

ARTICLE

Vegetation Ecology

Climate change and fire alter biotic interactions and tree growth in high-elevation forests

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Funding information

USFS Rocky Mountain Research Station,
Grant/Award Number: 19-JV-
11221639-098; BYU Redd Center

Handling Editor: Christopher Carcaillet

Abstract

Climate change and shifting fire regimes have the potential to alter forest structure and tree growth dynamics in high-elevation forests; however, the relative role of competitive and facilitative interactions in shaping postfire responses remains unclear. To investigate these dynamics, we studied tree growth across an elevational gradient in the subalpine and treeline forests of the Selway-Bitterroot Wilderness (Idaho and Montana, USA), where fire atlas data and a history of limited fire suppression enabled the implementation of a 2 × 2 factorial study design. We sampled burned and unburned stands in two elevation strata: within the transition from closed canopy subalpine forest to subalpine parkland (forest-parkland transition; FPT) and near the upper limit of single-stem upright tree growth (alpine treeline ecotone; ATE), which represent low environmental stress and high environmental stress conditions, respectively. We measured radial growth and tree neighborhood composition for focal trees (≥20 cm diameter at breast height [dbh]) of two functional groups informed by their ecological roles: stress-tolerant, early successional “benefactor” species (whitebark pine, *Pinus albicaulis* and subalpine larch, *Larix lyallii*), and shade-tolerant, late successional “beneficiary” species (subalpine fir, *Abies lasiocarpa* and Engelmann spruce, *Picea engelmannii*). Patterns of neighborhood stem density across our sites indicated a shift from competition to facilitation with increasing elevation, while fire served to reduce neighborhood stem density in focal tree plots. Growth responses to fire were group-specific: spruce/fir showed a clear fire-induced growth release, particularly at lower elevations, while whitebark pine/larch exhibited a more limited response. Although fire did not alter the sensitivity of tree growth to climate, relationships with winter precipitation shifted from uniformly negative (pre-1979) to neutral or positive (post-1979) across all species and elevations. Ultimately, our results suggest that while responses to disturbance are likely to vary across species and elevations, directional climate change is uniformly reducing

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abiotic limitations on tree growth in the high-elevation forests of the northern Rocky Mountains.

KEYWORDS

alpine treeline ecotone, climate change, competition, dendroecology, facilitation, fire, high-elevation forest, stress gradient hypothesis, subalpine forest

INTRODUCTION

Subalpine forests represent the highest elevation ecosystems dominated by trees (Millar & Rundel, 2016) and are composed of species that are well adapted to the cold temperatures and short growing seasons present in most high mountain environments (Jobbágy & Jackson, 2000; Körner, 2012). Increases in elevation within the subalpine zone generate shifts in forest structure, most notably the transitions from closed canopy forest to open park-like stands (i.e., timberline or forest–parkland transition [FPT]), from single-stem upright tree growth to stunted, krummholz form (i.e., treeline), and eventually to true alpine ecosystems where trees are completely absent (i.e., tree species limit) (Holtmeier, 2009; Körner, 2012; Rochefort et al., 1994). Here, we use the term “high-elevation forest” to discuss this entire zone—from closed canopy subalpine forest to tree limit—and further specify elevational positions and relative conditions when relevant. Ultimately, this gradient reflects a climate-driven increase in abiotic stress that at its upper limit is defined by conditions unsuitable for the survival and growth of tree species (Körner, 2012; Körner & Paulsen, 2004).

Predominant interactions between trees in high-elevation forests are expected to shift from negative (i.e., competition) near the boundary of closed canopy forest to positive (i.e., facilitation) as environmental stress increases with elevation, as described by the stress gradient hypothesis (SGH) (Bertness & Callaway, 1994; Callaway, 1998, 2007). Competition defines the negative effects of spatial association with other plants (both inter- and intraspecific) as they struggle to acquire resources, while facilitation describes a positive influence of spatial proximity to neighbors (Callaway, 2007). Differences in the nature of tree–tree interactions over this gradient suggest that removal of neighboring trees due to disturbance may result in differing growth responses for surviving trees: positive growth responses when competitors are removed in relatively low environmental stress sites and negative growth responses when facilitators are removed in more stressful sites.

Abiotic stress and climate are closely linked, especially in high-elevation forests where climate is often the

principal factor limiting tree growth and establishment (Körner & Paulsen, 2004; Millar et al., 2015, 2020; Paulsen et al., 2000; Peterson et al., 2002; Peterson & Peterson, 1994). Changes in climate have been strongly implicated in altitudinal and latitudinal shifts in many high-elevation forest boundaries (Beckage et al., 2008; Grace et al., 2002; Harsch et al., 2009; Lu et al., 2021; Malanson et al., 2011), emphasizing the sensitivity of high-elevation forest environments to global change (Smith et al., 2009). In addition to the direct effects of warming temperatures and shifting precipitation patterns, climate-induced shifts in both fire frequency and area burned are underway in high-elevation forests across the western United States (Alizadeh et al., 2021; Cansler et al., 2016). The response of treeline forest communities to the combined impact of fire and warming is complex (Cansler et al., 2018), and tree–tree interactions may play an important role in magnifying or buffering these responses (Wang et al., 2019). Our study aims to test whether the relationships predicted by the SGH (Bertness & Callaway, 1994; Callaway, 1998; Maestre et al., 2009) are impacted by disturbance and climate change, with the goal of understanding how interactions between trees across a stress gradient in high-elevation forests may change under future conditions.

The high-elevation forests of the northern Rocky Mountains display several characteristics that make them an ideal setting to investigate these dynamics. Environmental stress gradients which limit tree growth and survival have been documented within the region (Callaway, 1998), as has the occurrence of wildfires burning across high-elevation forests (Cansler et al., 2016, 2018). Furthermore, this region contains several federally designated wilderness areas where wildland fire dynamics can be studied in the absence of direct human manipulation (Kreider et al., 2023), and the dominant tree species in these high-elevation forest communities lend themselves to classification within the revised SGH framework proposed by Maestre et al. (2009).

Whitebark pine (*Pinus albicaulis*; WBP) is stress-tolerant and readily colonizes harsh sites (Arno & Hoff, 1989; McCune, 1988; Tomback, 1982; Ulrich et al., 2023), just as subalpine larch (*Larix lyallii*) thrives in severe environments (Arno & Habeck, 1972). Both are

relatively intolerant of shade as compared to co-occurring species—though WBP is more shade-tolerant than larch (Arno & Hoff, 1989)—and mature trees often provide shelter for the establishment and growth of other species in environmentally stressful sites (Arno & Habeck, 1972; Arno & Hoff, 1989; Callaway, 1998). For WBP specifically, seed dispersal by Clark’s nutcracker (*Nucifraga columbiana*) (Tomback, 1982) allows the species to initiate forest succession near treeline and in the interior of large disturbed patches following fire (Tomback, 1986; Tomback et al., 2001).

Alternatively, subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) are both shade and competition tolerant and require more favorable growing conditions (i.e., warmer, wetter, wind-protected) to succeed (Arno, 1986; Arno & Habeck, 1972). Under the refined SGH framework (Maestre et al., 2009), WBP and subalpine larch are “stress-tolerant benefactors,” whereas subalpine fir and Engelmann spruce are “competitive beneficiaries.” At high levels of environmental stress, beneficiary species are predicted to respond positively—in the form of enhanced growth or survival—from spatial association with benefactors (Bertness & Callaway, 1994; Brooker et al., 2008; Callaway, 1998). Alternatively, benefactor species are predicted to show a neutral to negative response from spatial association with beneficiaries (Callaway, 2007; Maestre et al., 2009).

Here, we investigate whether and how fire in high-elevation forests alters forest structure and the growth of residual trees across an environmental stress gradient. To characterize the two ends of the stress gradient present at our sites, we use the term FPT to describe the start of this gradient (near the elevational limit of closed canopy forest) and the term alpine treeline ecotone (ATE) (*sensu* Millar & Rundel, 2016) to refer to the zone near the upper elevational limit of single-stem upright tree growth. Given the importance of climate as a biophysical driver of growth in these ecosystems (Kichas et al., 2024; Millar et al., 2020; Peterson et al., 2002; Peterson & Peterson, 1994; van Mantgem et al., 2023), we also found it essential to quantify the direct effect of climate on growth in disturbed and undisturbed tree neighborhoods. Specifically, we ask:

1. How does the presence and species identity of large individual trees affect neighborhood stem density across an elevational stress gradient within high-elevation forests? How does fire affect stem density within these neighborhoods?
2. How do fire-associated changes in tree neighborhood environments affect the growth of surviving trees across species and elevational positions?

3. Do trees that survive fire show stronger growth–climate relationships in the postfire period as compared to individuals growing in adjacent unburned stands?

