



A short-interval reburn catalyzes departures from historical structure and composition in a mesic mixed-conifer forest

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ABSTRACT

Recent increases in fire frequency and severity across the western US are triggering abrupt changes in ecosystem structure and composition, especially in lower montane forests, but consequences of fire-regime change for mesic, mixed-conifer forests remain uncertain. Glacier National Park (Montana, USA) is characterized by a complex mosaic of species typical of Rocky Mountain, Pacific Northwest and boreal floras, creating opportunities for species composition to shift as species respond individualistically to environmental change. We quantified prefire and postfire stem density and composition in a recent anomalously short-interval fire (15 yrs) and historically typical long-interval fire (88–282 + yrs) to answer two questions: (1) How do the structure and composition of tree regeneration differ after long- and short-interval fires that burned in close proximity? (2) What drivers explain differences in postfire regeneration densities among species? We additionally compared understory cover in each fire to anticipate consequences of contemporary fire for the whole plant community. Mean postfire tree seedling density was 45 times higher after the long- than short-interval fire, and many stands in the short-interval fire lacked any tree regeneration. Postfire tree seedling densities were above prefire stem densities in the long-interval fire but well below in the short-interval fire. After both fires, fire-avoiding conifers (e.g., *Picea engelmannii*, *Abies lasiocarpa*) were generally replaced by fire-tolerating or fire-embracing species (e.g., *Larix occidentalis*, *Pinus contorta* var. *latifolia*). Some stands remained dominated by fire-sensitive conifers after long-interval fire but never after short-interval fire. Seedlings of *Thuja plicata* and *Tsuga heterophylla* were present after the long-interval fire but absent before and after the short-interval fire, despite historically occupying both burned areas. For all species, seedling density increased with indicators of proximate seed supply. Seedling density of dispersal-dependent species declined with distance to live trees, whereas *P. contorta* responded to serotiny. Seedlings of drought-intolerant species were more abundant on northerly aspects. Total understory cover was 50% lower after short-interval than long-interval fire, but shrub cover was twice as high. Our study suggests that persistent seed sources will allow *L. occidentalis* to expand following sequential high-severity fires, while dispersal-limited, drought-intolerant conifers may decline due to loss of seed sources and elevated postfire aridity. Increased fire activity will likely produce sparser forests that are dominated by fire-tolerating and fire-embracing conifers at the expense of fire-avoiding and fire-refuge species. Complete regeneration failure may be delayed by high fire-trait syndrome diversity, but the structure and composition of extant forests will shift.

1. Introduction

Increases in fire frequency and severity are widespread local symptoms of global climate change (Millar and Stephenson 2015, Abatzoglou and Williams 2016, Parks and Abatzoglou 2020). Climate conditions and fire activity that exceed the safe operating space within which fire-prone forests evolved (Johnstone et al. 2016) threaten postfire tree recovery through reduced propagule pressure (Keely et al. 1999, Enright et al.

2015, Gill et al. 2021) and arid postfire conditions that constrain establishment success (Harvey et al. 2016a, Hoecker et al. 2020). These compounding drivers are leading to major shifts in forest structure and composition that are likely to persist for decades to centuries (Bowman et al. 2014, Coop et al. 2020). Transitions from forest to sparse woodland, shrubland, or grassland are emerging in settings where drought and immaturity risk are high; for example, in forests dominated by obligate-seeder species (Bowman et al. 2014, Turner et al. 2019), at

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lower elevational treeline (Donato et al. 2016, Tepley et al. 2017, Davis et al. 2019) and in trailing-edge populations (Parks et al. 2019). However, fire-prone forests are diverse in species' traits and climatic setting, suggesting that responses to fire-regime change will be varied (Pellegrini et al. 2021).

In the species-rich subalpine forests of the far northern US Rocky Mountains, the response of forest ecosystems to fire-regime change remains uncertain. In the Crown of the Continent Ecosystem—straddling the border of western Montana and Alberta, Canada—flora from the Pacific Northwest, boreal forest and Rocky Mountains intersect (Rockwell 2007). Fostered by the spatially heterogeneous climate of the southern Canadian Rockies, interactions between species' traits and disturbance history enabled a diverse mosaic of communities to develop in this region during the Holocene (Rockwell 2007). Fire-regime change could alter the long-term (decades to centuries) character of these forests, but fire activity has only recently begun to depart from historical regimes. Further, the region's relatively cold and mesic climate may buffer tree seedlings from abiotic constraints on regeneration that have emerged in dry forests. In forests where fire was suppressed during 20th century, more fire could restore forests to 18th- and 19th-century densities (Hessburg et al. 2019). In forests where resilience to infrequent high-severity fire was historically high, fire-regime change could alter forest structure or shuffle species composition such that forests change but persist. Open questions about the fate of these diverse mixed-conifer forests remain. For example, whether tree species that established centuries ago can regenerate after disturbances in today's climate, or whether contemporary tree species assemblages can persist after short-interval fires, is unresolved. Fire-catalyzed changes in the structure and composition of subalpine forests would have cascading impacts on ecosystem functions and services, including wildlife habitat (Jones and Tingley 2021, Hoecker and Turner in review) and carbon stability (Anderegg et al. 2020, Mack et al. 2021, Turner et al. 2021), requiring scientists and managers today to anticipate the consequences of emerging trends.

Observations of tree regeneration following recent fires are needed to elucidate the consequences of more fire and a warmer climate for future development pathways in mesic mixed-conifer forests. Identifying tree species that may benefit from more fire, and those that may not, is relevant to regional managers and stakeholders and contributes to understanding of forest ecosystems globally. Experiments and observations point toward strong constraints on postfire regeneration from both biotic and abiotic drivers (Davis et al. 2018). Biotic drivers include variability in species traits (Keeley 2012, Stevens et al. 2020, Rodman et al. 2021) and interactions between vegetation and fire that determine the abundance of postfire seed sources and their proximity to disturbed patches (Harvey et al. 2016a, Kemp et al. 2016, Gill et al. 2021). Abiotic factors include variability in temperature and moisture at multiple scales (Dobrowski et al. 2015, Hansen and Turner 2019, Littlefield et al. 2020), topography and microclimate (Donato et al. 2016, Hoecker et al. 2020), and soils (Hansen and Turner 2019). Because juvenile trees are more sensitive to abiotic variation than adults (Jackson et al. 2009, Bell et al. 2014), forest self-replacement requires propagule pressure after disturbances to be high enough for natural mortality ("self-thinning") of the regenerating cohort and alignment with climatically suitable growing seasons (Kemp et al. 2019, Rodman et al. 2020, Littlefield et al. 2020). Differential establishment of tree species is thus difficult to predict.

We adapted the framework of fire-related trait syndromes developed by Keeley (2012)—which describes species as fire-avoider, fire-refugia, fire-tolerator, or fire-embracer—as a conceptual basis for comparisons among species and our expectations of species' responses to fire (Fig. 1). We refer to tolerator and embracer species as "fire-adapted" and refuge and avoider species as "fire-sensitive." Using published trait values or relative rankings, we ranked the seven focal conifers on six plant functional traits relevant to fire: serotiny, fecundity, adult drought tolerance, establishing germinant drought tolerance, light tolerance, and fire

