA Forest Service.

MacDonald, G. M., and L. C. Cwynar. 1986. "A Fossil Pollen Based Reconstruction of the Late Quaternary History of Lodgepole Pine (Pinus contorta ssp. latifolia) in the Western Interior of Canada." *Canadian Journal of Forest Research* 15: 1039–44.

MacDonald, G. M., K. V. Kremenetski, and D. W. Beilman. 2008. "Climate Change and the Northern Russian Treeline Zone." *Philosophical Transactions of the Royal Society London B Biological Sciences* 363: 2285–99.

Mack, M. C., X. J. Walker, J. F. Johnstone, H. D. Alexander, A. M. Melvin, M. Jean, and S. N. Miller. 2021. "Carbon Loss from Boreal Forest Wildfires Offset by Increased Dominance of Deciduous Trees." *Science* 372: 280–83.

Malhi, Y., D. D. Baldocchi, and P. G. Jarvis. 1999. "The Carbon Balance of Tropical, Temperate and Boreal Forests." *Plant, Cell and Environment* 22: 715–740.

Monserud, R. A., Y. Yang, S. Huang, and N. Tchebakova. 2008. "Potential Change in Lodgepole Pine Site Index and Distribution under Climatic Change in Alberta." *Canadian Journal of Forest Research* 38: 343–352.

Nelson, K. N., M. G. Turner, W. H. Romme, and D. B. Tinker. 2017. "Simulated Fire Behaviour in Young, Postfire Lodgepole Pine Forests." *International Journal of Wildland Fire* 26: 852–865.

Noad, N. C., P. P. Bonnaventure, G. F. Gilson, H. Jiskoot, and M. C. Garibaldi. 2023. "Surface-Based Temperature Inversion Characteristics and Impact on Surface Air Temperatures in Northwestern Canada from Radiosonde Data between 1990 and 2016." *Arctic Science* 9: 545–563.

Payette, S., P.-L. Couillard, M. Frégeau, J. Laflamme, and M. Lavoie. 2022. "The Velocity of Postglacial Migration of Fire-Adapted Boreal Tree Species in Eastern North America." *Proceedings of the National Academy of Sciences of the United States of America* 119: e2210496119.

Payette, S., and M. Frégeau. 2019. "Long-Term Succession of Closed Boreal Forests at their Range Limit in Eastern North America Shows Resilience to Fire and Climate Disturbances." *Forest Ecology and Management* 440: 101–112.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna: Foundation for Statistical Computing.

Rantanen, M., A. Y. Karpechko, A. Lipponen, K. Nordling, O. Hyvärinen, K. Ruosteenoja, T. Vihma, and A. Laaksonen. 2022. "The Arctic Has Warmed Nearly Four Times faster than the Globe since 1979." *Communications Earth & Environment* 3: 168.

Schwilk, D. W., and D. D. Ackerly. 2001. "Flammability and Serotiny as Strategies: Correlated Evolution in Pines." *Oikos* 94: 326–336.

Seidl, R., T. A. Spies, W. Rammer, E. A. Steel, R. J. Pabst, and K. Olsen. 2012. "Multi-Scale Drivers of Spatial Variation in Old-Growth Forest Carbon Density Disentangled with Lidar and an Individual-Based Landscape Model." *Ecosystems* 15: 1321–35.

Seidl, R., W. Rammer, R. M. Scheller, and T. A. Spies. 2012. "An Individual-Based Process Model to Simulate Landscape-Scale Forest Ecosystem Dynamics." *Ecological Modelling* 231: 87–100.

Seidl, R., and M. G. Turner. 2022. "Post-Disturbance Reorganization of Forest Ecosystems in a Changing World." *Proceedings of the National Academy of Sciences of the United States of America* 119: e2202190119.

Seliger, B. J., B. J. McGill, J.-C. Svenning, and J. L. Gill. 2021. "Widespread Underfilling of the Potential Ranges of North American Trees." *Journal of Biogeography* 48: 359–371.

Stralberg, D., D. Arseneault, J. L. Baltzer, Q. E. Barber, E. M. Bayne, Y. Boulanger, C. D. Brown, et al. 2020. "Climate-Change Refugia in Boreal North America: What, Where, and for How Long?" *Frontiers in Ecology and the Environment* 18(5): 261–270.

Strong, W. L., and L. V. Hills. 2013. "Holocene Migration of Lodgepole Pine (*Pinus contorta* var. *Latifolia*) in Southern Yukon, Canada." *The Holocene* 23: 1340–49.

Svenning, J. C., and F. Skov. 2007. "Could the Tree Diversity Pattern in Europe be Generated by Postglacial Dispersal Limitation?" *Ecology letters* 10(6): 453–460.

Svenning, J.-C., M. C. Fitzpatrick, S. Normand, C. H. Graham, P. B. Pearman, L. R. Iverson, and F. Skov. 2010. "Geography, Topography, and History Affect Realized-to-Potential Tree Species Richness Patterns in Europe." *Ecography* 33: 1070–80.

Thornton, P. E., R. Shrestha, M. Thornton, S.-C. Kao, Y. Wei, and B. E. Wilson. 2021. "Gridded Daily Weather Data for North America with Comprehensive Uncertainty Quantification." *Scientific Data* 8: 190.

Turner, M. G., D. M. Turner, W. H. Romme, and D. B. Tinker. 2007. "Cone Production in Young Post-Fire *Pinus contorta* Stands in Greater Yellowstone (USA)." *Forest Ecology and Management* 242: 119–126.

Turner, M. G., K. H. Braziunas, W. D. Hansen, T. J. Hoecker, W. Rammer, Z. Ratajczak, A. L. Westerling, and R. Seidl. 2022. "The Magnitude, Direction, and Tempo of Forest Change in Greater Yellowstone in a Warmer World with More Fire." *Ecological Monographs* 92(1): e01485.

Vannette, R. L., and T. Fukami. 2014. "Historical Contingency in Species Interactions: Towards Niche-Based Predictions." *Ecology letters* 17(1): 115–124.

Wickham, H. 2016. *ggplot2*. Cham: Springer International Publishing.

SUPPORTING INFORMATION

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

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