Following the SGH, we expected that the neighborhoods of large trees would have higher stem densities in ATE environments (high-stress, facilitation dominated) relative to arbitrary locations sampled with systematically located plots. In contrast, we predicted that neighborhood stem density around large trees would be similar to systematically sampled locations at sites in the FPT (lower stress, competition dominated). Fire was expected to reduce stem density across neighborhood types and elevations. We hypothesized that in lower elevation, low environmental stress FPT sites, all residual trees would see a growth release due to reduction of competition. In high-stress, facilitation dominated ATE sites at higher elevations, we expected growth to decrease after fire in beneficiary species and show a neutral to positive response for benefactor species. Regarding growth–climate relationships, we hypothesized that the annual growth of all trees that experienced fire would be more sensitive to (i.e., more highly correlated with) climate compared to growth of individuals in nearby unburned areas, and that these climatic effects would be most pronounced in beneficiary species.

METHODS

Study area and field sampling

We sampled 10 high-elevation forest sites across the Bitterroot Mountains (Figure 1) within the Selway-Bitterroot Wilderness (SBW) that burned between the years 1979 and 1998 (Table 1). The SBW is a 545,372-ha congressionally designated wilderness area with a unique history of limited fire suppression (Brown et al., 1994), making it a valuable “natural laboratory” for studying the impacts of fire on forest communities (Kreider et al., 2023). The high-elevation forest zone of the Bitterroot Range is snow-dominated, with annual precipitation averaging 170 cm and nearly 70% of this occurring as snowfall (Finklin, 1983).

At each site, we implemented a 2 × 2 factorial study design (burned/unburned at upper/lower elevation locations) with transects in each of these four factorials (Figure 2). We selected sites by using spatially explicit fire atlas data (Morgan et al., 2017; Parks et al., 2015) to identify areas that had burned once during the period of record (1870–2022) and had adjacent forest which was undisturbed during that same period. Site selection was further constrained to fires which occurred during the period 1979–1998 to limit the

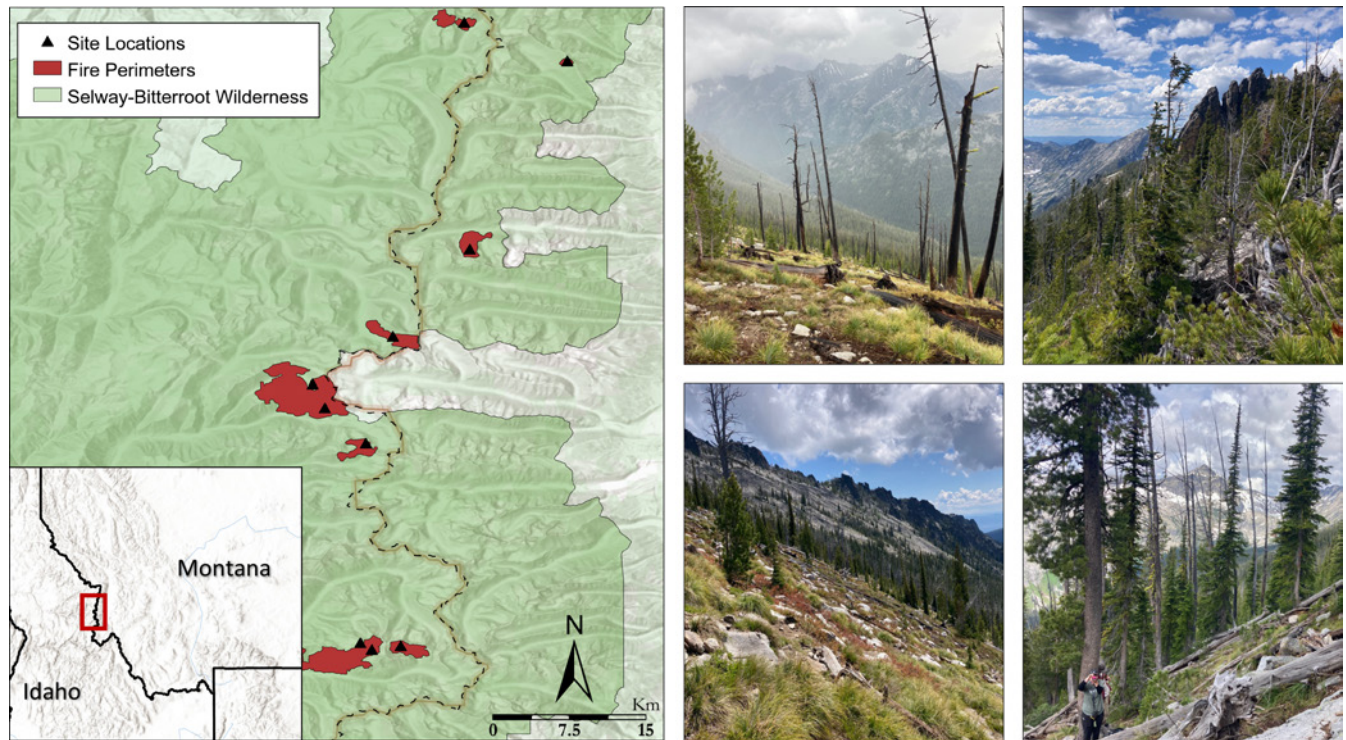


FIGURE 1 Map of study area, fire perimeters, sample sites, and plot photos showing representative conditions across 2×2 factorial study design in the forest–parkland transition (FPT) zone and alpine treeline ecotone (ATE). Plot photographs are from a site near Gash Point, Montana, USA, and show (clockwise from upper left): ATE burned, ATE unburned, FPT unburned, and FPT burned. Photo credit: Josh Beisel.

TABLE 1 Summary of fire events and plot counts across all study sites.

Site	Fire year	Fire size (ha)	Elevation (m)		Spruce/fir (n)	Whitebark/ larch (n)	Systematic (n)	Total (n)
			Minimum	Maximum				
Vance 1 ^a	1979	2057	2099	2453	32	36	21	89
Vance 2 ^a	1979	2057	2184	2552	32	24	16	72
Twelve mile	1981	446	2053	2431	33	31	17	81
Blodgett	1987	620	1996	2434	32	34	22	88
Bear 2 ^b	1988	2931	1952	2263	32	35	17	84
Bear 3 ^b	1988	2931	1961	2268	16	14	11	41
Sawtooth	1998	702	2142	2461	6	6	3	15
Gash Pt.	1991	49	2378	2644	32	32	16	80
Packbox	1998	276	1980	2384	36	22	20	78
Spruce	1998	284	2049	2332	32	32	20	84

Note: Superscripts (a, b) denote sites that burned in the same fire event. Details regarding the number of samples within each fire $\times$ elevation transect at a given site, along with dendrochronological statistics by species group, can be found in Appendix S2: Table S1.

extent of postfire forest structural development while ensuring an adequate postfire growth record (≥ 25 years) could be captured. Fires were selected that burned within the elevational range of 1900–2700 m with at least 400 m between minimum and maximum mapped elevations (Table 1).

Sampling was focused in two elevational strata which represent two distinct points along the environmental stress gradient present at our sites. Within a given study site, our lower elevation sample (relatively low environmental stress) targeted the zone of transition from closed canopy subalpine forest to the subalpine parkland (FPT).

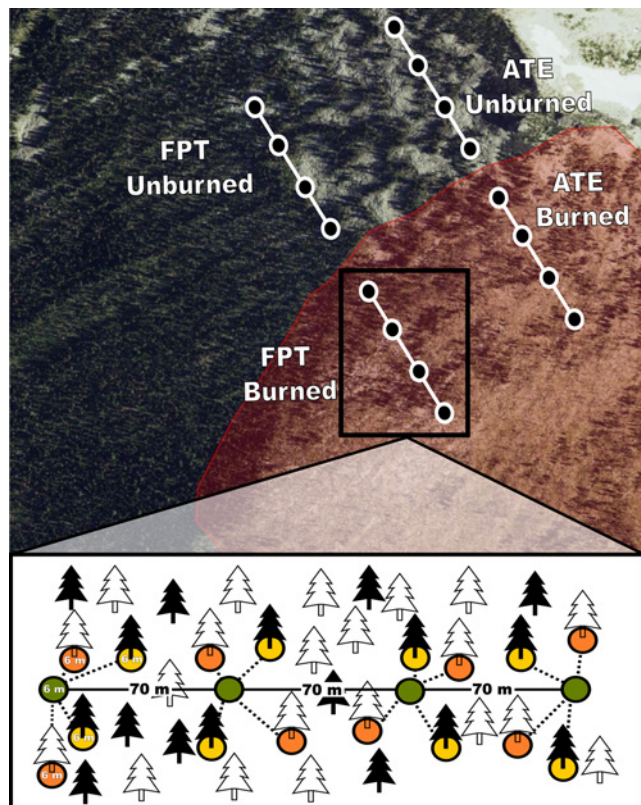


FIGURE 2 Visualization of sampling design at a representative burned/unburned high-elevation forest site across forest–parkland transition (FPT) zone and alpine treeline ecotone (ATE) in the Bitterroot Mountains, Montana. Sample transects (white lines) are distributed across four treatments: ATE unburned, FPT unburned, ATE burned, and FPT burned. The satellite-derived burn perimeter is delineated in red. The bottom panel illustrates the plot layout within each transect, where green circles represent systematic sample plots at evenly spaced 70-m intervals. From each systematic plot, the nearest two individuals of each species group (≥ 20 cm dbh) were located and focal tree plots (orange and yellow circles) were established. All plots were circular and had a fixed radius of 6 m. Image courtesy of US Geological Survey National Aerial Image Program (NAIP). Illustration credit: Josh Beisel.