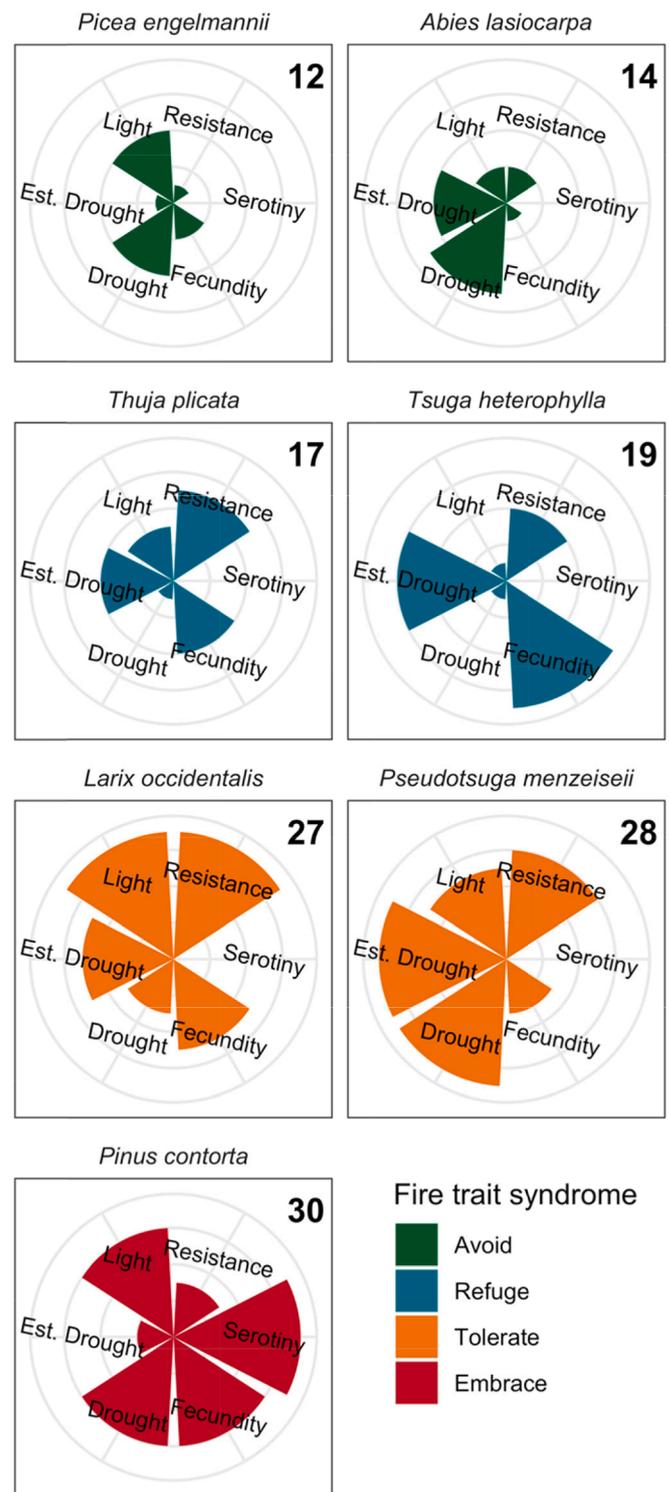


Fig. 1. Fire-relevant functional traits ranked and grouped into syndromes for seven focal species. Each species was assigned a relative rank (1–7) based on published trait values for fire resistance (Stevens et al. 2020), serotiny, fecundity (Seidl et al. 2012, Braziunas et al. 2018), adult drought tolerance ("Drought") and drought tolerance of establishing germinants ("Est. Drought"; Seidl et al. 2012, Braziunas et al. 2018), and light tolerance (Niinemets and Valladares 2006). The sums of each species' ranks is shown in bold in the upper-right corner of each panel.

resistance (see Supplemental Information). Species were assigned higher ranks when they had high fire-adaptive trait values, and we used these rankings to assign each species to a fire trait syndrome (Fig. 1).

We used a natural experiment in Glacier National Park (Montana, USA) to quantify early tree regeneration after high-severity fire in two contrasting contexts likely to become more common as climate change progresses: a long-interval fire (88–282 yr) in mature forests—with individual trees > 400 yrs old—that established under cooler climate conditions; and an unusual short-interval fire (15 yr), or reburn, that burned young trees regenerating from a previous fire.

The fires occurred in otherwise similar biophysical settings and in areas occupied by both fire-sensitive and fire-adapted conifers, making them ideally suited for comparison of early postfire regeneration trajectories. While early regeneration (here, two years postfire) after stand-replacing fire does not reflect all potential recruitment, it often establishes the trajectory of stand development and species composition for decades to centuries (Kashian et al. 2005, Turner et al. 2016) or until a stand is affected by another disturbance (Gill et al. 2017). The conifers we studied typically establish from seed on bare mineral soil, which is abundant after fire (Burns and Honkala 1990), and even slow-growing or shade-tolerant species are often present within 2 yrs following fire (Stevens-Rumann et al. 2018, Littlefield 2019). Furthermore, we contrast outcomes after short- and long-interval fires sampled at the same time-since-fire, indicating relative, rather than absolute, differences in the effects of fire return interval. We sought to identify which species benefit from contemporary fire activity, and at whose expense, and to untangle the sensitivity of different species to potential drivers. We organized our study around two questions (Table 1).

(1) Effect of fire return interval. *How do the structure and composition of tree regeneration differ after long- and short-interval fires that burned in close proximity?* We hypothesized that reburns in young forests would result in lower postfire seedling density relative to mature forests because of reduced seed availability and greater aridity. We hypothesized that postfire tree seedling densities would meet or exceed prefire stem densities following long-interval fire but would be lower than prefire stem densities following short-interval fires. We expected fire in mature forests to favor regeneration by fire-tolerators like western larch (*Larix occidentalis*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), that are more likely to survive and harbor residual seed sources, and fire-embracing lodgepole pine (*Pinus contorta* var. *latifolia*), for which serotinous cones can lead to prolific regeneration. We expected that drought-intolerant species might fail to regenerate because climate conditions may have exceeded their limits of tolerance. We hypothesized further that short-interval fire in young forests would favor western larch (*Larix occidentalis*), Douglas-fir and lodgepole pine because of their ability to resist fire (western larch and Douglas-fir) and/or prolifically disperse seed into burned areas (serotinous lodgepole pine and larch). We expected little regeneration of fire-sensitive, shade-tolerant species like western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in short-interval fire because of limited seed sources and xeric, exposed conditions.

Secondarily, we compared postfire understory cover and functional type after short- and long-interval fires to anticipate effects of fire return interval on the whole plant community and on potential interactions with tree regeneration. We hypothesized percent cover of forbs would be greater following long-interval fire, whereas percent cover of shrubs and graminoids would be greater following short-interval fire, because of differences in seed availability and drought tolerance. In addition, shrubs that were abundant in the young forests could resprout from surviving roots even if stems were top-killed by fire.

(2) Differences among tree species. *What drivers explain differences in postfire regeneration densities among species?* We hypothesized that seedling densities of all species would decrease with distance to areas of low burn severity, which harbor seed sources, and would increase with prefire conspecific basal area—or in the case of lodgepole pine, the

Table 1
Summary of organizing questions, hypotheses and rationale.

	Question	Hypothesis	Rationale
Effect of fire return interval	How does the structure of tree seedling regeneration differ after long- and short-interval fires?	Lower postfire seedling density after short-interval than after long-interval fire Stronger relationship between prefire and postfire density in long-interval than short-interval fires	Reduced seed availability; elevated microclimate aridity Young trees are immature and lack seed-bearing cones
	How does the composition of tree regeneration differ?	Fire in mature forests should favor regeneration by fire-tolerators and serotinous species Fire in young forest will favor shade-intolerant species and prolific seeders Low regeneration of shade-tolerant fire-avoider species after short-interval fire	Persistent seed sources High light exposure, mineral seedbed, low competition Limited seed sources; light exposure, elevated aridity
Differences among tree species	How does understory cover differ?	Higher forb cover after long- than short-interval fire and higher shrub cover after short- than long-interval fire	Reduced seed availability; resprouting advantage of shrubs
	What drivers explain postfire regeneration densities and differences among species?	Seedling density of all species except lodgepole pine will decrease with distance to areas of low burn severity Seedling density of all species will increase with conspecific prefire basal area or presence of serotinous cones Seedling density of drought-intolerant species will decrease with proxies of microclimate aridity (northeastness, vapor pressure deficit)	Long dispersal distances reduce propagule pressure Stands with high basal area/serotiny more likely to harbor seeds sources Relative tolerance to moisture limitations

presence of *in situ* serotinous cones—because stands with higher basal area (or serotinous cones) are more likely to contain residual seed sources. We expected that vapor pressure deficit (VPD) and aspect (northeastness), proxies for microclimate aridity, would affect regeneration density of all species, but the effects would be stronger for the relatively drought-intolerant Engelmann spruce and subalpine fir, than for more drought-tolerant species like Douglas-fir. Finally, we expected soil organic matter to negatively impact regeneration of all species because these conifers preferentially establish on mineral soils, and that drought-intolerant species would have higher seedling densities on clay-rich soils because of higher water-holding capacity.

