Growth and spatial patterns of natural regeneration in Sierra Nevada mixed-conifer forests with a restored fire regime

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ABSTRACT

Many dry conifer forests in the western United States were historically adapted to frequent low-to-moderate severity fires, but are increasingly susceptible to large, stand-replacing wildfires due to dramatically altered stand conditions and changing climate. The historic tree spatial patterns of mature stands in fire-adapted forests – individual trees, clumps of trees, and openings (ICO) – are associated with heightened resistance and resilience to fire. How this pattern develops over time, however, is not well understood and could help inform reforestation practices better designed to increase fire resistance in developing stands. We investigated growth rates and spatial patterns among regenerating trees in mixed-conifer forests with restored fire regimes in California's Sierra Nevada. We compared average stocking densities across tree species, size classes, shrub cover, and fire histories. We also examined the effects of microsite topography on spatial patterning of these juvenile trees, and the effects of clump patterning, local stem density and adjacent shrubs on tree growth rates. We found that the majority (75%) of sampled stems were found in clumps. Our mixed-effect models indicated that for trees growing within clumps, increased crowding slowed tree growth, as expected. Surprisingly, however, compared with individual trees growing outside clumps, trees growing within clumps grew significantly faster. Shrub cover in proximity to juvenile trees did not have a consistent impact across our models, but was associated with increased annual height growth. Additionally, plots with high shrub cover had higher stocking rates among the tallest regenerating stems (height > 137 cm). Our findings indicate that clumped spatial patterns of natural tree recruitment may favor the establishment and early growth of regenerating conifers in active-fire forests. While our study focused only on the early stages (<30 years old) of regeneration, our results contrast with common reforestation strategies favoring regular, widely-spaced plantings and aggressive shrub reduction. Our research suggests we need a better understanding of how heterogeneity in the spatial patterns of juvenile trees and shrubs may enhance the resilience of regenerating stands as they mature.

1. Introduction

Historical and contemporary forests with active fire regimes, including mixed-conifer and yellow pine forest types, had frequent (<30 years) low-intensity fire regimes that strongly influenced (and were influenced by) their spatial structure, composition and ecological functions (Steel et al., 2015). However, intensive and widespread fire-suppression during most of the past century has produced dense, homogeneous stands susceptible to high-severity wildfires (Stephens et al., 2016). Recent research has shown that highly heterogeneous tree spatial patterns characterized by individual trees (I), clumps of trees (C), and openings (O) (hereafter, ICO) (Fry et al., 2014; Kane et al., 2019; Lydersen et al., 2013) can result in greater stand resilience, in part because it slows fire spread and decreases the potential for crown fires, especially at local scales (Churchill et al, 2013, Koontz et al., 2020). This spatial heterogeneity of frequent-fire forests may also support a range of other important ecosystem functions across spatial scales (Churchill et al., 2018). These include providing variable microclimates (Ma et al., 2010; Norris et al., 2012), with different temperature and moisture niches leading to greater understory plant diversity (Wayman and North, 2007; Knapp et al., 2013; Stevens et al., 2016), and increased snow retention (Stevens, 2017). The variability in structure ranging

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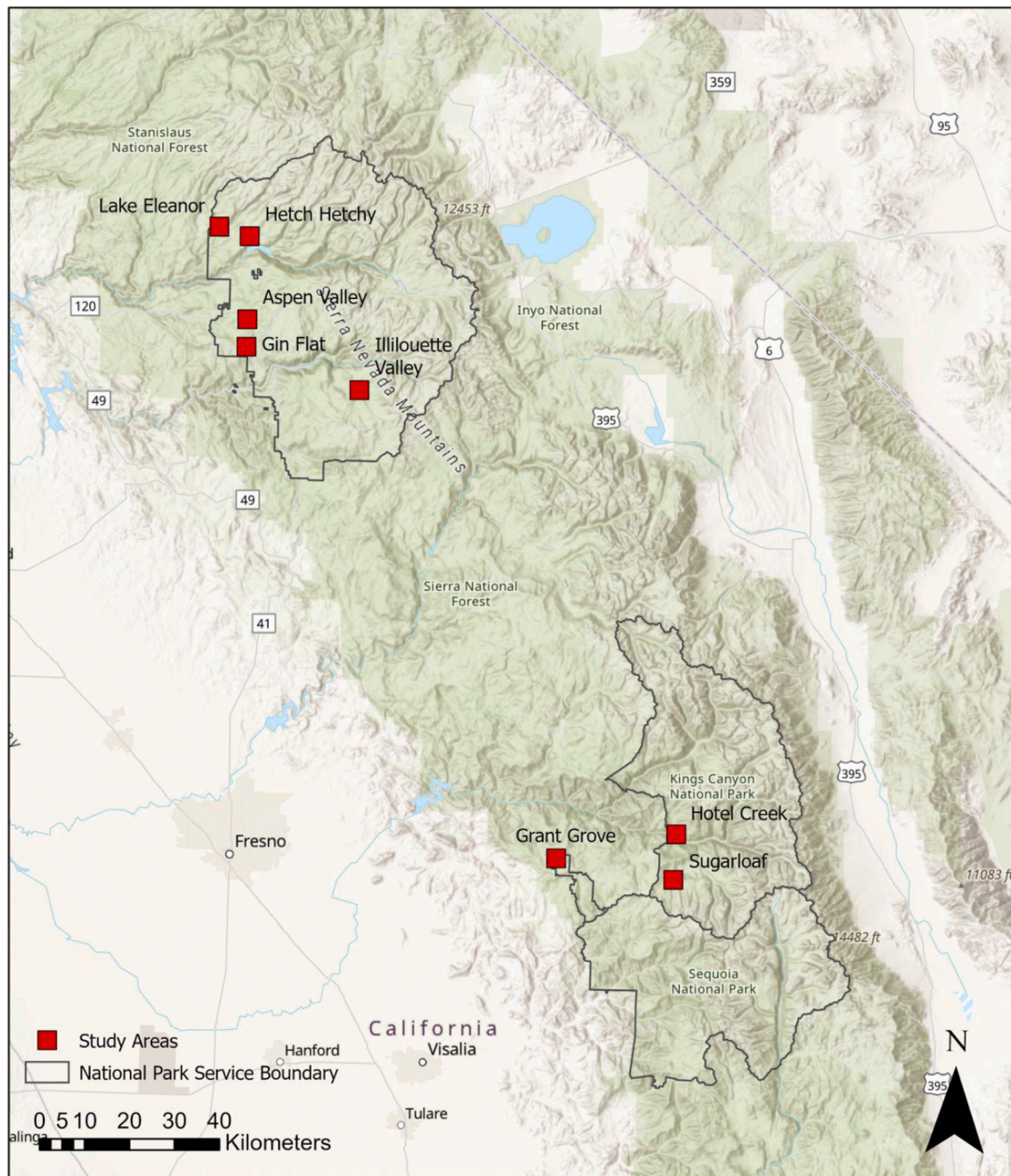*E-mail address:* hmfertel@berkeley.edu (H.M. Fertel).