Our higher elevation sampling (relatively high environmental stress) targeted the zone near the upper elevational limit of single-stem, upright tree growth near the transition to the krummholz growth form (ATE). The elevational range for each of these strata was based on observations from the Bitterroot Mountains where a switch from competitive to facilitative interactions has been demonstrated, as predicted by the SGH (Callaway, 1998). In addition to the well-understood decrease in temperature resulting from adiabatic cooling, a 200–300-m increase in elevation in these systems also corresponds with an increase in the rate of leaf cuticle wax abrasion for exposed leaves (i.e., increased physical stress/winter damage) (Hadley & Smith, 1989).

Transect origins were established at randomized coordinates within a given elevation band and 50 m from the mapped burn edge (randomized point location within 50-m buffer polygon), running perpendicular to the prevailing slope and oriented either towards the interior of the burn (burned transects) or away from the burn edge (unburned transects). Sampling occurred at four evenly spaced points at every 70 m along the line (Figure 2). Each of these points became the plot center for a “systematic plot,” where forest structure was assessed. Systematic plots allowed for an unbiased estimate of response variables across each of our sites. From each point (i.e., systematic plot), four additional “focal tree plots” were also sampled. Using a laser rangefinder and compass, we identified and mapped the nearest two individual “benefactor” species (*P. albicaulis* or *L. lyallii*) and “beneficiary” species (*A. lasiocarpa* or *P. engelmannii*) ≥ 20 cm dbh (Figure 2). Procedures to adjust this protocol for cases where field conditions prevented sampling under the standard protocol (e.g., safety, cliffs) are detailed in Appendix S1: Section 1.1.

Plot-level measurements

To quantify the neighborhood environment at each systematic or focal tree plot, we used fixed-area 6-m radius circular plots centered on either a systematic point or focal tree. All trees ≥ 8 cm dbh within the plots were identified to species and binned into diameter classes (8–20, >20–30, >30–40, and >40 cm). For each focal tree, we recorded species, dbh (in centimeters), and a visual estimate of crown volume ratio (CVR; proportion of crown height to total stem height). To measure annual growth for postfire growth response and climate–growth analysis, we extracted two increment cores from each focal tree at ~ 30 cm above the root collar. Increment cores were extracted at two opposite radii, perpendicular to the prevailing slope to account for uneven radial growth. We also recorded percentage crown dieback (US Forest Service, 2022) as a proxy for tree vigor. GPS coordinates for all systematic plot centers were recorded using a submeter GPS unit (Juniper Systems Geode GNS3), and focal tree locations were calculated from distance and azimuth measurements originating from these points.

Dendroecology

Tree cores were air dried and processed using standard methods (Speer, 2010). Processed cores were measured in the CooRecorder program and cross-dating was carried out in the accompanying CDendro program v9.8.1 (Larsson & Larsson, 2023). Cores that did not meet

statistical thresholds (cross-correlation ≥ 0.30 or t test ≥ 5.0) were examined further to identify and account for missing and/or false rings following methods of Dial et al. (2024), with modified thresholds to account for the greater complexity of our dataset (i.e., multiple species across elevations with disparate disturbance histories). Measurements from the two cores extracted from each tree were averaged to obtain annual raw ring width measurements (in millimeters) for each tree, which was the basis for all subsequent growth analysis. In several instances, an adequate growth record could not be obtained from both cores, in which case only a single core was used. Dendrochronology summary statistics for each growth chronology are available in Appendix S2: Tables S1 and S2.

Chronology building and detrending were carried out using the *dplR* package (Bunn, 2008) in R (R Core Team, 2024). Two response variables for growth were derived from raw ring width measurements to address our different research questions: relative basal area increment (rBAI) and ring width index (RWI). Both metrics are unitless ratios which describe growth in relation to an average across some period. rBAI represents relative growth of a given tree in year n since fire (Keyser et al., 2010; Reinhardt & Ryan, 1988; Skov et al., 2005). To obtain rBAI, annual raw ring width measurements were first converted to basal area increment (BAI) for each individual tree using the *bai.out* method in *dplR* (Bunn, 2008). The value for rBAI in year n since fire can be represented by the following equation:

$$\text{rBAI}_{i,n} = \frac{\text{BAI}_{i,n}}{\frac{1}{10} \sum_{k=-10}^{-1} \text{BAI}_{i,k}} \quad (1)$$

where BAI for tree i in year n since fire is divided by the average annual growth across the 10-year period prior to the year of the fire event. We used a 10-year window given that this was available for all sampled trees prefire and the window postfire captures the immediate growth response (Reinhardt & Ryan, 1988; Skov et al., 2005). This metric was chosen for growth response analysis because BAI is less tied to age- and size-related trends than radial ring width (Biondi & Qeadan, 2008; LeBlanc & Foster, 1992), and the relativization allows each tree to act as its own control (Salonius et al., 1982). This enabled us to capture individual tree response to fire while minimizing potential size- and age-related influences on total growth.

To analyze climate–growth relationships, we used the same annual BAI measurements but expanded the temporal window to include up to ± 30 years from fire occurrence at each site (Appendix S2: Figure S1). We divided these observations into pre- and postfire categories, and annual growth

for an individual tree was detrended by dividing through by the mean 30-year growth of the tree over the given period (i.e., a value of 1 corresponds to an average year of growth, >1 indicates above average, and <1 is below average). These series were modeled using a first-order autoregressive process (AR-1) to address serial autocorrelation, the residuals of which were used as our RWI series for each tree. Final chronologies (the unit of observation for climate–growth analysis) were developed by aggregating individual tree RWI values by period (pre- vs. postfire), species group, and transect using Tukey’s bi-weight robust mean.

Climate data

We obtained 4-km gridded raster datasets for monthly precipitation (PPT, in millimeters), minimum temperature ($T_{\min}$, in degrees Celsius), and maximum temperature ($T_{\max}$, in degrees Celsius) from PRISM Climate Group (Daly et al., 2008) for all months spanning the period from 1930 to 2023. Site-level records were extracted from these grids using bilinear interpolation from the coordinate center point of each transect. We used monthly PRISM precipitation and temperature data to estimate climatic water deficit (CWD) for all months via a Thornthwaite-type water balance model (Thornthwaite, 1948; Thornthwaite & Mather, 1957) following the general methods of Lutz et al. (2010) (see Appendix S1: Section 1.2). Thornthwaite-type models are considered the best choice for estimating water balance parameters when only temperature and precipitation data are available (Dingman, 2015).

Temporal windows for final climate analysis were identified using the *climwin* package (van de Pol et al., 2016) within R statistical software (R Core Team, 2024). *Climwin* analysis identified the three seasonal/monthly windows which best explained annual growth and became the basis for our analysis: previous August CWD (pAugust CWD; in millimeter), January–March precipitation (Winter PPT; in millimeter) and mean April temperature (April T_{mean} ; in degrees Celsius). A description and visual example of climate window selection is provided in Appendix S1: Section 1.3 and Appendix S2: Figure S2.

Statistical analysis

To address each of our research questions, we fit separate linear mixed-effects models tailored to each research question and its associated data. Estimated marginal means (EMM) were calculated for all models using the *emmeans* package in R (Lenth, 2024). The Sawtooth site (Table 1) could not be completed due to inclement weather; measurements of forest structure are included

in Appendix S2: Table S3, but this site was excluded from all analyses.

To analyze differences in neighborhood stem density across plot types (*Question 1*), we fit a zero inflated negative binomial model (ZINB) with stems per hectare as the response using the *glmmTMB* package in R (Brooks et al., 2017). This modeling framework provided the best fit for our stem density data as it accounts for the non-Gaussian, zero inflated distribution we observed—a common feature of forest structure/ingrowth data (R. Li et al., 2011). Fixed effects included fire status, elevational position (FPT vs. ATE), plot type, delta normalized difference vegetation index (dNDVI), years since fire, percent cover of rock, and various interaction terms. We also included a random effect for transect, nested within site. Model output summary with more detailed information is available in Appendix S2: Table S4. Satellite-derived dNDVI was obtained from plot coordinates using bilinear interpolation from the same fire atlas data used in site selection (Morgan et al., 2017; Parks et al., 2015). Focal trees were omitted when calculating neighborhood stem density and basal area to provide a fair comparison of neighborhood structure between focal tree and systematic plots.