2. Methods

2.1. Study area

We conducted our study on the west side of the continental divide in the far northern US Rocky Mountains on traditional homelands of the Blackfeet, Kalispel, and Salish-Kootenai indigenous groups, which are

now managed as Glacier National Park (hereafter “Glacier”). We focused on recently burned forests in the vicinity of Lake McDonald (Fig. 2a). A low-elevation band around the lake is characterized by a moist, temperate microclimate that resists burning and supports old-growth (200–400 + yr old) stands of western hemlock and western redcedar forests, that are interspersed with western white pine (*Pinus monticola*) and grand fir (*Abies grandis*). Moving upslope, Douglas-fir, western larch and lodgepole pine comprise stands of monotypic and mixed dominance. The proportion of Engelmann spruce and subalpine fir dominated stands increases with elevation, which take on krummholz forms and give way to whitebark pine (*Pinus albicaulis*) at the boundary of the alpine zone (Barrett et al. 1991, Hop et al. 2007, Rockwell 2007).

Glacier’s climate varies with elevation, with temperate conditions around Lake McDonald yielding to lower temperatures and increased precipitation at higher elevations. Orographic effects of the Continental Divide trap moist Pacific weather systems on Glacier’s west side. At West Glacier (~10 km south of our study area) average (1990–2020) maximum temperatures of 18.3 °C occur in July and average minimum temperatures of –4.2 °C occur in December and January (ncei.noaa.gov). August is the driest month, receiving 30 mm of rainfall on average, while winter months are snowy, with > 800 mm of precipitation falling as snow in December and January. Glacier is underlain by Precambrian age sedimentary argillite and quartzite from the Belt Supergroup, which have been dissected by glacial activity for the past 2 million years (Rockwell 2007). Soils are a mix of Luvisols, Cambisols and Podzol (soilgrids.org).

2.2. Fire history and historical forest composition

The subalpine forests of Glacier’s west side have been affected by fire for millennia, and numerous fires have been observed in the recent past (Arno 1980, Barrett et al. 1991, Power et al. 2006, Marlon et al. 2012). Historical (based on fire-scar and stand-origin reconstructions for 1650 CE to present) fire return intervals were 140–340 years, and fires affected extensive (10^3 ha) areas at high severity (Barrett et al. 1991). Most of the area burned on Glacier’s west side occurs during large infrequent fires, driven by synoptic climate patterns. Regionally extensive fire years in the northern Rockies during the 20th century were associated with positive phases of the Pacific Decadal Oscillation (Morgan et al. 2008). Extreme aridity in 1910 produced an historic fire year, burning > 12,000 km² across the region and > 30,000 ha in Glacier. Drought was also associated with regional fire years and extensive burning in Glacier in 1929 (Barrett et al. 1991) and 2003 (McKenzie and Tinker 2012). However, most of the moist cedar-hemlock forests around Lake McDonald had not burned at high severity for several centuries prior to 2003, allowing the easternmost population of this forest type to persist.

2.3. Data collection

We studied regeneration after two recent fires. The long-interval Sprague Fire of 2017 burned 7000 ha of subalpine forests across several drainages south of Lake McDonald. These forests were mature; stand age and composition were a mosaic shaped by fires that burned in the 18th and 19th centuries. Stand age generally exceeded 200 years and

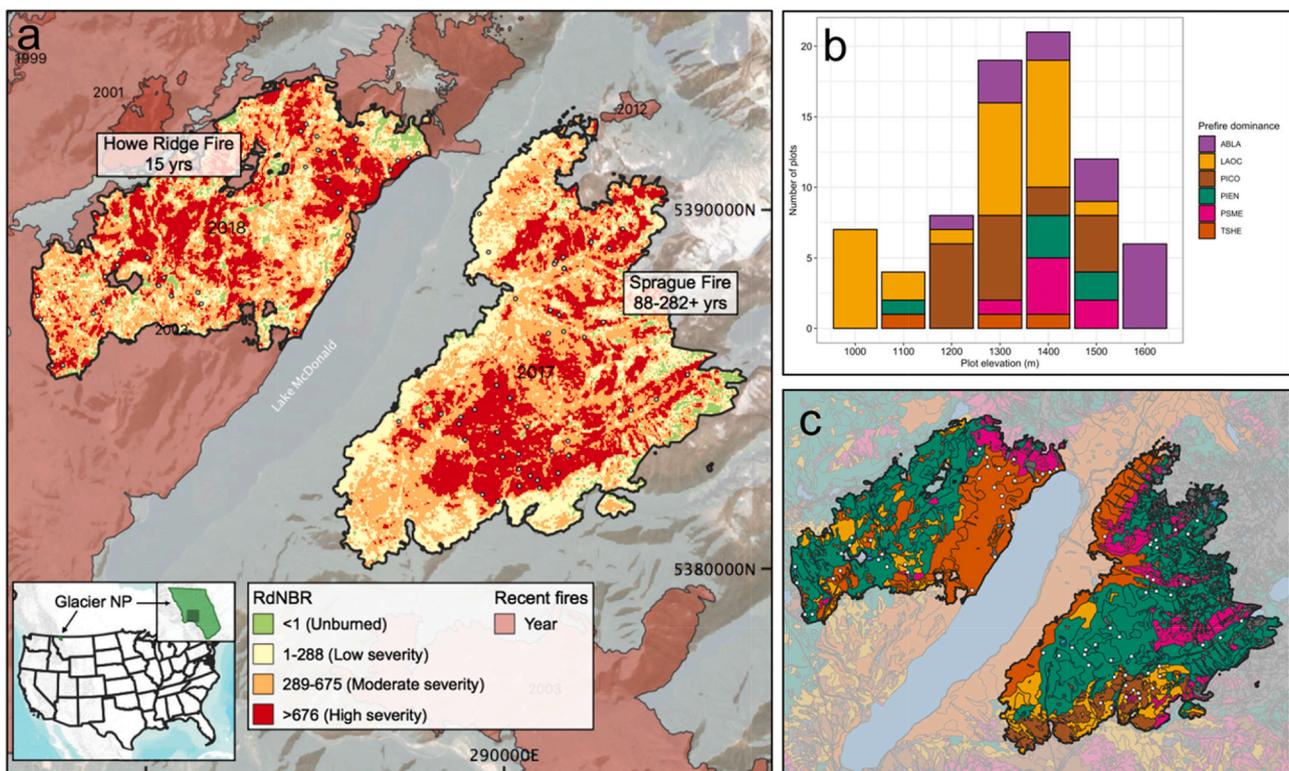


Fig. 2. Study area map and prefire stand composition. (a) Inset maps show study area within Glacier National Park (green polygon). Red polygons show fire perimeters in the observational record, labeled with their year of occurrence and shaded with recent fires in darker reds. The perimeter of the Howe Ridge Fire of 2018 that reburned young forest and the perimeter of Sprague Fire of 2017, which burned entirely in mature forest, are outlined in black. Focal fires are colored by relativized delta normalized burn severity ratio (RdNBR) from MTBS (mtbs.gov); RdNBR cutoffs for severity are based on Harvey et al. (2016b). Field plot locations are indicated by grey points. (b) The composition of plots, colored by the dominant species, and plotted in 1000-m elevational bins. PIEN: Engelmann spruce (*Picea engelmannii*), ABLA: subalpine fir (*Abies lasiocarpa*), PICO: lodgepole pine (*Pinus contorta*), LAOC: western larch (*Larix occidentalis*), PSME: Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), TSHE: western hemlock (*Tsuga heterophylla*), THPL: (*Thuja plicata*). (c) Tree species composition before 2003 (Hop et al. 2007); colors are the same as (b), but here “TSHE” represents mixed western hemlock and western redcedar stands and “PIEN” represents mixed Engelmann spruce and subalpine fir stands. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

these forests included individuals or stands of trees that were likely older (Barrett et al. 1991). Before the fire, stands upslope from Lake McDonald were pure and mixed dominance of lodgepole pine, Douglas-fir, larch, and spruce-fir, depending on specific disturbance histories, site conditions and topographic position. Stands adjacent to Lake McDonald were predominantly cedar-hemlock (Fig. 2c; Hop et al. 2007).