Fig. 1. Map of study areas sampled in California's Yosemite and Sequoia and Kings Canyon National Parks in 2019 and 2020.

from dense patches to sparse open areas also provides a diverse suite of habitats for wildlife species (Meyer et al., 2007; Steel et al. 2022).

The patchy "mosaic" structure characteristic of frequent fire forests is believed to be rooted both in the high-frequency, low-severity fire regime and the highly heterogeneous, clumped regeneration patterns of these forest types (Larson and Churchill, 2012; North et al., 2019). As frequent low-to-moderate severity fires historically swept through the forest with high spatial variability, small gaps and openings in the forest canopy as well as understory patches of bare mineral soil were created, providing favorable microsites for young regenerating seedlings (Larson and Churchill, 2012). As these trees aged, repeated disturbance and

intra-clump competition may have led to the highly heterogeneous stands now identified as possessing "ICO" structure (Larson and Churchill, 2012; Stephens and Fry, 2005; Churchill et al., 2013). Though a small number of studies in pre-suppression (pre-1910) and modern reference sites have confirmed that regeneration patterns in Sierra Nevada mixed-conifer forest were likely highly heterogeneous with high-density clumps in forest canopy gaps, less is known about the dimensions and dynamics of seedling clumps, or to what extent clumped spatial patterning in these forest types might impact growth rates as regenerating stands mature (North et al., 2019).

With millions of hectares of forest now burning in Western North

American forests each year, and with an increasing proportion of those burns occurring at high severity (Hoover and Hanson, 2021; Miller and Safford, 2012), it is important to investigate both the stand conditions and management practices that promote the development and maintenance of fire-resilient forests. Much attention has been focused on restoring fire- resistant and -resilient western forests through reinstating historic fire regimes and strategically lowering fuel loads and tree densities, using prescribed fire and mechanical thinning (Innes et al. 2006, Larson and Churchill, 2012; North et al., 2021; North et al., 2009; Stephens, 2017). As forest spatial patterning is now recognized as an important influence on fire behavior (Koontz et al., 2020, Ziegler et al 2017; Ziegler et al., 2021), forest management strategies to improve resilience may focus on increasing structural heterogeneity in stands (Knapp et al. 2017; Prichard et al., 2021; Reynolds et al., 2013). However, design and implementation of treatments that accomplish these conditions at the landscape scale in mature forest stands are understudied and logistically complicated (Stephens et al., 2021).

One possible method for landscape-scale restoration of structurally heterogeneous and fire-resilient dry-conifer forests may be to focus on restoration "from the ground up" — i.e., through forest regeneration (North et al., 2019; Stevens-Rumann and Morgan, 2019) — and by supporting ecological processes that lead to heterogeneous stand structures. If larger patches of high severity become the norm, leading to a reduced likelihood of natural recruitment in burned areas from surviving seed sources (Welch et al, 2016), then reforestation practices are likely to become an even more critical component of landscape-scale forest restoration efforts in the future (Coop et al., 2020). Many current reforestation practices use a regularly-spaced planting pattern focused on regenerating fast-growing pines to help shade out competing vegetation, particularly shrubs that vigorously germinate and re-sprout after high-intensity fire (Coppoletta et al., 2016). For several decades after planting, however, this spatial pattern may be at increased risk for burning at high severity and, in the absence of natural recruitment, can produce regularly-spaced mature pine plantations (Zald and Dunn, 2017). While there could be fire resistance and ecological benefits to more varied planting patterns, to date there has been little research on different spatial planting patterns in part due to the greater challenges associated with design and implementation of irregular patterns. As manipulative experiments investigating the effects of clumped patterning on growth rates can be time consuming and costly to implement, a complementary approach is to analyze *in situ* growth and regeneration dynamics in areas with a restored frequent-fire regime.

1.1. Project objectives

Initial scouting of our study areas found a high degree of clumping (i. e., stems growing with overlapping neighborhoods of potential influence) among regenerating trees. To examine this further, we sought to quantify the establishment, growth, and spatial pattern of juvenile trees in old-growth, mixed-conifer forests with restored fire regimes, including a comparison of growth rates for clumped trees versus individual trees and for trees across clumps of different sizes and densities. Specifically, we focused on the following questions:

(1) What are the regeneration spatial patterns in active-fire forests (i. e., relative percentages of juvenile trees growing as individuals or in clumps by species), and how do they vary with tree age, site fire history, and topographic variables?
(2) What are the relationships between spatial patterns (i.e., individuals vs. clumps of varying sizes and densities) and growth

rates of juvenile trees, and how does this vary across species and tree age?
(3) How do site fire history and shrub cover affect juvenile tree growth and spatial patterns?