Focal tree growth responses to fire (*Question 2*) were quantified by fitting a linear mixed-effects model with rBAI as our response variable using the *nlme* package in R (Pinheiro et al., 2025). Due to non-normality in the distribution of our response, rBAI was transformed using a Box-Cox transformation ($\lambda = -0.06$; Box & Cox, 1964) prior to model fitting. This transformation was preferred to a generalized linear mixed model (GLMM) approach because the necessary inclusion of an autocorrelation term led to issues with model fitting within a non-Gaussian framework. Continuous predictors included live basal area (LBA) of the plot as well as tree-level diameter (dbh), CVR, and crown dieback (Dieback). Our growth response model can be represented by the equation:

$$\begin{aligned} BC(rBAI_{ijkl}) = & \beta_0 + \beta_1(\text{Group}_{ijl}) + \beta_2(\text{Elevation}_{jl}) \\ & + \beta_3(\text{Fire}_{jl}) + \beta_4(\text{Group}_{ijl} \times \text{Elevation}_{jl}) \\ & + \beta_5(\text{Group}_{ijl} \times \text{Fire}_{jl}) \\ & + \beta_6(\text{Elevation}_{jl} \times \text{Fire}_{jl}) \\ & + \beta_7(\text{Group}_{ijl} \times \text{Elevation}_{jl} \times \text{Fire}_{jl}) \\ & + \beta_8(\text{TSF}_{jlk}) + \beta_9(\text{TSF}_{jlk} \times \text{Fire}_{jl}) \\ & + \beta_{10}(\text{LBA}_{ijl}) + \beta_{11}(\text{DBH}_{ijl}) + \beta_{12}(\text{CVR}_{ijl}) \\ & + \beta_{13}(\text{Dieback}_{ijl}) + u_k + u_j + u_{jl} + \epsilon_{ijkl} \end{aligned} \quad (2)$$

Response variable $BC(rBAI_{ijkl})$ represents the transformed rBAI for tree i , on site j , within transect l , in year k . Fixed effects ($\beta_1, \beta_2, \dots, \beta_{13}$) include coefficient estimates for categorical variables (species group, transect elevation group, and fire occurrence) and their interactions, as well as the continuous predictors. The time-since-fire (TSF) term and its interaction with burned status ($\text{TSF} \times \text{Fire}$) account for the influence of time for both burned and unburned trees. Random effects represent the nested structure of our data and account for calendar year (u_k), site (u_j), and transect (u_{jl}) variations that are confounding factors not focal to this analysis. The variance structure of the residual errors (ϵ_{ijkl}) included an autoregressive term to account for within-tree temporal autocorrelation.

To analyze growth–climate relationships (*Question 3*), we fit linear models for annual RWI in the pre- and postfire periods for each climate variable identified in our moving window analysis—previous August CWD (pAugust CWD, in millimeter), January–March precipitation (Winter PPT, in millimeter), and mean April temperature (April T_{mean} , in degrees Celsius). This resulted in six models (one for each variable and period combination) with the form:

$$\begin{aligned} RWI_{ijk} = & \beta_0 + \beta_1(\text{Climate}_{ijk}) + \beta_2(\text{Fire}_{ijk}) \\ & + \beta_3(\text{Elevation}_{ijk}) + \beta_4(\text{Group}_{ijk}) \\ & + \beta_5(\text{Climate}_{ijk} \times \text{Fire}_{ijk}) \\ & + \beta_6(\text{Climate}_{ijk} \times \text{Elevation}_{ijk}) \\ & + \beta_7(\text{Climate}_{ijk} \times \text{Group}_{ijk}) \\ & + \beta_8(\text{Fire}_{ijk} \times \text{Elevation}_{ijk}) \\ & + \beta_9(\text{Fire}_{ijk} \times \text{Group}_{ijk}) \\ & + \beta_{10}(\text{Elevation}_{ijk} \times \text{Group}_{ijk}) \\ & + \beta_{11}(\text{Climate}_{ijk} \times \text{Fire}_{ijk} \times \text{Elevation}_{ijk}) \\ & + \beta_{12}(\text{Climate}_{ijk} \times \text{Fire}_{ijk} \times \text{Group}_{ijk}) \\ & + \beta_{13}(\text{Climate}_{ijk} \times \text{Elevation}_{ijk} \times \text{Group}_{ijk}) \\ & + \beta_{14}(\text{Fire}_{ijk} \times \text{Elevation}_{ijk} \times \text{Group}_{ijk}) \\ & + \beta_{15}(\text{Climate}_{ijk} \times \text{Fire}_{ijk} \times \text{Elevation}_{ijk} \times \text{Group}_{ijk}) \\ & + \epsilon_{ijk} \end{aligned} \quad (3)$$

where RWI_{ij} represents growth of a given chronology i in time period k as a function of climate variable j with fixed effects $\beta_1, \beta_2, \dots, \beta_{15}$. β_n represents the coefficient estimates for a given term and ϵ_{ijk} represents the residual error for given model.

RESULTS

Fire effects and forest structure

In the ATE, neighborhood stem density was similar between unburned spruce/fir and unburned whitebark/larch focal tree plots ($p = 0.974$; Figure 3, Table 2). However, unburned spruce/fir plots and whitebark/larch plots exhibited average stem densities that were over twice that of systematically placed plots ($p < 0.001$). This follows the density patterns predicted by the SGH, with greater aggregation of stems around focal trees compared to background densities at high-stress, high-elevation sites. In FPT transects, stem densities in unburned plots exhibited little to no evidence of difference from one another ($p = 0.243$, $p = 0.343$, $p = 0.999$), consistent with predictions for competition-dominated biotic interactions in low environmental stress locations.

A primary effect of fire was a decrease in mean neighborhood density (Figure 3; Table 2); however, the strength and consistency of these decreases differed between elevation groups. We observed a consistent decrease in density between burned and unburned spruce/fir neighborhoods and systematic neighborhoods in the FPT ($p < 0.001$), while there was less evidence of

consistent stem density reductions across whitebark/larch neighborhoods at this lower elevation band ($p = 0.102$). In higher elevation ATE transects, spruce/fir and whitebark/larch exhibited density reduction ($p = 0.042$, $p = 0.001$) while systematic plots showed more moderate evidence of reduction ($p = 0.077$). A study-wide summary of attributes by plot type and factorial combination is presented in Table 3.

Tree growth response to fire

Tree growth response differed across burn history, species group, elevation (FPT vs. ATE), and time (Figures 4 and 5). Time since fire was associated with increased relative growth in all factorial combinations. However, trees that experienced fire exhibited greater relative growth over time compared to trees in unburned locations (Figure 4). Time series of postfire growth showed immediate postfire declines for whitebark/larch that were not apparent in spruce/fir (Figure 4). Model results showed that larger trees (dbh), trees in crowded neighborhoods (LBA), and trees with crown dieback all had reduced relative growth compared to those with contrasting characteristics. On the other hand, trees with larger CVRs had

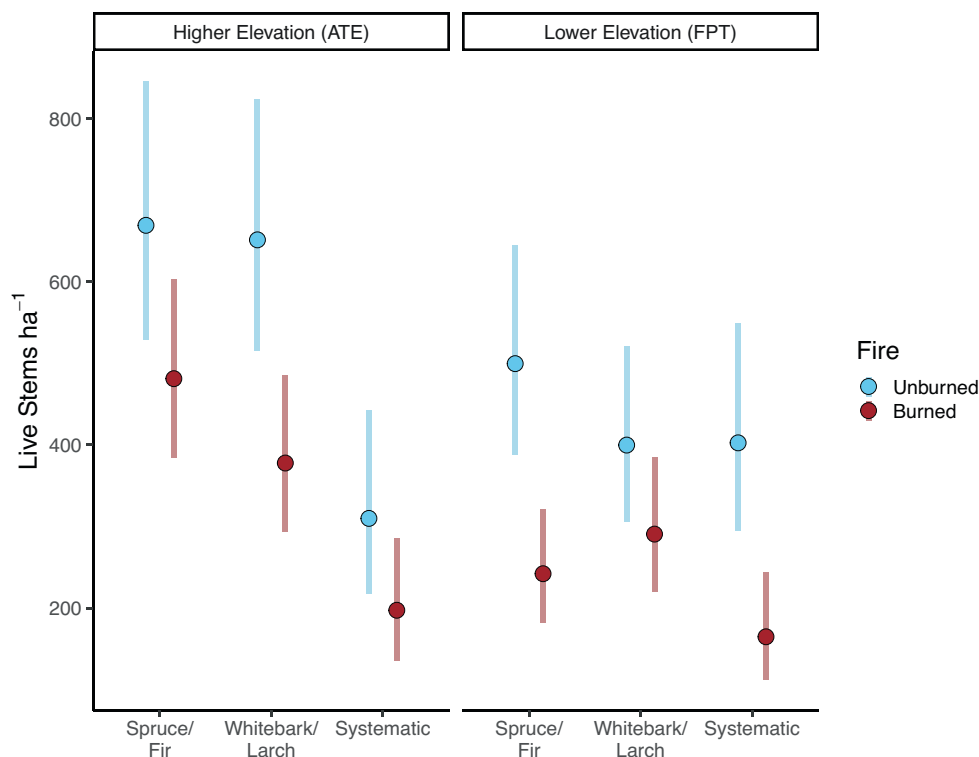


FIGURE 3 Estimated marginal means of live stem density per hectare with 95% CIs for each combination of crossed fire treatments (unburned, burned), plot type (spruce/fir, whitebark/larch, and systematic), and elevation zones within the alpine treeline ecotone (ATE; higher elevation, higher stress) and forest-parkland transition (FPT; lower elevation, lower stress).