The short-interval Howe Ridge Fire of 2018 reburned areas of young postfire forests that regenerated following the 2003 Robert Fire, a 23,000-ha high-severity event (Fig. 2a). Prior to the 2003 fire, these forests were predominantly cedar-hemlock for several hundred meters upslope along the lake edge, grading into spruce-fir dominated forests interspersed with discontinuous pockets of larch and lodgepole pine (Fig. 2c; Hop et al. 2007). The Howe Ridge Fire in 2018 burned nearly 6000 ha at high severity through young forest and abundant downed coarse wood, almost entirely within the 2003 fire perimeter (Fig. 2a).

We measured prefire forest structure and composition and the density and identity of postfire tree seedlings two years after stand-replacing fire at 77 plots ($n = 43$ in long-interval and $n = 34$ in short-interval burned areas). The long-interval Sprague Fire was sampled in July 2019, and the short-interval Howe Ridge Fire was sampled in July 2020. Areas of stand-replacing fire were determined in the field based on observed tree mortality (all but three plots had 100% tree mortality) and bole scorch height. Plots were chosen to reflect the distribution of aspects and elevations that burned (Fig. 2b) and to avoid inaccessibly steep slopes and trail closures due to fire damage. We also quantified burn severity post-hoc at our plots using relativized delta normalized burn severity ratio (RdNBR) data from the Monitoring Trends in Burn Severity (MTBS) dataset (Fig. 2a), and compared values to qualitative severity ranges defined by Harvey et al. (2016b). Based on RdNBR, two plots were classified as low severity fire (< 288), 19 plots were in moderate severity (288–675), and 56 plots were in high severity patches (> 675). However, the moderate severity category (RdNBR 288–675) represents a wide range of basal area mortality (50–93%; Harvey et al. 2016b, 2019). In our plot data, only three plots, in burned mature stands that were dominated by western hemlock, had live cone-bearing trees; thus, our plot locations were skewed toward high severity, even where RdNBR indicated low or moderate severity.

Upon reaching the desired elevation and aspect, plots were located within areas of homogenous, high burn severity, and a compass bearing to orient the plot was selected using a random number generator. All but two plots were separated by at least 200 m (two plots were 79 m apart). A semivariogram of postfire seedling density of all tree species vs. lag distance showed no evidence of spatial autocorrelation among plots (Fig. S1). At plot center we recorded GPS coordinates, aspect, and slope angle. We then laid two perpendicular 30-m transects with their intersection at plot center and quantified prefire structure and composition in a circular plot defined by these axes. We measured stem diameter at 1.37 m and recorded the species of every conifer stem > 1.37 m tall in at least one quadrant of the circular plot. If < 50 stems were recorded in one quadrant we measured every stem in additional quadrants until > 50 stems (or all stems in the plot) were recorded, always recording every stem in each additional quadrant. Prefire species identity was determined from the stem's morphology and bark; we did not record stems that were determined to be dead before the fire based on scorching underneath bark.

To measure postfire tree regeneration, we counted and identified the species of every regenerating tree seedling in two 2-m wide variable-length transects along perpendicular tapes while avoiding the intersection. If > 50 seedlings were recorded in the first meter of the transect we reduced the transect lengths, but always measured a portion of both transects. Transects in 64 plots were 28 m long each and transects in 13 plots < 28 m. Percent cover of understory vegetation was estimated by functional type (graminoid, forb, shrub) in six 0.25-m² quadrats evenly spaced along the full length each of transect ($n = 12$ quadrats per plot). We collected three soil cores at each site (5 cm \times 15 cm deep), which were later dried in an oven at 60 °C until their mass stabilized (~ 72 h),

composited, ground, sieved to 2 mm and analyzed for total percent organic matter (OM) and nutrient content at the University of Wisconsin's Soil and Forage Analysis Laboratory.

We measured the distance to potentially live cone-bearing trees by calculating the distance from each plot center to a point burned at low severity using gridded 30x30-m RdNBR data from MTBS; following Harvey et al. (2016b), RdNBR values < 288 defined low severity. Elevation and aspect were calculated for each site using a 100-m DEM with the *raster* R package (Hijmans and van Etten 2015), then aspect was converted to deviation from northeast, an index ranging from 0 to 2 with 2 facing directly northeast. Growing-season climate data for the first complete growing season (May 1 – Sept. 1) and partial second growing season (May 1 – July 1) were obtained from Daymet at 1-km resolution (Thornton et al. 2020). We averaged daily maximum temperature and vapor pressure deficit (which we calculated from absolute vapor pressure and temperature using standard equations) across all days during these periods. We accounted for differences in snowpack between sampling years using snow water equivalent (SWE) data from snow telemetry (SNOTEL) station nearest to our plots, 15–20 km away, and at approximately the same median elevation, 1325 m (wcc.nrcs.usda.gov/snow/). We averaged May 1st SWE of the two years prior to our sampling (Fig S3). The mature (long-interval fire) and young (short-interval fire) study sites represented a similar range of topographic conditions and burn severity (Figs S2).

2.4. Statistical analyses

(1) Effect of fire return interval. To test for differences in postfire tree regeneration after long- vs. short-interval fires, we compared mean seedling density after each fire. To evaluate stand self-replacement in each fire, we fit a log-log model of total postfire seedling density (normalized by sample area) of all species as a function of total prefire stem density of all species, separately for each fire, and compared the partial-slope coefficients of these models. We excluded densities of zero in the log-log regression. We compared the percent cover of understory vegetation by functional type in each fire using an analysis of variance (F-test, ANOVA).

We evaluated fire-driven changes in composition by identifying the dominant tree species at each plot, defined as the species with the highest importance value (IV), before and after fire. Prefire IV was calculated as the relative basal area plus relative stem density by species (range from 0 to 2), and postfire IV was calculated as relative seedling density (because basal area is not calculated for seedlings; range from 0 to 1). Change in plot-level species dominance was depicted as an "alluvial diagram" that shows changes in prefire and postfire dominance as flows between groups. To test for shifts in overall community composition, we used non-metric multidimensional scaling (NMDS) based on species presence or absence in each plot, rotated the ordination using principal component analysis to maximize the variance explained by each of two dimensions and plotted the location of each tree species in that space. We grouped plots in ordination space based on their site and stage ("burned mature" [post-long-interval], "long-unburned mature" [pre-long-interval], "burned young" [post-short-interval], "15 yrs-unburned young" [pre-short-interval]) and then calculated the centroid of each group using the mean in each dimension, indicating the tendency of compositional change in each group. Finally, we quantified change between prefire and postfire composition of individual plots using the Bray-Curtis dissimilarity index based on normalized abundance (i.e., stem density) of each species, and compared the prefire and postfire composition dissimilarity between fires using an ANOVA.

(2) Differences among tree species. We evaluated the effect of biotic and abiotic drivers on the postfire density of each species, in both fires together, using generalized linear models (GLMs). Postfire seedling densities were highly overdispersed, so we applied a negative binomial error distribution and a log link function. We selected predictor variables by identifying a set of available predictors for which we had strong

ecological rationale for their importance. We did not perform a model selection procedure or compare competing models, avoiding type-I errors associated with multiple comparisons. We selected conspecific prefire basal area ($\text{m}^2 \text{ha}^{-1}$), distance to low burn severity (m), mean daily vapor pressure deficit (kPa) during the growing seasons prior to our sampling (one complete growing season [May 1 – September 1] and one partial growing season [May 1 – July 1]), aspect (index from 0 to 2 relative to northeast), soil organic matter content (%), and soil clay content (g kg^{-1}). In the model of lodgepole pine we replaced prefire basal area with the presence of serotinous cones (a binary index). We did not include collinear predictors ($|r| > 0.5$), which eliminated mean growing season maximum temperature (correlated with vapor pressure deficit). We centered predictors by subtracting the mean and rescaled by dividing by their standard deviation (a “z-score”). We interpreted coefficients based on the p -values from a Wald test and measured the explanatory power of each full model using a likelihood ratio test against an intercept-only null model. We then compared effect sizes, the change in the expected log-count of the response species with a one-unit change in the standardized predictor, among predictors within models and among species. We did not model western redcedar or western hemlock seedling densities because they were only present in the long-interval fire (substantially reducing the predictor range). We fit models using the *glmmTMB* package (Magnusson et al. 2017). All statistical analyses were conducted in R v4.0.2 (R Core Team 2018) with the use of pre-loaded (“base”) packages; data wrangling tasks were accomplished using *tidyverse* packages (Wickham et al. 2019).