2. Methods

2.1. Study locations

Broad study areas for this project were selected among mature, unlogged stands in Yosemite National Park and Sequoia and Kings Canyon National Parks, located between 600 m and 2,100 m in elevation in California's Sierra Nevada Mountains (Fig. 1). Study areas were primarily in mixed-conifer and ponderosa pine forest types that historically experienced frequent low-to moderate-severity fires. Principal species included ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), and black oak (*Quercus kelloggii*). Less common species included western juniper (*Juniperus occidentalis*), lodgepole pine (*Pinus contorta*), and canyon live oak (*Quercus chrysolepis*), whose sample sizes were too small in our study to support statistical analysis.

Broad study areas were selected based on the criteria of having at least two fires in the past 60 years, with the most recent fire having occurred in the 20 years directly preceding 2018 (Lydersen and North 2012). These criteria were used to select areas that approximated the historical range of variation in fire return interval for the dominant forest types (Barrett et al., 2010) and based on an earlier study suggesting that two burns may drive dry western forest stands to approach pre-suppression structure (Taylor, 2010). Local sampling sites within the broad study areas were identified in ArcGIS Desktop 10.7 (ESRI 2018) using CAL FIRE Fire and Resource Assessment Program's (FRAP) Fire Perimeter dataset. We dissolved overlapping fire perimeters that met the selection criteria, creating individual polygons with a unique "fire history" consisting of the number of burns the site experienced and year of the most recent burn event. We then further filtered these polygons using CalVeg GIS database map identification to limit our sites to "mixed-conifer" or "ponderosa pine" forest types.

Identified local sampling sites were ground-truthed in the field to ensure that the species composition and overstory conditions were consistent with what was identified through remote site identification. Overstory stand conditions in these "active fire" forest types have been quantified in earlier publications (Lydersen and North, 2012; Ng et al., 2020). All study sites were in low and moderate burn severity areas where canopies were relatively open (mean percent canopy cover ranged between approximately 30% − 45%) and overstory tree densities were fairly low (see Ng et al., 2020, Tables 2 and 5).

2.2. Data collection

Data collection took place in eight broad study areas over two summer field seasons in 2019 and 2020. Each broad study area contained one or more local sampling sites, where sampling sites were classified by both the number of fires the site had experienced and time-since-last-fire, because these factors can affect the biotic community (McLauchlan et al., 2020). In total, this categorization resulted in 26 unique "fire histories" for our analysis to help determine what relationship may exist between number of burns, time since burn, and site regeneration patterns.

2.2.1. Circular plots

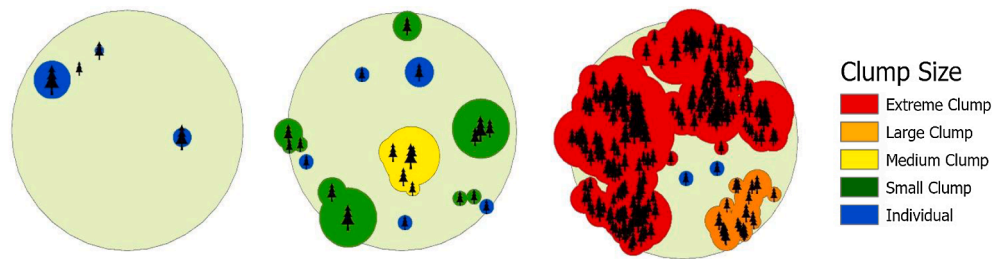Within each local sampling site, variable-diameter circular plots

Fig. 2. Example plots featuring different clump patterns and identified buffers ranging from very sparse with a few individual trees (plot on the far left) to highly clumped, dense patterning (plot on the far right).

were sampled to efficiently census regeneration and examine spatial patterns and density of seedlings. Plots were established in a grid pattern with a randomly generated starting point and azimuth, except in cases where the identified sampling site was too small to implement the grid pattern, in which case plots were randomly distributed (without overlap) in the site. The diameters of circular plots were determined by juvenile tree density, beginning at a plot diameter of 1 m and increasing in fixed gradations (2 m, 4 m, 5.64 m, 8 m, 12.6 m) until at least 20 stems were recorded or the maximum plot radius (12.6 m) was reached. Within each plot, we recorded species, height, ground diameter, condition (live or dead) and location relative to a GPS-recorded plot center (azimuth measured using a global sighting compass and distance measured to the nearest 0.01 m) for every regenerating stem ≥ 10 cm in height and < 5 cm in diameter at breast height (DBH, taken at 1.37 m). We limited our data collection to conifer and oak species. Stems under 10 cm in height were excluded due to their high mortality rate and probable ephemerality (Shepperd et al., 2006). The age of each regenerating stem was approximated using visual whorl counts (Hättenschwiler and Smith, 1999), with age estimates calibrated using destructive sampling of seedlings and saplings from locations outside of our study areas and National Park lands. Additionally, for each individual regenerating stem in our study, the percent shrub cover and dominant shrub species within a 2 m radius were recorded to estimate shrub cover effects on growth rate and spatial patterning. Physiographic information including aspect, slope, and GPS coordinates of plot center were recorded for each plot.

2.2.2. Belt transects

Within each local sampling site, we also sampled belt transects between circular plots or at randomly selected azimuths out from circular plots (without overlap) in order to census regeneration across landscape topographic changes. Transects were 25 m in length, and belt width varied with juvenile tree density. Each transect width began at 4 m and, for every 12 trees measured along the length of the transect, would subsequently shrink by half for the remaining length of the transect down to a minimum width of 1 m. This resulted in transect areas ranging from 100 m^2 in low density areas to a minimum of roughly 25 m^2 in extremely high-density areas. For every stem within the transects, we recorded species, height, ground diameter, and approximate age, as well as percentage shrub cover within a 2 m radius. We measured aspect and slope for each transect in the field; a subset of these incurred measurement errors and were subsequently extrapolated from a 1 m digital elevation model. We used this topographic data to categorize transects by cardinal direction and relative steepness: flat (1–15%), moderate (16–35%), and steep (>35%) slopes. Any changes in either variable were recorded along the transect to capture topographical variation across the sampling site.