TABLE 2 Pairwise contrasts for estimated marginal means (EMM) derived from stem density GLMM.

Contrast	Elevation stratum	Plot/transect type	Ratio	SE	<i>p</i>
Unburned × Burned	ATE	Spruce/fir	1.390	0.225	0.042
Unburned × Burned	FPT	Spruce/fir	2.062	0.398	<0.001
Unburned × Burned	ATE	Whitebark/larch	1.724	0.290	0.001
Unburned × Burned	FPT	Whitebark/larch	1.375	0.268	0.102
Unburned × Burned	ATE	Systematic	1.570	0.400	0.077
Unburned × Burned	FPT	Systematic	2.440	0.624	0.000
Spruce/fir × Whitebark/larch	ATE	Unburned	1.027	0.127	0.974
Spruce/fir × Systematic	ATE	Unburned	2.158	0.393	<0.001
Whitebark/larch × Systematic	ATE	Unburned	2.101	0.379	<0.001
Spruce/fir × Whitebark/larch	FPT	Unburned	1.250	0.173	0.243
Spruce/fir × Systematic	FPT	Unburned	1.241	0.192	0.343
Whitebark/larch × Systematic	FPT	Unburned	0.993	0.162	0.999
Spruce/fir × Whitebark/larch	ATE	Burned	1.273	0.176	0.189
Spruce/fir × Systematic	ATE	Burned	2.437	0.474	<0.001
Whitebark/larch × Systematic	ATE	Burned	1.913	0.382	0.003
Spruce/fir × Whitebark/larch	FPT	Burned	0.833	0.138	0.514
Spruce/fir × Systematic	FPT	Burned	1.468	0.301	0.146
Whitebark/larch × Systematic	FPT	Burned	1.762	0.375	0.021

Note: Ratios and SE indicate difference between the two groups and associated uncertainty. Full model output summary is available in Appendix S2: Table S4. Abbreviations: ATE, alpine treeline ecotone; FPT, forest–parkland transition.

slightly higher growth across our study. Within functional groups, species-specific responses differed in some cases. Most notably, subalpine larch that experienced fire in the FPT showed a positive growth response—relative to unburned trees—after 6 years postfire, whereas WBP did not (Appendix S2: Figure S3). Species-level responses were not analyzed statistically due to small sample sizes for subalpine larch and Engelmann spruce.

Differences in EMM of transformed rBAI over the 10-year postfire period show that spruce/fir individuals that experienced fire had greater increases in average relative growth in both elevational strata compared to whitebark/larch (Figures 4B and 5). Spruce/fir in the FPT that burned had the largest magnitude increase across all species × elevation groups, nearly doubling average growth over the 10 years postfire ($p < 0.001$). Postfire growth of whitebark/larch exhibited strong temporal trends whereby growth was reduced in the years immediately following fire but recovered to levels greater than adjacent unburned trees after approximately 6 years. EMMs for whitebark/larch that burned in the FPT indicate that growth did not differ from unburned conspecifics when averaged over the 10 years postfire ($p > 0.9$); however, these species did show a small growth increase in ATE transects over that same period ($p = 0.01$).

Effect of fire on climate–growth relationships

Average climate across our sites has trended warmer and drier over the last century, albeit with pronounced interannual variability (Figure 6). In particular, winter precipitation (January–March) has steadily declined while August CWD has increased slightly. Across all groups, differences in climate–growth correlations were more pronounced between periods (prefire vs. postfire) than between burned and unburned neighborhoods (Figure 7; Appendix S2: Table S5), indicating that regional climate trends over time were more important than fire history.

Baseline climate–growth relationships in the prefire period were consistent among groups; winter precipitation and previous August CWD exhibited clear negative relationships with RWI (Figure 7; Appendix S2: Table S5), and April mean temperature showed a positive relationship. Coefficients pertaining to winter precipitation shifted for all groups in the postfire period, and these shifts were group-specific. The clear negative effect of winter precipitation on growth during the prefire period became neutral for spruce/fir and slightly positive for whitebark/larch, coinciding with the downward trend in winter precipitation between these two periods

TABLE 3 Summary of forest structure for all sites across full factorial study design (means for each group across all sites ± 1 SE).

Forest type	Fire status	Focal tree dbh (cm)	Live basal area ($\text{m}^2 \text{ha}^{-1}$)	Snag basal area ($\text{m}^2 \text{ha}^{-1}$)	Live stems (ha^{-1})	Dead stems (ha^{-1})
Alpine treeline ecotone (ATE)						
Spruce/fir	Burned	28.9 ± 0.8	18.6 ± 2.4	12.4 ± 2.4	537.0 ± 51.3	147.9 ± 23.5
	Unburned	26.1 ± 0.6	20.7 ± 2.0	16.3 ± 2.4	695.7 ± 53.2	199.1 ± 28.5
Whitebark/larch	Burned	34.2 ± 1.3	12.5 ± 1.8	7.8 ± 1.7	351.4 ± 48.9	137.9 ± 27.6
	Unburned	28.7 ± 0.9	19.7 ± 2.4	12.9 ± 2.2	677.7 ± 73.6	246.1 ± 43.1
Systematic	Burned	...	5.9 ± 1.6	5.8 ± 1.7	165.3 ± 50.1	107.1 ± 33.7
	Unburned	...	7.3 ± 1.6	4.3 ± 1.6	280.2 ± 58.7	86.0 ± 33.4
Forest–parkland transition (FPT)						
Spruce/fir	Burned	36.8 ± 1.7	12.2 ± 1.6	5.1 ± 1.3	336.6 ± 35.6	72.4 ± 13.6
	Unburned	36.5 ± 2.1	36.5 ± 3.4	7.3 ± 1.2	656.3 ± 57.3	111.8 ± 15.4
Whitebark/larch	Burned	33.1 ± 1.3	12.0 ± 2.0	8.3 ± 1.7	326.0 ± 36.0	128.9 ± 25.7
	Unburned	38.8 ± 1.9	25.6 ± 2.8	6.1 ± 1.4	442.5 ± 41.5	118.9 ± 20.7
Systematic	Burned	...	6.0 ± 1.7	5.4 ± 1.8	153.2 ± 34.8	77.7 ± 30.0
	Unburned	...	0.5 ± 5.6	8.5 ± 2.5	440.5 ± 71.8	74.4 ± 18.9

(Figure 6). The negative relationship with previous August CWD remained constant for all groups in the postfire period (Figure 7). Coefficients for April mean temperature remained similar across groups and time periods. Elevational position (FPT vs. ATE) did not have an influence on interannual climate–growth relationships (Appendix S2: Table S5).

DISCUSSION

Forest structure and fire effects

The presence of a large focal tree in ATE sites was associated with a twofold increase in stem density as compared to systematically located points. This was not the case in FPT transects where we observed similar densities near focal trees and systematic points, indicating differences in the spatial distribution of trees between our two strata. The observed shift from even dispersion in the FPT to strong clustering in the ATE follows the patterns predicted by the SGH (Callaway, 1998; Dearborn & Danby, 2020). Facilitation promotes positive density dependence (Callaway, 1998, 2007), while competitive exclusion produces a more spatially uniform distribution of trees (Kenkel, 1988; Larson et al., 2015). Other processes that may play a role in the long-term development of tree spatial distributions include patterns of seed dispersal (e.g., Seidler & Plotkin, 2006) and/or strong abiotic microsite effects (Resler et al., 2005). However, there was no indication of these mechanisms

acting in a consistent manner throughout our study given the topographic heterogeneity across sites and differences in seed dispersal mechanisms between our focal species (both animal and wind). As such, changes in tree–tree interactions appear to be the most likely explanation for the patterns we observed over this elevational stress gradient.