3. Results

3.1. Effect of FRI

Mean postfire tree seedling densities were approximately 45 times greater following long-interval than short-interval fire ($65,534$ vs. 1455 ha^{-1} ; Fig. S4). Relative to prefire stem densities, postfire seedling densities were much higher after long-interval fire (mean \pm CV = $903 \pm 79 \text{ ha}^{-1}$ prefire and $65,534 \pm 268 \text{ ha}^{-1}$ postfire), and much lower after short-interval fire ($4342 \pm 84 \text{ ha}^{-1}$ prefire and $1455 \pm 147 \text{ ha}^{-1}$ postfire; Fig. S5). Pre- and postfire densities were positively correlated following both long and short-interval fire, but this relationship was much stronger after long-interval vs. short-interval fire (Fig. 3). The partial-slope coefficient of 1.78 ($p = 0.003$) for a linear log-log model of postfire seedling density vs. prefire stem density in the long-interval fire indicates that postfire seedling density increases by 106% with a 50% increase in prefire density and is likely adequate for self-replacement. By contrast, the partial-slope coefficient of only 0.36 ($p = 0.032$) in the short-interval fire indicates that postfire seedling density increases by only 16% with a 50% increase in prefire stem density, and the slope is less than the 1:1 line indicating a lack of initial stand self-replacement densities (Fig. 3).

Prior to the long-interval fire, there were mature forest plots dominated by all of the conifer species we studied. Following the long-interval fire, plots that were dominated by lodgepole pine were still dominated by lodgepole pine (Fig. 4). Larch-dominated plots were either self-replaced or dominated by lodgepole pine. However, nearly all plots dominated by Engelmann spruce, subalpine fir, western hemlock or

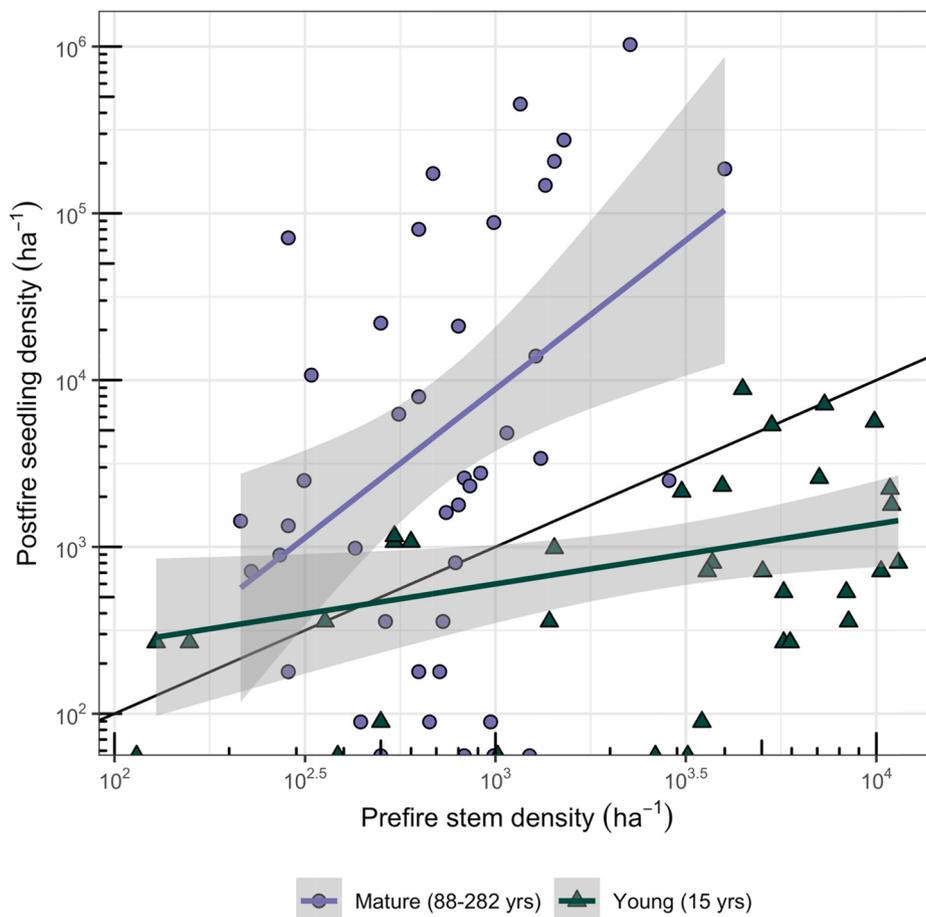


Fig. 3. Relationship between prefire stem (all stems taller than 1.37 m) density and postfire tree seedling density after long-interval fire in a mature forest (purple) and short-interval fire in young forest (green) fit with a linear log-log model. Black line is a 1:1 relationship. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