2.2.3. Plot sampling summary

In total, we sampled 216 circular plots and 213 belt transects, with a final count of 9,915 stems. The total area sampled across all circular plots totaled over 6.5 ha of censused regenerating trees.

2.3. Analysis and modeling

All analyses were performed in R software V.3.6.3 (R Core Team 2020) unless otherwise noted.

2.3.1. Stem-mapping and clump spatial pattern detection

Location data for trees sampled in circular plots (azimuth and distance to the nearest 0.1 m from a GPS-recorded plot center) were used to generate spatially-explicit stem maps. We calculated the X and Y offset for each tree relative to plot center, then added the offsets to the UTM coordinates of plot center to generate a dataset with UTM coordinates for each measured tree. We used these tree coordinates, to generate a spatial point layer in ArcGIS Desktop 10.7 (ESRI 2018). Regenerating trees sampled within circular plots were categorized as either individual (i.e., growing alone) or clumped (i.e., members of clumps) to determine the impact of belonging to a clump on juvenile tree growth and mortality. To assess whether a given stem was a member of a clump, circular buffer polygons were generated outward from the base of each geolocated stem. The use of a user-defined buffer as a means of identifying clumped or singular trees through buffer overlap has been previously used for tree spatial pattern analyses (see Lydersen et al., 2013; Ng et al., 2020; Plotkin et al., 2002; Sánchez Meador et al., 2011), though not at the scale of regenerating seedlings or saplings. We assigned buffer diameters based on tree height (0.25 m for trees 10–49 cm, 0.50 m for trees 50–99 cm, 1.0 m for trees 100–137 cm, and 2.0 m for trees > 137 cm in height) to approximate a "neighborhood" of influence based on estimated lateral root spread. The lateral root spread of seedlings varies significantly across species and among individuals, and may be highly dependent on environmental and microsite conditions (Stein, 1978). In young conifer seedlings, root lengths tend to far outstrip shoot lengths and canopy spread, with this trend even more pronounced in arid and semiarid areas (Casper et al., 2003). Given these trends, our choice of buffer sizes is likely conservative (Stein, 1978; Casper and Jackson, 1997). To determine how our results might vary with different buffer sizes and resulting clump outcomes, we ran all analyses pertaining to clump identification with an additional range of buffer sizes, resulting in the following buffer schemas: a) base schema as described above, b) 25% larger, c) 25% smaller, d) equal to 0.5 m, or e) equal to stem height with a maximum buffer diameter of 2 m).

Regenerating trees were assigned either individual or clumped status based on the absence or presence of overlapping buffers. Overlapping buffer polygons were spatially dissolved to generate clump polygons, and stems within each given clump were summed inclusively to

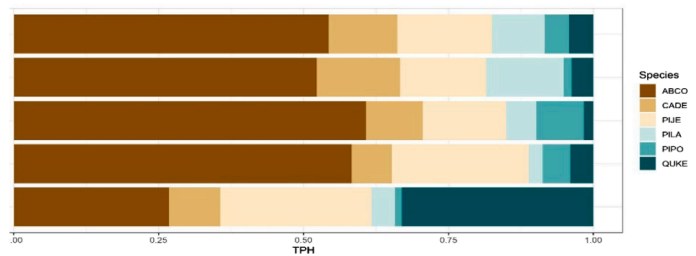| Height Class | Age Estimates (years) | | Species TPH Estimates | | | | | | |
	Mean(Median)	Range	ABCO	CADE	PIJE	PILA	PIPO	QUKE	All Species
All Regeneration >10cm	7 (6)	1-44	510	111	153	85	39	39	1,074
10-25 cm	3 (3)	1-33	241	66	68	61	7	17	520
25-75 cm	8 (8)	2-30	187	30	44	16	25	5	351
75-137 cm	13 (13)	4-35	48	6	19	2	4	3	93
>137 cm	18 (18)	5-44	12	4	12	2	1	15	65

Fig. 3. Table of stocking densities for juvenile trees by size class and species with adjacent graph showing relative proportions of species within each size class.

determine the number of trees in that clump. The number of trees in each clump was then used to label clumps (and their associated trees) with size categories to be used in determining the effect of clump size on growth metrics (Kane et al., 2019) (see Fig. 2 for example plots with clump size variation within and among plots). The size categories were: small clump (2–5 trees), medium clump (6–14 trees), large clump (15–49 trees), or extreme clump (>50 trees).

2.3.2. Summary Statistics: Stocking densities across species, height class, fire history, and shrub cover

We calculated stocking densities of regenerating stems using count data from our entire sampling effort (circular plots and belt transects combined), ultimately averaging across plots (weighted by relative plot size) to obtain estimates of average (mean) trees per hectare (TPH). We subdivided our estimates by species, topographic category, shrub cover, and fire history for comparison purposes. We also grouped TPH values by height class as a proxy for estimating stocking densities at different tree ages. We used height class values for our stocking density estimates rather than estimated ages as we wanted to include species that we were not able to age through whorl counts or felt less confident in our estimated ages (i.e., oak species).

2.3.3. Summary statistics: intra-cluster dynamics

Stem counts by species and clump size within circular plots were evaluated across topographic and specific site fire history to characterize establishment, clumping patterns, and density across the study area. To characterize demographic patterns, clumped trees were grouped by clump size category to obtain average number of species, average height, and standard deviation of height for each clump size. To compare diversity across clump sizes, we calculated within-clump diversity using Shannon's Diversity Index and within-clump evenness using Pielou's evenness metric. Both calculations utilized the Vegan R package (Oksanen et al., 2020). We then conducted ANOVA comparisons of calculated diversity metrics by clump size followed by Tukey's Honest Significant Difference (HSD) post hoc tests to determine if significant differences (α = 0.05) among clump size categories could be detected.