Burned plots generally exhibited lower stem densities than their unburned counterparts. However, there was variation in the magnitude of density reduction across elevations and plot types. This variation is likely attributable to differences in prefire density, postfire development, and local fire severity. Microsite effects may partially explain the lower magnitude reductions we observed in burned larch plots at lower elevations given that subalpine larch are known to prefer moist, rocky microsites which may act as fire refugia (Arno & Habeck, 1972). Contemporary WBP populations have experienced high adult mortality at the hotter, drier trailing edge of their distributional range, and survival at lower elevation may increasingly depend on cooler, more mesic site conditions (Young et al., 2023). Both of these trends suggest whitebark/larch in lower elevation transects were more likely to be located in cooler, wetter microsites which may have experienced reduced fire severity. In the case of ATE systematic plots, the patchy tree cover at this elevation (Figure 3) is associated with more variable fire effects (Cansler et al., 2018), which may explain the less clear reductions we observed. Despite this variability, fire acted as a mechanism to reduce neighborhood stem density but did not disrupt

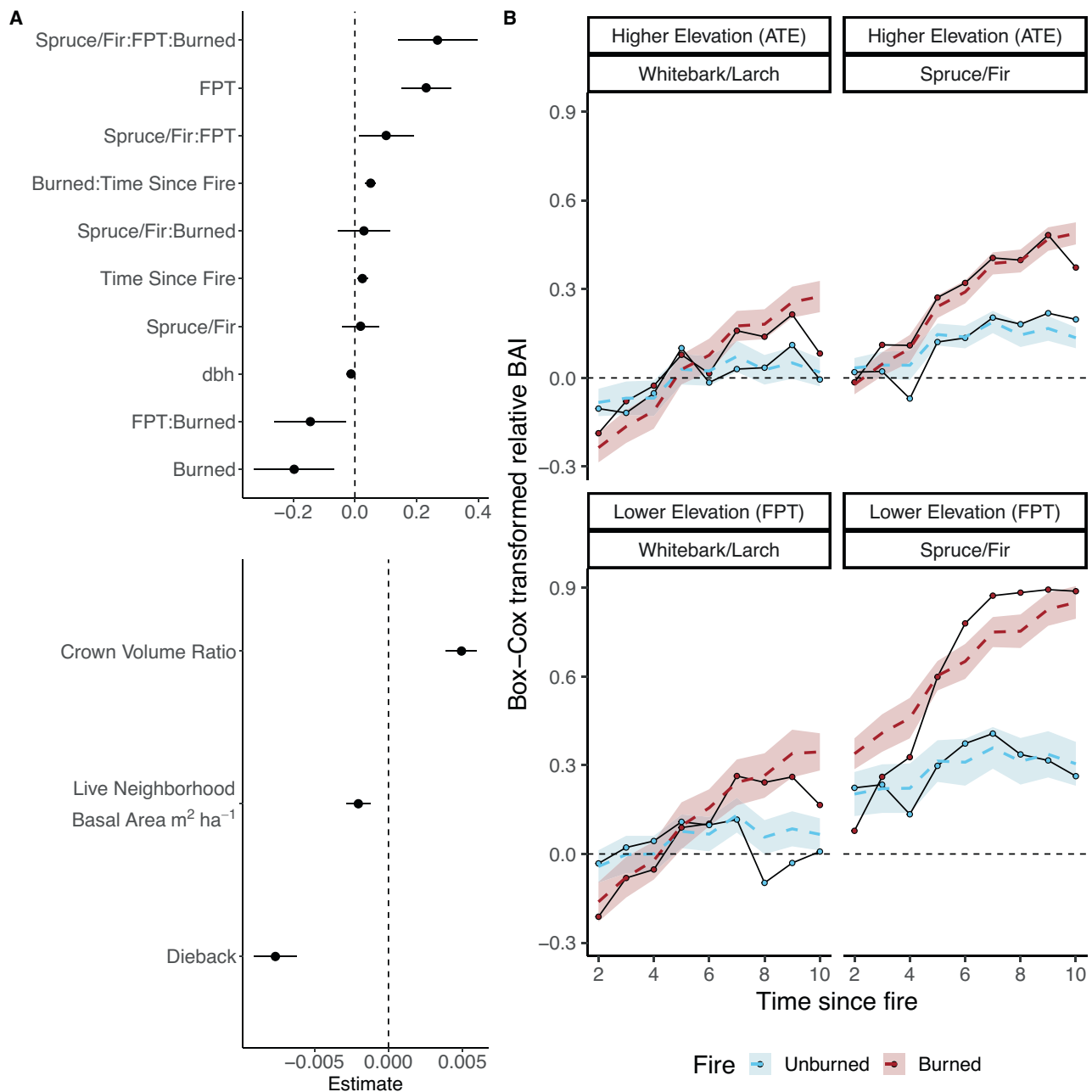


FIGURE 4 (A) Coefficient plot (estimate ± 2 SE) for model of Box-Cox transformed 10-year relative basal area increment (rBAI) predicted from individual trees across all sites and (B) observed means (circles, solid lines) overlaid with model predicted means and 95% CIs (dashed lines, shaded areas). Burned and unburned trees are summarized by species group and elevation zone across the alpine treeline ecotone (ATE; higher elevation, higher stress) and forest–parkland transition (FPT; lower elevation, lower stress). Different scales were used for the x-axis of coefficient plots in (A) to better visualize small coefficients.

the stem density patterns we observed in adjacent unburned sites in a meaningful way.

Residual tree growth response to fire

The strong, positive growth response of spruce/fir that experienced fire in the FPT relative to unburned trees in

the same group (Figures 4 and 5) supports our hypothesis that these species would see the greatest benefit of reduced competition from declines in neighborhood density. However, we did not observe the expected negative responses of beneficiary species in the ATE and instead detected a more muted, positive response (Figures 4 and 5). This suggests that competition remained the dominant mode of interaction between trees in ATE transects

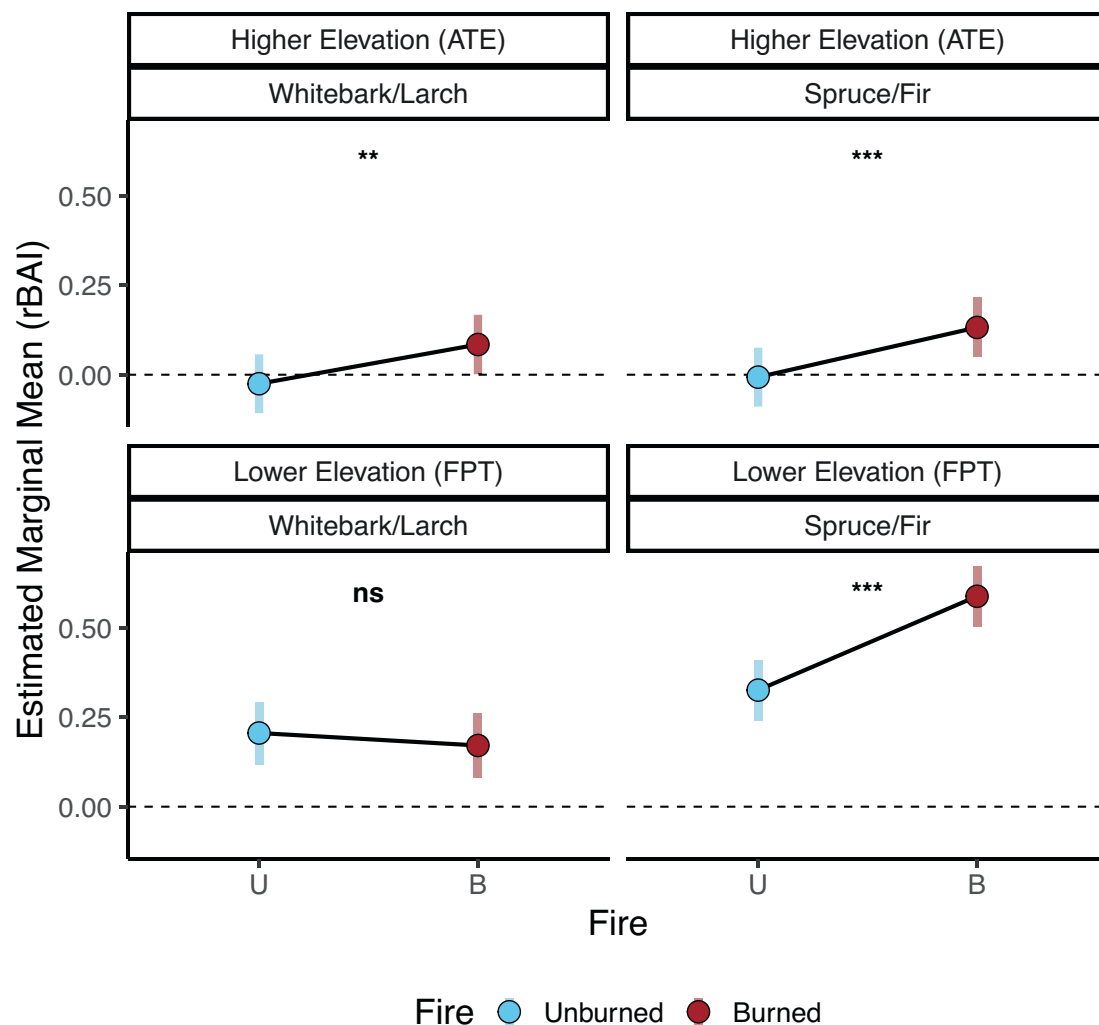


FIGURE 5 Estimated marginal means of unburned and burned categories across plot type $\times$ elevation interactions. Elevational strata are alpine treeline ecotone (ATE; higher elevation, higher stress) and forest–parkland transition (FPT; lower elevation, lower stress). Points represent estimated marginal means, and shaded bars represent 95% CIs. Differences between mean estimates were assessed via two-sample t test for each plot type $\times$ elevation. Asterisks denote significance for pairwise comparisons ($*p < 0.05$, $**p < 0.01$, $***p < 0.001$, $ns = p > 0.05$).

when fire occurred, although the lower magnitude response indicates that trade-offs between competitive and facilitative interactions were likely more pronounced at higher elevations.