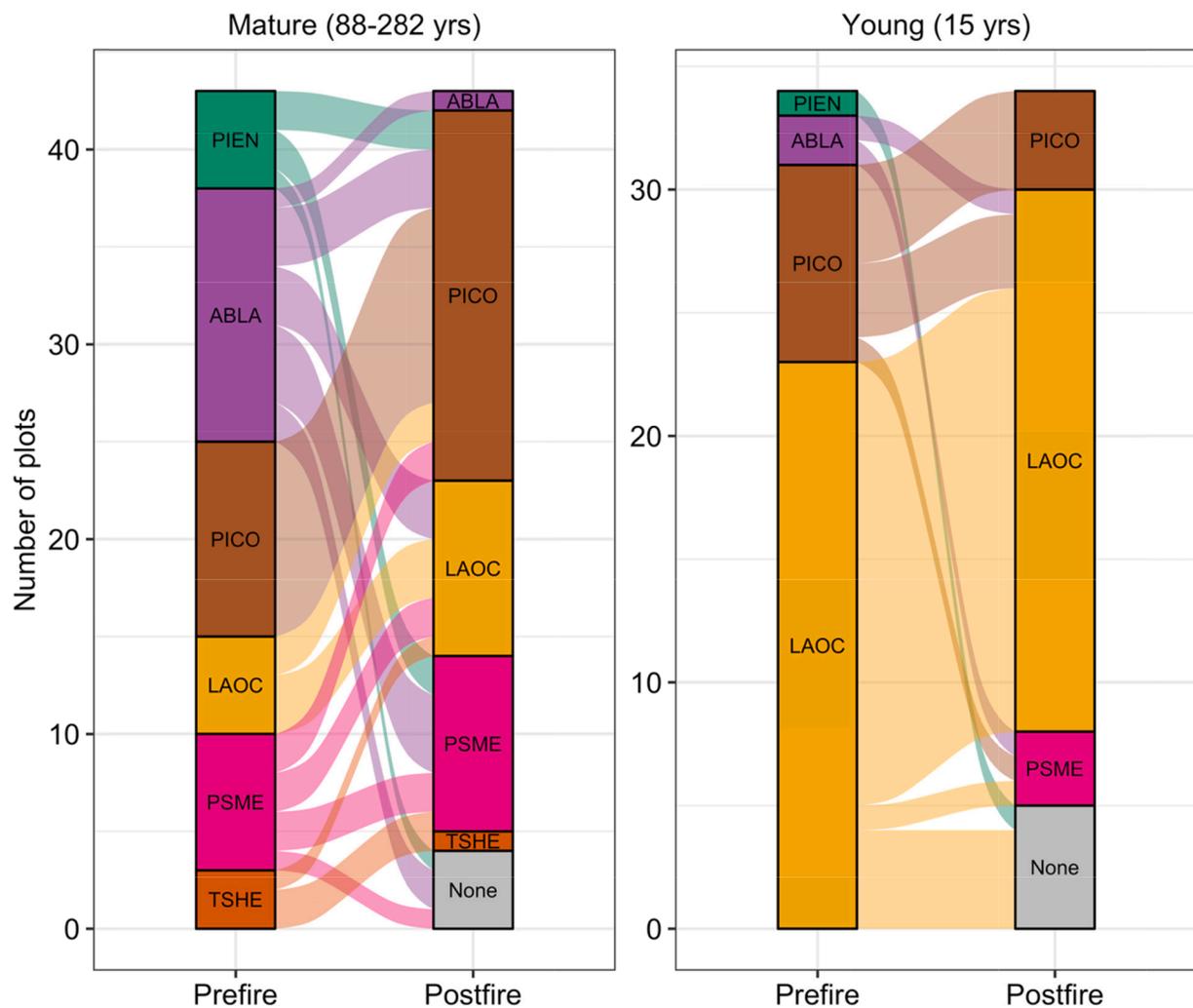


Fig. 4. Alluvial diagram depicting the dominant species of plots (based on importance values) in mature and young forests before and after high-severity fires. Note that y-axes are scaled differently because the total number of plots in each site was different. PIEN: Engelmann spruce (*Picea engelmannii*), ABLA: subalpine fir (*Abies lasiocarpa*), PICO: lodgepole pine (*Pinus contorta*), LAOC: western larch (*Larix occidentalis*), PSME: Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), TSHE: western hemlock (*Tsuga heterophylla*).

western redcedar before the long-interval fire were replaced by other species or had no postfire regeneration at all (Fig. 4); only one subalpine fir and one western hemlock stand regenerated as such. Plots that had been dominated by subalpine fir before the fire transitioned to lodgepole pine, western larch or Douglas-fir. Plots dominated by western hemlock transitioned to western larch or Douglas-fir. Plots dominated by Douglas-fir before the fire also followed multiple pathways postfire; about one-third were self-replaced, about half transitioned to lodgepole pine or larch, and two had no postfire seedlings (Fig. 4).

Prior to the short-interval fire, the young forest was dominated by larch and lodgepole pine, with a few plots dominated by Engelmann spruce or subalpine fir (Fig. 4). Nearly all plots dominated by western larch before fire were also dominated by western larch after the fire. One stand transitioned to Douglas-fir, and four had no postfire tree seedlings. Nearly all plots dominated by lodgepole pine before the short-interval fire either self-replaced or transitioned to western larch dominance postfire. Plots that were spruce- or fir-dominated before fire transitioned to Douglas-fir, western larch, or had no regeneration; no plots were dominated by spruce or fir seedlings after the short-interval fire (Fig. 4).

When considering the tree species assemblage in each plot, the mature forests were associated with Engelmann spruce, subalpine fir, western hemlock and western redcedar before the long-interval fire and became more associated with lodgepole pine and western larch after the

fire (Fig. 5a). Prefire mature forest plots were distinct from all other groups in ordination space. Young (15 yr old) forests and the 2-yr postfire seedling assemblages were all associated with lodgepole pine and/or western larch. (Fig. 5a). Douglas-fir was most strongly related to unburned mature forest, but it was present before and after fire in mature forest and the number of plots dominated by Douglas-fir increased after fire in young forests. Higher Bray-Curtis indices of dissimilarity in plot-level species composition before and after long- vs. short-interval fire indicated that composition was changed more by fire in mature than in young forest (Fig. 5b). Mean dissimilarity (\pm SE) pre- vs post-fire was 0.78 ± 0.04 in mature forest and 0.57 ± 0.06 in young forest was ($F = 12.5$, $p = 0.001$).

Mean percent cover (\pm SE) of all understory vegetation and of annual forbs was higher after long-interval fire ($36 \pm 2\%$ and $28 \pm 3\%$, respectively) than after short-interval fire ($24 \pm 2\%$ and $13 \pm 1\%$; Fig. S6). In contrast, mean percent cover of shrubs after short-interval fire ($9 \pm 1\%$) was nearly two times greater compared to long-interval fire ($5 \pm 1\%$). Percent cover of graminoids was very low and did not differ with fire interval ($2 \pm 1\%$).

3.2. Differences among species

Across both fires, postfire tree seedling density varied substantially

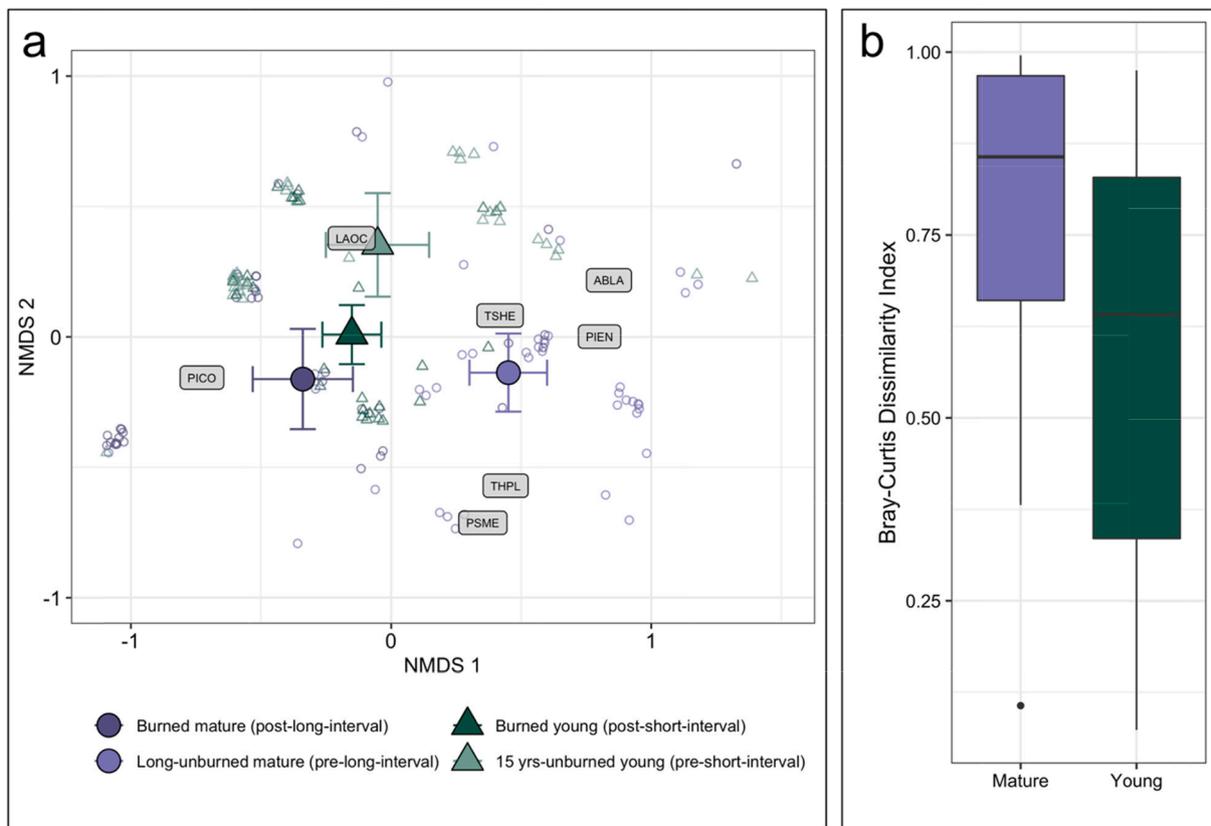


Fig. 5. Plot-level tree species composition and Bray-Curtis dissimilarity before and after fire. (a) Field plots (small points) in a non-metric multidimensional scaling (NMDS) ordination space of presence/absence. Axes are rotated and scaled to maximize variation in each dimension, and points are randomly jittered, to aid interpretation. The centroids of each group are indicated by a large dot, with error bars representing a 95% confidence interval around the mean. Tree species are plotted in ordination space: PIEN: Engelmann spruce (*Picea engelmannii*), ABLA: subalpine fir (*Abies lasiocarpa*), PICO: lodgepole pine (*Pinus contorta*), LAOC: western larch (*Larix occidentalis*), PSME: Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), and TSHE: western hemlock (*Tsuga heterophylla*).

among species (Table S2). Lodgepole pine had the highest mean (\pm SE) postfire seedling density ($30,012 \text{ ha}^{-1} \pm 15,097$); larch and Douglas-fir were also abundant, with mean densities $> 2500 \text{ ha}^{-1}$. Western hemlock was slightly less abundant ($1732 \text{ ha}^{-1} \pm 1545$), and western redcedar, Engelmann spruce and subalpine fir had the lowest mean postfire seedling densities ($<40 \text{ ha}^{-1}$; Table S2).