We calculated mean annual growth rates (two forms) for each regenerating tree by dividing the ground diameter and height of each stem by the estimated age of the tree. We averaged growth rates by species, clump status (i.e., if the tree was found as an individual versus in a clump of any size), and age group. ANOVA comparisons of calculated metrics were made (again, followed by Tukey's HSD post hoc tests) to test for differences (α = 0.05) in growth rates between clumped and individual trees across species and age classes.

2.3.4. Modeling effect of topographic variables and fire history on spatial pattern of juvenile trees

To evaluate the influence of topographic variables and fire histories on spatial patterning, we fit generalized linear mixed-effects models (GLMMs) using the glmer function in the lme4 R package (Bates et al., 2015) on clump and individual tree data from our circular plots. We used a binomial GLMM to model the probability that trees would be members of a clump versus growing as isolated individuals. Fixed effect variables included the number of fires on record during the last 60 years, timing of the most recent fire (categorized as recent:< 10 years or older: $\geq$ 10 years), slope (categorized as flat, moderate, or steep), aspect categorized as SW (180-270°) or non-SW (all other azimuths), and scaled continuous variables for elevation and tree age. To control for unmeasured differences among sites that might affect clump membership, we included sampling site as a random effect. Models were evaluated and selected based on Akaike's Information Criterion (AIC) scores, where a more complex model was selected if its AIC value was at least two points lower than the simpler model. Predicted bootstrapped probability estimates (n = 500) generated from an expanded grid combination of all predictor variable values (with continuous variables included at set intervals across the range of measured values) from our model were used to visualize and interpret our model results.

2.3.5. Modeling effect of spatial pattern on annual growth rate

Hierarchical Linear Mixed Effects Models were applied using the lme4 package function lmer (Bates et al., 2015) to compare how spatial pattern and specific fire site history affected annual growth rates of regenerating trees. Separate models were generated to look at diameter growth and height growth. For all growth rate models, we included plot as a random effect to control for unmeasured variation in small-scale local factors (e.g. light availability as influenced by overstory canopy, upper-strata soil moisture, etc.). Mean annual height and diameter growth for each juvenile tree were used as response variables. Scaled continuous variables for tree age and clump density, as well as categorical variables for tree species and clump size (levels of this variable were: individual tree, small clump, medium clump, large clump, and extreme clump) were used as predictors. The density of each clump was calculated by dividing the number of stems in each clump by the area of the clump (i.e. area of the polygon of intersecting tree buffers) to obtain a "stems per square meter" metric. For individuals outside of clumps, distance to nearest neighbor was used as a radius for calculating a neighborhood area. A local density "stem per meter" metric for use in our model was then obtained by dividing one (i.e. the number of stems for an individual tree) by the calculated neighborhood area. Models were evaluated and selected based on calculated AIC scores where a
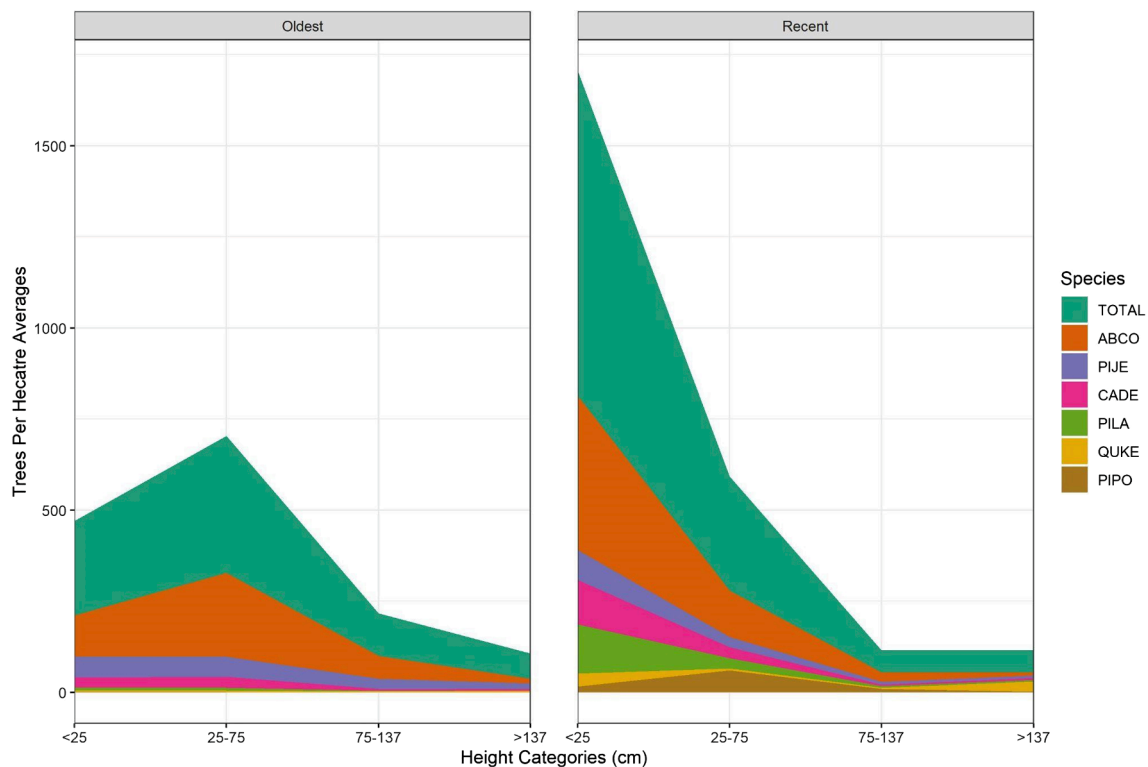
Fig. 4. Mean stocking densities of juvenile trees (by species and for all species combined) across height classes for two fire history categories: Oldest (fires occurring greater than or equal to 10 years before sampling) and Recent (fires occurring <10 years before sampling).

more complex model was selected if its AIC value was at least two points lower than the simpler model. Predicted bootstrapped estimates (n = 500) generated from an expanded grid combination of all predictor variable values (with continuous variables included at set intervals across the range of measured values) from our models were used to visualize and interpret our model results.