Observable beneficial outcomes resulting from facilitation are the result of a “net effect,” wherein positive (i.e., facilitative) interactions outweigh the impact of negative (i.e., competitive) interactions (Callaway, 2007) that are occurring simultaneously. Given that the strength of positive interactions is greater with increasing stress (Callaway, 2007; Maestre et al., 2009), moderate stress could create a scenario where net tree–tree interactions are closer to neutral. Declining winter precipitation at our sites (Figure 6) provides the most likely explanation for mechanisms that may be shifting the balance of tree–tree interactions. Reduced winter precipitation

results in decreased snowpack, extending growing season duration and leading to increased growth, as observed in subalpine fir populations in the North Cascade Mountains (Peterson & Peterson, 1994) and WBP populations in the Sierra Nevada (van Mantgem et al., 2023). As directional climate change attenuates environmental stress in high-elevation forests, negative impacts stemming from the loss of facilitators may be compensated for by the benefits of competition reduction under less stressful conditions.

Growth response to fire in whitebark/larch followed our predictions at ATE sites (neutral to slightly positive). However, the lack of response in lower elevation transects contrasts with the clear release in spruce/fir individuals at that elevation (Figures 4 and 5). WBP growth response to density reduction treatments is often variable

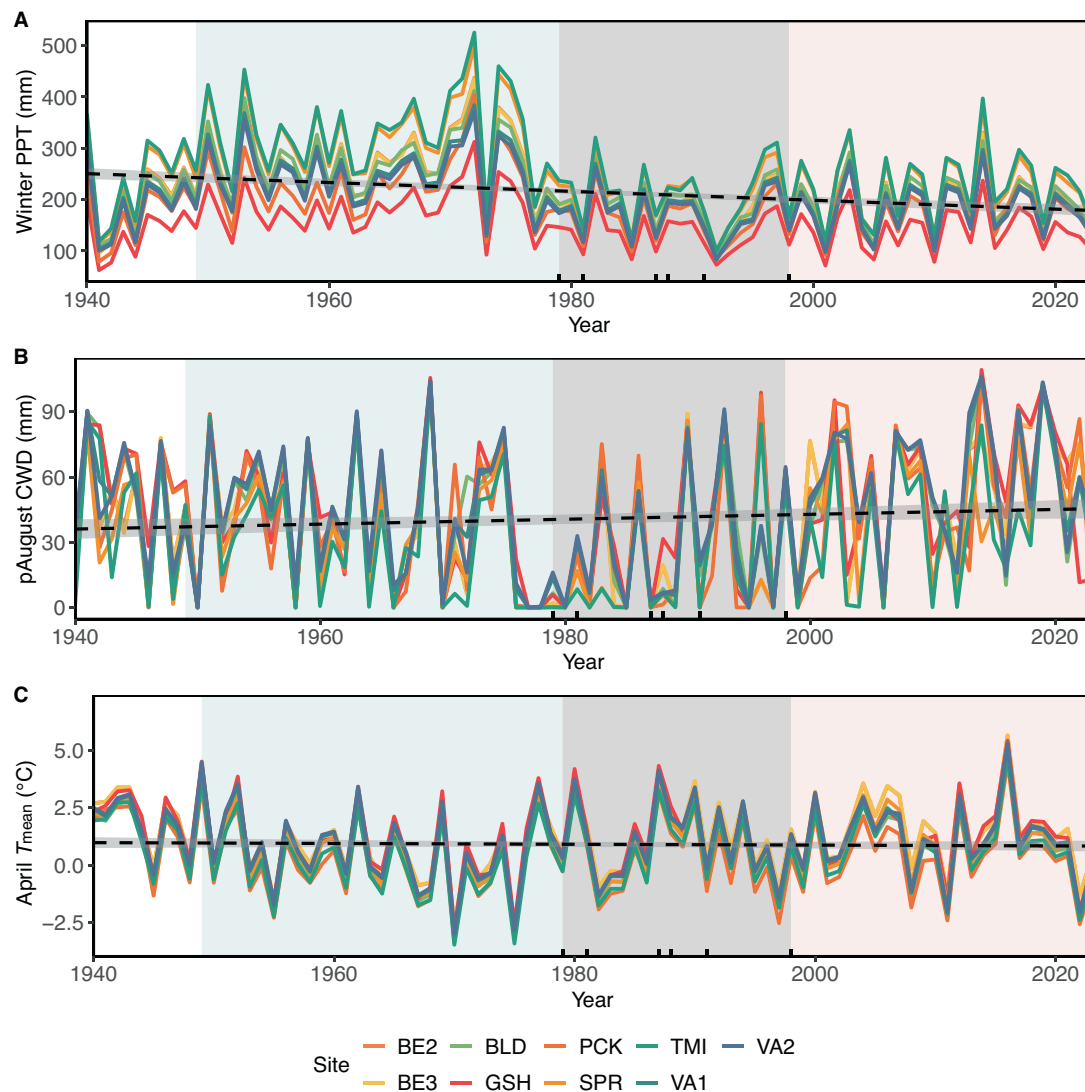


FIGURE 6 Time series showing (A) winter precipitation (PPT) from January to March, (B) summer climatic water deficit (CWD) in August of the previous year, and (C) mean April temperature (T_{mean}) from 1940 to 2023. Colors denote sites—values represent site-level averages (across elevation and fire transects). The dashed black line represents the linear trend for all sites during the displayed period. Blue and red shading indicates years before and after all fires, respectively. Gray shading delineates the period when fires occurred, rug plots indicate specific fire years.

in high-elevation stands (Maher et al., 2018; Retzlaff et al., 2018) though more consistent positive responses have also been observed (Kichas et al., 2024). In subalpine forests at elevations below our FPT stratum, response to competition reduction is expected to be uniformly positive (Keane et al., 2007). Species-specific responses within the whitebark/larch functional group (Appendix S2: Figure S3) indicate that subalpine larch in the FPT benefitted from fire—relative to unburned trees—but WBP did not. This discrepancy may in part be explained by the range-wide reductions in the growth of WBP during the latter half of the 20th century—not observed in subalpine larch—potentially related to nonlinear snowpack dynamics (Kipfmüller, 2008;

Youngblut & Luckman, 2013) or species-specific threats such as WPBR and MPB favoring survival of trees that prioritize defense at the expense of radial growth (Kichas et al., 2020).

The negative effects of postfire neighborhood density and crown dieback, as well as the positive effect of CVR (Figure 4A) follow the expectations that trees with well-developed, undamaged crowns (Camarero et al., 2022; Pretzsch, 2021), and trees growing with less density-dependent competition (van Mantgem et al., 2018; Wenderott et al., 2022) will show increased postfire growth. However, determining the direction of causality is limited by our retrospective approach. Crown measurements were taken decades after the fire events, making it