Seedling densities of lodgepole pine and western larch, the most abundant postfire species, were positively associated with indicators of seed supply (serotiny or conspecific prefire basal area) and for larch, a negative relationship with distance to low-severity burn was also important. None of the climatic variables were significant predictors (Table S2; Fig. 6), but soil clay content had a negative effect on

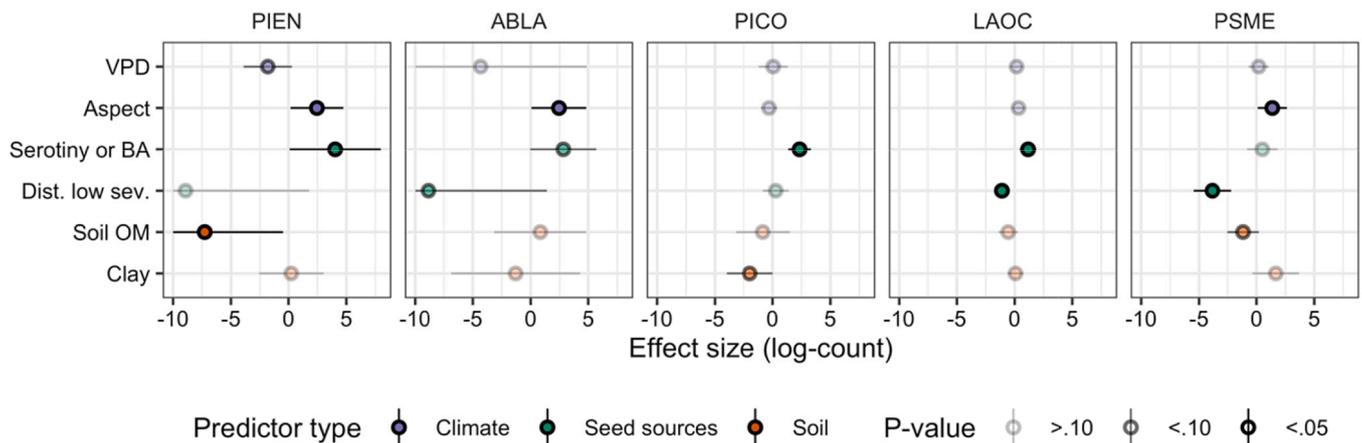


Fig. 6. Effect sizes estimated by generalized linear models of postfire seedling density as a function of mean daily vapor pressure deficit during the growing season months before sampling (VPD; kPa), aspect (index from 0 to 2 relative to northeast), conspecific prefire basal area ($\text{m}^2 \text{ ha}^{-1}$), distance to low burn severity (m), soil organic matter content (%), and soil clay content (%). The lodgepole pine model used presence of serotinous cones instead of prefire basal area. See Table S1 for summary statistics of predictors on their original scale. PIEN: Engelmann spruce (*Picea engelmannii*), ABLA: subalpine fir (*Abies lasiocarpa*), PICO: lodgepole pine (*Pinus contorta* var. *latifolia*), LAOC: western larch (*Larix occidentalis*), PSME: Douglas-fir (*Pseudotsuga menziesii* var. *glauca*). Low values were truncated to -10 for plotting.

lodgepole pine. Postfire seedling densities of Engelmann spruce and subalpine fir were positively associated with conspecific prefire basal area and subalpine fir was negatively associated with distance to low-severity burn. Northeastness (aspect) had a positive effect on both species and soil OM was negatively associated with spruce seedling density (Table S2; Fig. 6). Douglas-fir density was negatively associated with distance to low-severity burn, positively associated with northeastness, and soil OM had a negative effect.

4. Discussion

Our study provides evidence that successive fires (i.e., short-interval reburns) in mesic mixed-conifer forests initiate a regenerating seedling cohort that is less dense and less diverse than after historically typical long-interval fires. Substantial relative differences between the structure and composition of tree seedling regeneration after long- and short-interval burns at the same time-since-fire could signal a departure from historical recovery pathways. The trajectory of stand structure and composition set by postfire regeneration in the first two years after fire may also foreshadow long-lasting change because seed sources for fire-sensitive species are no longer within dispersal distance (Kemp et al. 2016, Stevens-Rumann and Morgan 2016, Gill et al. 2021), site conditions for conifer germination are ephemeral (Fischer 1987), and the regional climate is becoming increasingly inhospitable for the establishment of drought-intolerant species (Harvey et al. 2016a, Whitlock et al. 2017). While the forests we studied did not exhibit fire-catalyzed regeneration failure, reduced seedling densities and a simplification of species composition have implications for the provisioning of wildlife habitat and stable carbon stores that would be challenging to mitigate with current management tools. However, the shift to dominance by western larch, a species well adapted to both resist burning and reseed after fire, could maintain forest cover even as the fire regime changes.

4.1. Effects of return interval on the structure and composition of regenerating forests

Our study documents the potential for short-interval fires to reduce tree density relative both to long-interval fires and to prefire stem densities in young forests. As we hypothesized, postfire tree seedling densities were substantially reduced in the short- vs. long-interval fire; mean total seedling density was 45 times higher after the long-interval fire than after the short-interval fire. Importantly, the density of post-fire regeneration was within historical and contemporary forest densities for the region (10^2 - 10^4 trees ha^{-1}) following both fires (McKenzie and Tinker 2012, Harvey et al. 2016b, Urza and Sibold 2017, Stevens-Rumann et al. 2018), indicating that conversion to non-forest was unlikely, but the density of seedlings in young forests was just a third of the prefire stem density. Subalpine forests in this region historically recovered to postfire seedling densities that met or exceeded prefire stem densities within a few years of fire (McKenzie and Tinker 2012, Urza and Sibold 2017) and the mature forests we studied appear similarly resilient to long-interval fire. However, we found a weak relationship between pre- and postfire density after short-interval fire (Fig. 3), suggesting that repeated burning after a short fire-free period may incrementally erode the capacity for forests to sustain historical stand densities (Turner et al. 2019).

Prefire composition of the mature forest reflected the historical richness of species in the study area, and species dominance was relatively evenly distributed (Fig. 4). Consistent with our hypotheses (Table 1), plots that were dominated by fire-adapted species were self-replaced, whereas plots dominated by fire-sensitive species were converted to fire-adapted ones (Fig. 4). The short-interval fire in young forests reinforced this shift such that recovery of fire-sensitive conifers will be constrained by seed availability into the future. Our observations are consistent with previous findings that indicate fire in mature forests promotes the expansion of fire-embracing lodgepole pine and fire-

tolerating western larch at the expense of fire-avoiding Engelmann spruce and subalpine fir (McKenzie and Tinker 2012, Urza and Sibold 2017, Steed and Goeking 2020). However, our findings also demonstrate the potential for a second short-interval fire to further erode seed sources, simplifying species richness and reinforcing the expansion of monotypic stands of highly fire-adapted species to a degree that a single fire does not. We recognize that a lack of field measurements representing forest conditions before 2003 (the first fire in the short-interval reburn sequence) limits our inference about sequential changes in forest structure following each fire.