2.3.6. Spatial point pattern analysis: mark correlation and growth rates

Spatial point pattern analysis (SPPA) is a method widely used in plant ecology to analyze relationships, interactions, and patterns in spatially explicit datasets (Ben-Said, 2021, Velázquez et al 2016). In cases where quantitative variables, commonly referred to as "marks" (such as DBH or height) are included in the analysis to explore distance-dependent relationships among points, the mark correlation function is the most commonly used tool (Ben-Said, 2021). As an additional analysis to investigate the effects of spatial patterning (especially at close proximity) on regenerating tree growth rates, we applied the mark correlation function from the R package *spatstat* Ver. 2.2.0 (Baddeley et al., 2015) to point patterns of tree locations generated from each stem-mapped plot to analyze distance-dependence between our "marks", in this case, diameter and height growth rates (Ben-Said 2021, Velázquez et al., 2016, Wälder and Wälder, 2008). Height and diameter growth rates were standardized for each seedling using the standard deviation from the mean for each species and age group. We opted for this method rather than scaling and centering as mark correlation functions require positive values for analysis. We removed any plots containing <20 trees, unaged trees (i.e. oak species), and containing species with very small sample sizes. This left us with a sample of 72 plots and 3190 total trees, where number of trees per plot ranged from 21 to 376, with an average

of 44 trees per plot. We applied the mark correlation function, and ran 500 simulations with an independent labeling null model, by which observed mark values are randomly assigned among plot points, and used the fifth lowest and highest values to generate an envelope with a significance level of 99% across tested distances (Ben-Said et al 2020). The analysis provides an estimate of $k_{mm}(r)$, or correlation among marks relative to a value of 1, which indicates "lack of correlation". We used the default equation included in the mark correlation function, Stoyan's mark correlation (Stoyan and Stoyan, 1994), meaning that observed $k_{mm}(r)$ values that fall outside the upper bounds of the envelope indicate a positive association of marks at the given distance, while values that were lower than the lower envelope bound indicate inhibition, or lower than average mark values given proximity to another point (Baddeley et al., 2015, Ben-Said et al., 2020; Ben-Said, 2021).

For all analyzed plots, we looked specifically at the distances, direction, and magnitude of deviations from the generated significance envelope. To do this, we calculated the proportion of plots at each .1m distance where positive correlations (observed value above simulation envelope bound), negative correlations (observed value below simulation envelope bound), or no correlation (observed value did not exit the simulation envelope) were detected (Zhang et al.,2013). Additionally, we calculated the difference between the observed value and envelope boundary (in cases where the observed value did not exit the envelope, this value was 0) across tested distances. These values were subsequently averaged at .1m distance increments to calculate the mean deviation of confidence envelope "exits" and examine where significant correlations between our mark (i.e., seedling) growth rates and spatial proximity could be detected across our plots.
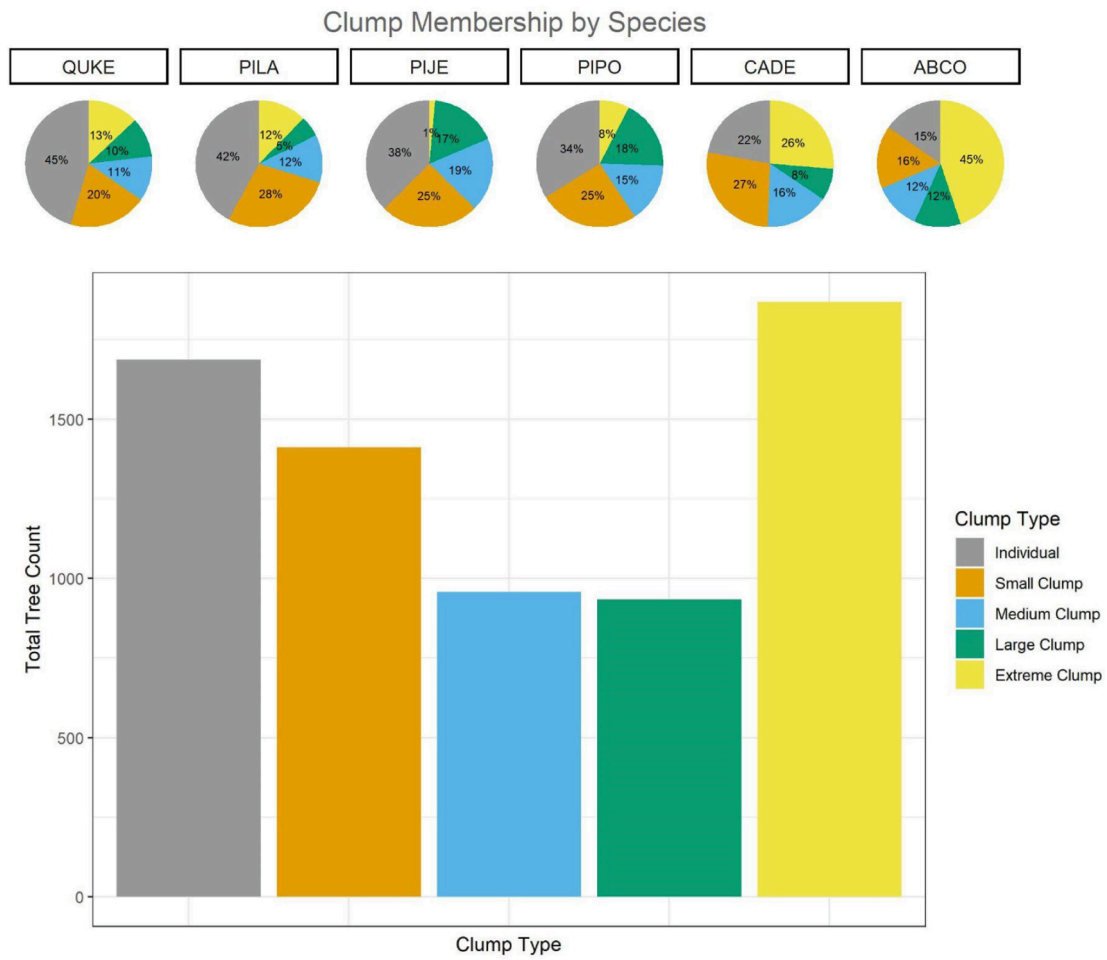
Fig. 5. Clump membership overall and by species. For all species (individually and overall combined), the majority of stems were found in clumps of some kind.