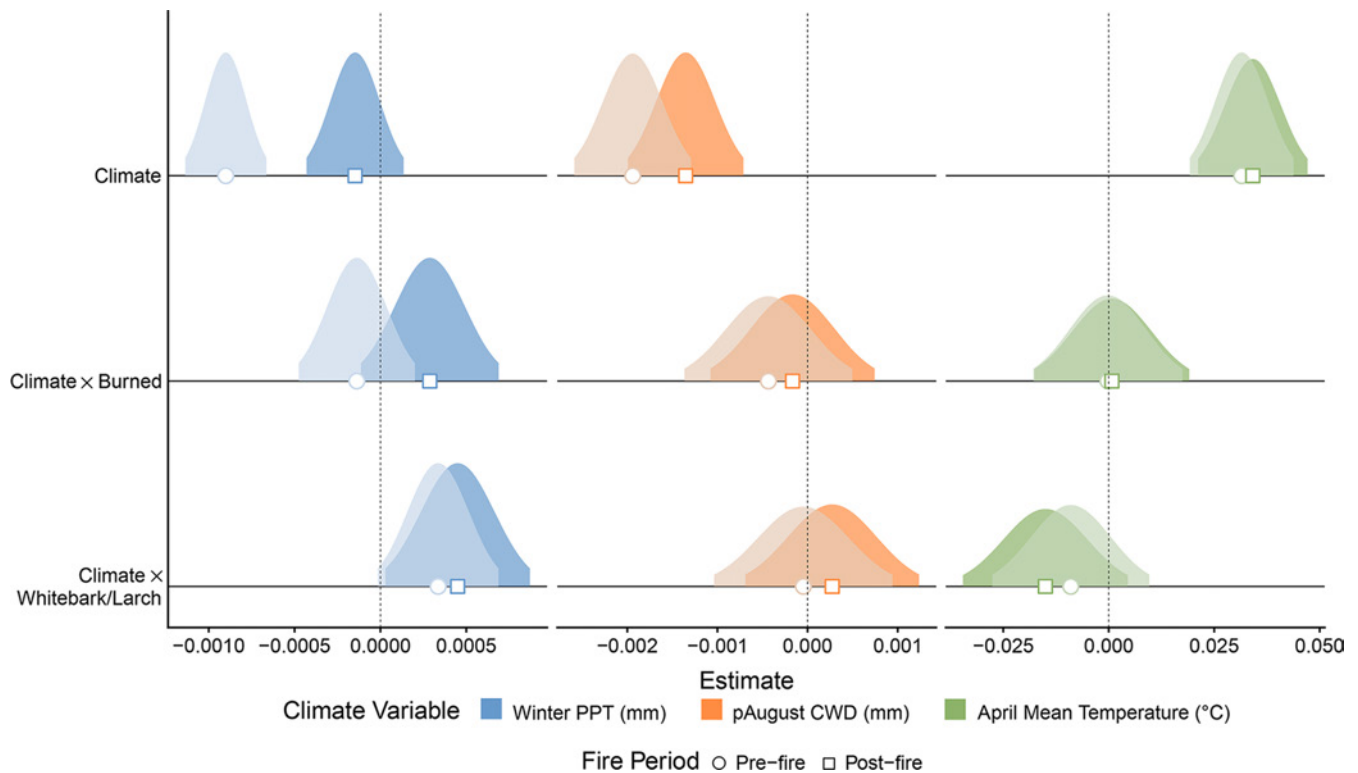


FIGURE 7 Coefficient estimates and their associated uncertainty (visualized as normal distributions) for the effects of winter precipitation (PPT), April mean temperature, and previous August climatic water deficit (pAugust CWD) on ring width index (RWI). Each estimate is derived from a separate model fit for a given variable in the prefire period (circles) or postfire period (squares) with RWI as the response. Distributions that do not overlap zero (vertical dashed lines) indicate statistical significance at $\alpha = 0.05$.

impossible to discern if trees that benefitted from competition reduction responded positively with increased crown volume and resistance to dieback, or if trees that were already more vigorous were able to respond with a greater increase in growth. Similarly, we cannot speak directly to the prefire stand structure or quantify the relationship between neighborhood mortality and magnitude of growth release; rather, we must rely on adjacent unburned transects as a reference. Such limitations are inherent to studying these dynamics in a congressionally designated wilderness area where experimental manipulation is prohibited.

Effect of fire on climate–growth relationships

Our climate–growth analysis indicates that the sensitivity of growth to climate in trees which experienced fire did not differ from their undisturbed counterparts. Rather, directional environmental change at our sites during the period of study appears to have eclipsed any potential interactive effects with disturbance (Figure 7). We expected that because fire reduces neighborhood

competition, trees in low-stress environments which experience fire would respond more strongly to favorable growing conditions (see Ford et al., 2016). We also expected that where positive interactions were occurring, the opposite might be true—trees would face greater exposure to conditions which negatively affect growth in the absence of facilitators and show stronger negative responses as a result. Despite evidence in closed canopy systems that competition is a more important driver of growth than climate (Clark et al., 2011; Ford et al., 2016; Sánchez-Salguero et al., 2015), our results here suggest that directional climate change over the last half-century in the high-elevation forests of the northern Rocky Mountains has outweighed any potential effects of disturbance on climate–growth relationships.

Warmer, drier conditions brought on by current climatic trends may shift the primary growth control in high-elevation tree populations from energy limitation (i.e., low temperature growth inhibition and/or short growing season length) towards moisture limitation (i.e., unmet evaporative demand limiting carbon gain and subsequent radial growth) (Dudney et al., 2023). The negative relationship we found between winter precipitation and growth in the prefire period is indicative of energy

limitation and consistent with previous work in WBP (Kichas et al., 2020, 2024; van Mantgem et al., 2023) as well as subalpine fir and Engelmann spruce (Peterson et al., 2002; Peterson & Peterson, 1994). The deterioration of this relationship in the postfire period suggests that the magnitude of winter precipitation—likely acting through reduced growing season length via greater snowpack depth and snow cover duration, as well as snow-caused physical damage (Nykänen et al., 1997)—is no longer adequate to act as a strong limitation on growth. Furthermore, the emergence of a positive relationship between growth and winter precipitation for whitebark/larch (Figure 7) may indicate a shift towards moisture limitation, with low snow years potentially leading to unmet evaporative demand during the growing season.

The changes we observed regarding the role of winter precipitation in governing growth are reflected by its general downward trend during our study period (1949–2023; Figure 6), and the shift between our two periods corroborates other lines of evidence for a climate change breakpoint in the western United States during the early 1980s (Perret et al., 2024). Tree growth relationships in subalpine environments can also be sensitive to intermediate climate variability (Nakawatase & Peterson, 2006; Peterson et al., 2002) driven by processes such as the Pacific Decadal Oscillation (PDO) (Mantua & Hare, 2002). However, PDO trends have been quite variable during most of our postfire period (2000–2020) (Xiang et al., 2024), suggesting the shifts we observed are the result of broader directional climate change rather than annual to decadal oscillations.

The strength and consistency of previous August CWD as a constraint on growth in high-elevation forests aligns with trends observed in several of our focal species across other regions (Peterson et al., 2002; Peterson & Peterson, 1994). Potential mechanisms for this relationship include carbohydrate depletion due to increased respiration and stomatal closure under drought conditions (McDowell et al., 2008) or diversion of resources to cone production following warm, dry years (Woodward et al., 1994). Trees in high-elevation forests actively store carbohydrates during the growing season (Li et al., 2018); however, the ultimate fate of that carbon—whether for long-term storage (Huang et al., 2021), osmoregulation (Badalotti et al., 2000), reproduction (Woodward et al., 1994), or cold tolerance (Ögren et al., 1997) can be difficult to discern. In our case, we are limited to our measurements of radial growth, but these findings provide further motivation for research to disentangle mechanisms related to carbon allocation in high-elevation tree species.

CONCLUSIONS AND IMPLICATIONS FOR FUTURE HIGH-ELEVATION FOREST DYNAMICS

Our results suggest that as shifting fire regimes and climate continue to impact the high-elevation forests of the northern Rocky Mountains, the growth response of trees will not be uniform. Specifically, contemporary postfire conditions seem to favor enhanced growth of residual spruce/fir, especially those individuals at lower elevations, while unmanaged fire in lower elevation WBP stands risk mortality without any clear benefit (i.e., growth release) for surviving trees.

While spatial patterns of stem density indicate that facilitation influenced historical forest structural development within our high-elevation transects (Callaway, 1998; Dearborn & Danby, 2020), the environmental stress gradient we sampled appears to have moderated in recent decades. Contemporary environmental conditions appear to be driving net-competitive interactions such that the beneficiary spruce/fir functional group responded to fire with growth increases even in ATE sites. The changes we observed in the direction and magnitude of relationships between winter precipitation and growth provide a general mechanism for the weakening of winter climate as a constraint on growth in these forests. These changes appear to be driven by temporal period more so than disturbance history, indicating that directional climate change has superseded the role of biotic interactions in governing growth near treeline.

AUTHOR CONTRIBUTIONS

Josh Beisel, C. Alina Cansler, Sean A. Parks, and Andrew J. Larson conceived the project and research hypotheses. Josh Beisel carried out field data collection, processing, analysis, visualization, and wrote the first draft of the manuscript. David L.R. Affleck and Ashley P. Ballantyne assisted with statistical methods and analysis. All authors contributed detailed revisions to the manuscript and approved the final version.

ACKNOWLEDGMENTS

Funding for this research was provided by the USFS Rocky Mountain Research Station (agreement number 19-JV-11221639-098). Additional support was provided by the BYU Redd Center. We thank the USFS Selway-Bitterroot Wilderness management team for their assistance in facilitating our fieldwork; specifically, Matthew Anderson and Cheryl Probert for their help with permitting and approval, as well as Kearstin Edwards and Jacob Long for their support with field logistics. We also thank Sharon Hood, Charlotte Reed, Mark Kreider, and

Colin Maher for their help with methods related to dendrochronology. Field data collection would not have been possible without the hard work and diligence of technicians Olivia Vergin, Hayes Henderson, and Meg Leonardi. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or US Government determination or policy.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Beisel, 2026) are available from Figshare: <https://doi.org/10.6084/m9.figshare.31356322>.

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SUPPORTING INFORMATION

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

How to cite this article: Beisel, Josh, C. Alina Cansler, Sean A. Parks, David L. R. Affleck, Ashley P. Ballantyne, and Andrew J. Larson. 2026. "Climate Change and Fire Alter Biotic Interactions and Tree Growth in High-Elevation Forests." *Ecosphere* 17(4): e70612. <https://doi.org/10.1002/ecs2.70612>