4.2. Differences in driver importance among species

Among species, we found that drivers related to seed availability were consistently important but effects of abiotic variables were equivocal. All of the conifers we modeled (i.e., excluding western hemlock and western redcedar) are obligate seeders and were strongly limited by seed availability; studies from a range of conifer systems identify the importance of seed supply for post-disturbance establishment (Bowman et al. 2014, Kemp et al. 2016, Stevens-Rumann and Morgan 2016, Gill et al. 2021). Although our study is consistent with findings that aridity reduces postfire regeneration of drought-intolerant species like spruce and fir (Andrus et al. 2018, Schapira et al. 2021), the effect of aspect (our proxy for microclimate) was lower than for conspecific prefire basal area or distance to potential seed sources. For species that tolerate a wider range of climatic conditions—lodgepole pine and western larch—our findings align with studies from mesic forests that suggest seed availability is frequently a more important limitation on regeneration than climate (Steed and Goeking 2020, Povak et al. 2020). However, our ability to detect constraints on regeneration from interannual climate variability was limited because our study only reflects the climate of two growing seasons.

4.3. Species traits mediate responses to increasing fire

The shifts in composition we observed suggest that fire-regime change is altering the relative fitness advantage conferred by species' traits. Western larch are well-positioned to succeed in a future with more fire because of their multiple adaptations to both high- and low-severity fire and a range of frequencies (Burns and Honkala 1990). After high-severity fire, western larch can quickly repopulate disturbed areas from a single survivor; mature individuals frequently exceed 30 m in height, produce hundreds of cones per tree that are positioned in the upper canopy, and disperse their small, winged seeds widely onto the mineral soils they prefer (Burns and Honkala 1990). Once established, fast growth rates allow individuals to outcompete co-occurring species (Burns and Honkala 1990). Larch can also succeed in a frequent, low-severity fire regime because they have thick bark that enables them to survive fires (Stevens et al. 2020), self-prune lower branches, and replace scorched branches epicormically (Burns and Honkala 1990). In larch forests adjacent to Glacier, fires restored forest structure to low densities and increased tree vigor relative to unburned sites (Hopkins et al. 2014). In contrast, lodgepole pine relies largely on the fire resilience conferred by serotinous cones, in which seeds are bound by resin until heated. Serotiny is advantageous in ecosystems where infrequent, high-severity fires expose large patches of mineral soil denuded of competitors (Schwilk and Ackerly 2001, Schoennagel et al. 2003). Then, prolific seeding from mature trees promotes the self-replacement of dense postfire cohorts (i.e., fire-embracing), as was the case in stands of lodgepole pine in our long-interval plots. However, serotiny in lodgepole pine doesn't become dominant until trees reach ~30 years old and requires that cones avoid complete combustion (Brown and Johnstone 2012, Turner et al. 2019). Cones held in short-stature canopies are more likely to be consumed by fire and travel shorter distances from unburned islands or edges (Gill et al. 2021).

If the short-interval fire we studied is a harbinger of future

conditions, increased fire activity may eventually shift these systems toward a more fuel-limited regime characterized by low-density forests and woodlands composed of fire-resistant tree species and fire-embracing shrubs and grasses (Donato et al. 2009, Larson et al. 2013, Serra-Diaz et al. 2018). When fire return intervals fall below the time required for trees to mature and produce serotinous cones, serotiny loses its adaptive advantage, and fire-resistant traits are favored over fire-embracing ones (Pellegrini et al. 2017, Stevens et al. 2020, Rodman et al. 2021). Douglas-fir, western larch and Ponderosa pine (*Pinus ponderosa*), for example, grow thick insulating bark that allows mature individuals to survive fire and provide seed to the burned patch (Pellegrini et al. 2017, Stevens et al. 2020). Ponderosa pine is found in warm, dry river valleys in Glacier and benefits from frequent fire, even after decades without burning (Larson et al. 2013). Self-reinforcing feedbacks between fire and vegetation in a warm and dry future climate scenario could promote semi-stable alternative ecosystem states (Ratajczak et al. 2014, Johnstone et al. 2016), but determining whether immediate shifts in postfire ecosystem structure and composition are temporary or indefinite remains extremely challenging (Hastings et al. 2018, Miller et al. 2019).

4.4. Persistence of fire-avoiding and fire-refuge conifers is uncertain

An ongoing challenge for scientists and managers in this region will be to determine when fire events are within the historical range of variability and when they represent fire-regime departures that will drive persistent shifts in the local distribution of tree species. For example, fire activity increased during Holocene warm periods, like the Medieval Climate Anomaly ca. 1000–700 years before present, and decreased during cool wet periods, including the Little Ice Age ca. 600–100 years before present (Power et al. 2006, Whitlock et al. 2008). Patterns of repeated high-severity fire activity within several decades, like we observed, are not unprecedented in the observational record (Habeck 1968, Arno 1980, Davis 1980, Barrett et al. 1991). However, old-growth cedar-hemlock stands in Glacier were not affected by extensive high-severity fire for several centuries until 2003. Of the four western hemlock-dominated stands in our study, just one was dominated by western hemlock after fire. In the short-interval fire, although much of the area was cedar-hemlock forest before the 2003 fire, none of the stands we sampled were dominated by western redcedar or western hemlock before the 2018 reburn and their seedlings were absent afterward. Regardless of whether these species will eventually dominate in the burned areas we studied, such a process would take centuries. Given the strong likelihood that temperatures will be $> 2^{\circ}\text{C}$ warmer by the end of the 21st century (Whitlock et al. 2017), and evidence that recently burned subalpine forests are at risk of burning again within decades (Turner et al. 2019, Higuera et al. 2021), the fire-driven loss of these forest types today could effectively be permanent.

4.5. Climate adaptation in subalpine forests

Changes in the age, density and composition of species-rich subalpine forests could have lasting impacts on wildlife biodiversity and carbon storage in these ecosystems into the future. Loss of old large individual trees (Jones et al. 2018), simplification of forest structure and pyrogenic residuals (Bowman et al. 2016, Jones and Tingley 2021) and declines in forest extent (Jones et al. 2016) are already implicated in the decline of forest-specialist vertebrates. Similarly, fire-driven changes in forest age structure could jeopardize the potential of forests to safeguard Earth's climate by storing atmospheric carbon (Fargione et al. 2018, Anderegg et al. 2020). For example, old-growth larch and Douglas-fir stands (>150 years old) near our study sites held $> 200 \text{ Mg ha}^{-1}$ more total ecosystem aboveground carbon than young (< 50 years old) stands (Bisbing et al. 2010).

Managers will be challenged to determine where resisting changes to historical forest structure and composition is feasible and where

directing or adapting to ecosystem transformation is more appropriate (Schoorman et al. 2020). Resisting climate- and fire-driven vegetation change could involve active suppression around culturally important old-growth trees; directing change could include assisted migration of fire- and drought-adapted native species, like ponderosa pine, to areas of the park it currently does not occupy; accepting change might involve an approach where fire and vegetation are not actively managed and public education of change is emphasized. Decisions about whether and how to intervene in vegetation trajectories or fire activity will be local, context-dependent and vary with a unit's management objectives.

4.6. Conclusions

Climate-driven models of future fire activity indicate that burned area and fire severity will continue to increase in the northern Rockies (Westerling et al. 2006, Abatzoglou and Williams 2016, Holden et al. 2018, Parks and Abatzoglou 2020, Turner et al. 2021) until there is a fundamental change in system properties (McKenzie and Littell 2017, Littell et al. 2018), and our findings indicate the potential for two types of forest change in response. First, more frequent burning in historically dense subalpine mixed-conifer forests will promote the expansion of fire-adapted conifers and could drive a transition toward sparser forests. Ultimately, if fire-resistant species (e.g., western larch, Douglas-fir, ponderosa pine) become dominant, a frequent, low-severity fire regime could emerge. Second, longer and more extreme fire-season weather will enable more burning in old-growth cedar-hemlock forests, as occurred during the 2003 Robert Fire (initiating our young forest study site) and the 2017 Sprague Fire (our mature forest study site), and postfire regeneration of these species is likely to be strongly constrained by seed availability, and increasingly, climate. These factors could interact to reduce the extent of this iconic forest type in the northern Rockies, but the diverse assemblage of tree species in Glacier may facilitate compositional shifts to fire-tolerant species that prevent or delay loss of forests altogether.

CRediT authorship contribution statement

Tyler J. Hoecker: Conceptualization, Methodology, Software, Investigation, Formal analysis, Writing – original draft, Visualization. **Monica G. Turner:** Conceptualization, Resources, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119814>.

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