3. Results

3.1. Inventory and stocking density of juvenile trees

Stocking estimates of regenerating stems varied widely across plots and sites, ranging from estimates of 0 TPH (plots with no regeneration) to > 400,000 TPH (plots located within dense thickets of regenerating white fir). For all tree species combined (total TPH), trees per hectare estimates declined with increasing height classes (Fig. 3). For every species individually, densities at the shortest height class were greater than densities at the tallest height class. Regenerating white fir stems were the principal driver of high counts in our plots across all but the tallest height classes.

The distribution of stocking density by height class differed between sites where the most recent fire occurred less than 10 years ago ("recent" fire sites) versus occurring greater than or equal to 10 years ago ("oldest" fire sites). Total regeneration densities were higher overall in sampling sites with more recent fires, specifically among stems in the smallest height class (10–25 cm) (Fig. 4).

Stocking density was lower for the shortest stems (10–25 cm) in plots with higher shrub cover (≥50%) than in plots with lower shrub cover (<50%) for white fir (ABCO), black oak (QUKE), sugar pine (PILA), and Jeffrey pine (PIJE) species. However, stocking density was higher for taller stems (>75 cm) in plots with high shrub cover for ABCO and PIJE. Stocking density was higher across all height classes for incense cedar (CADE) and ponderosa pine (PIPO) stems in plots with high shrub cover, and lower across all height classes for QUKE stems (Fig. A.1).

3.2. Spatial patterns of juvenile trees

Altering the sizes of buffers around each stem (see Section 2.3.1) did have a small impact on our parameter coefficient estimates, as well as the percentage of regenerating trees in each clump size. However, trends in our results remained generally consistent: across all tested buffer sizes, the majority of sampled trees were found to belong to clumps, and our probability models found that the likelihood of belonging to a clump increased with tree age and time since fire (Table A2). Additionally, for all tested buffer sizes, being a member of a clump was positively associated with increased growth. For the remainder of this section, we have opted to present the values and estimates calculated from our original tiered buffering schema "a", but model coefficient estimates from our other tested buffering schemas can be found in Table A.2.

3.2.1. Spatial pattern dynamics: clump membership across species

The majority of regenerating stems across plots, fire histories, and species were found in clumps, defined here as all groupings of greater than one regenerating stem with intersecting buffers. Exact breakdown of clump membership varied by species, with white fir having the highest percentage of trees in clumps (85%), whereas black oak had the highest percentage of trees growing as individuals (45%) (Fig. 5).

White fir made up the highest percentage of stems out of total stem counts (all species combined) for individual trees and all clump sizes; for extreme clumps (>50 trees) in particular, it accounted for nearly 80% of all stems (Table A4). Pines collectively accounted for 43% of individual trees. Jeffrey pine made up a sizable proportion of trees across all spatial pattern categories (from individuals to large clumps) – all between 19 and 25% – but less than one percent were in extreme clumps.

3.2.2. Spatial pattern dynamics: diversity within and across clump types

Significant differences were detected across cluster types by our applied metrics. Large clumps had significantly higher (p < 0.001) average number of species (2.9), average height (68 cm), and standard deviation of height (43) within the clump, when compared to all other clump sizes. Small clumps had the lowest values in all three categories (Table A.5).

Average diversity and evenness index values were significantly higher in large clumps and medium clumps when compared to small clumps. Although the average values of both metrics for extreme clumps were smaller than those for large clumps, they were not found to be significantly different from small, medium, or large clumps (Table A.6).

3.2.3. Logistic model of clumping across topographic patterns and fire history

Predicted values from our binomial mixed model indicated that regenerating stems in sites which had experienced their most recent fire greater than 10 years prior to sampling (i.e. had an older fire history) were significantly more likely to be in clumps compared to stems in sites with a more recent fire history. The probability of any given tree being a member of a clump also increased significantly with tree age, as well as for trees growing on a southwest aspect, and on flatter slopes (Fig. A4 and Table A2). Among the species included in the analysis, white fir was the most likely to be growing in a clump (mean estimates > 50% across the age range 1–30 years).

3.3. Clumping and growth rate analysis

3.3.1. Growth rate significance testing across age groups

Trees in clumps grew significantly faster in height when averaged across stems of all ages for white fir, Jeffrey pine, sugar pine and ponderosa pine, and significantly faster in diameter for all species except sugar pine (p < 0.05) (Table 1). A comparison between individual and clumped trees within different age categories (ages 1–5, 6–11, 12–19, and > 20 years) between white fir and yellow pines (Jeffrey and ponderosa pine grouped together for comparison) revealed that diameter growth rate averages among Clumped trees were significantly greater (p < 0.05) for yellow pines ages 1–5 and 6–11 years, as well as for white fir ages 1–5 years. Older age groups in yellow pine did not demonstrate significant differences in mean diameter growth, and white fir demonstrated a negative significant difference between mean growth rates of clumped and individual trees for stems aged 12–19 years (Table A.1).

Table 1

Results of Tukey HSD tests across all ages for different species. Across all species, Clumped trees displayed significantly higher growth rates for height, and the same was true for diameter growth rates for all species except sugar pine.

	Estimated differences in growth rates of clumped versus individual trees by species					
	Diameter			**Height**		
Species	**Diff. Est.**	**P**		**Diff. Est.**	**P**	**N Individual Trees**	**N Clumped Trees**
ABCO	0.053	**0.032**	0.691	**<0.001**	505	2810
PIJE	0.248	**<0.001**	1.884	**<0.001**	416	692
PILA	0.065	0.135	0.490	**0.004**	214	296
PIPO	0.523	**0.007**	1.669	**0.010**	89	174

Estimates are mean differences (mm/yr) between Clumped and Individual tree growth rates. A positive value indicates a faster growth rate among Clumped trees. **Bold font indicates significant result.**

By comparison, height growth among clumped trees was significantly greater across all age groups for white fir, and for yellow pines ages 1–5 and 6–11 years. The proportion of trees in clumps grew dramatically as tree age increased (75% of white fir and 56% of yellow pine at ages 1–5 years compared to 92% of both groups when stems were > 20 years).

3.3.2. Growth rate modeling results

Selected mixed models indicated that individuals demonstrated significantly slower growth in both height and diameter than clumped trees. For both our height and diameter growth rate models, there were no significant differences between (non-individual) clump sizes (See Fig. 6 and Table A.4).
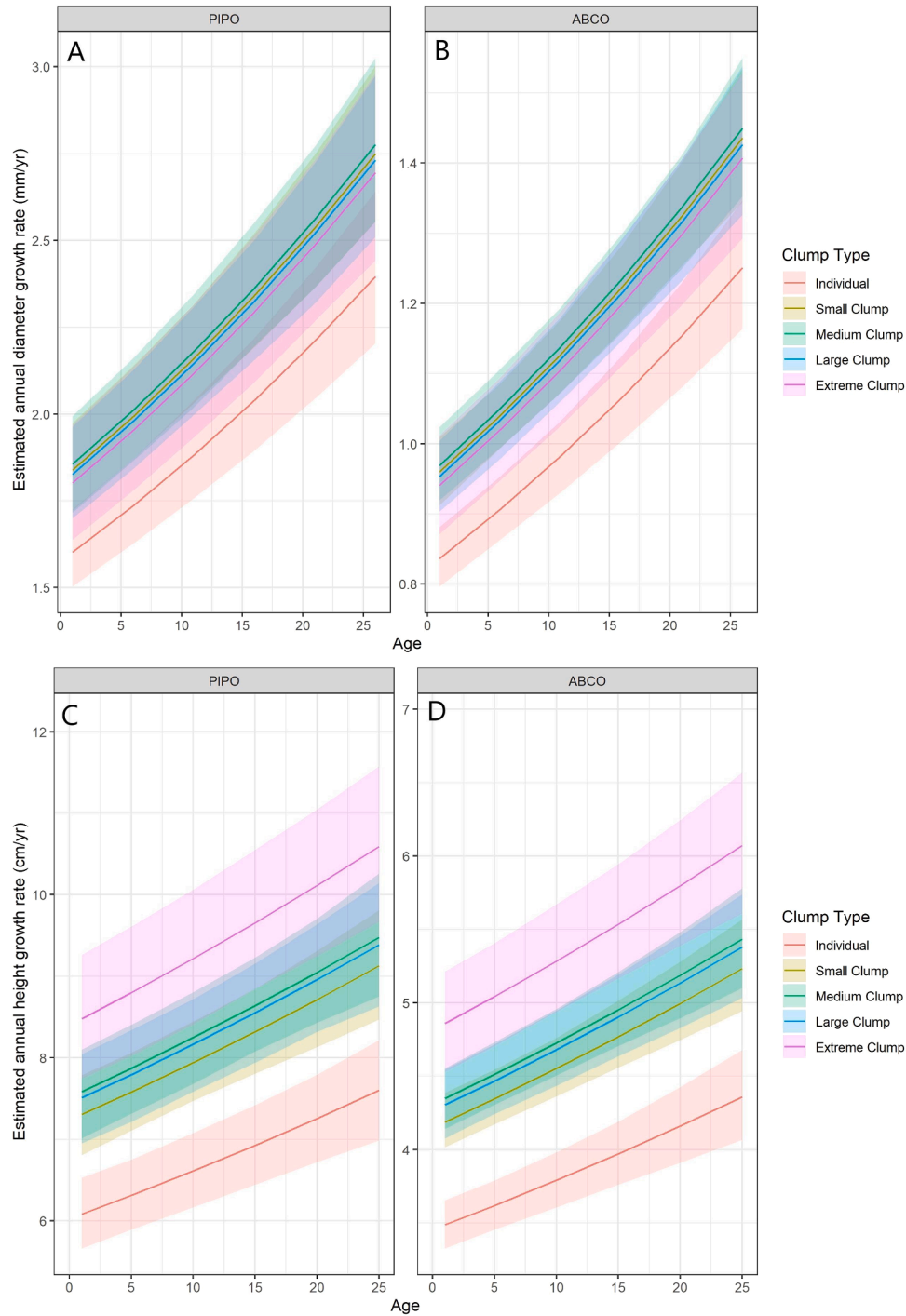

Fig. 6. Bootstrapped predictions from growth rate models for ponderosa pine (left) and white fir (right). Diameter growth: graphs A and B. Height growth: graphs C and D. Envelopes represent 95% confidence interval on calculated estimates.

In our diameter growth model, shrub cover was not significantly related to differences in growth rates between clumped and individual trees. For our selected height growth model, shrub cover was significantly *positively* correlated with juvenile tree growth. The estimated coefficient for our predictive variable measuring regenerating tree density or crowding within clumps was significantly negative (Table A2). However, bootstrapped model predictions estimated that clumped trees at the median age in our sample (6 years) grew faster than individual trees for the smallest measured density (0.0005 stems per meter) up to a density of about 7 stems per meter.

3.3.3. Mark correlation analysis results

For both diameter and height growth rates, the majority of analyzed plots (43 and 40 out of 72 total plots for diameter and height growth analyses, respectively) did not have distances where the observed $k_{mm}(r)$ value exceeded the confidence envelope at any tested distance value, indicating that for most plots, significant correlation among marks could not be detected. Additionally, summarized correlation results at each .1m distance increment across plots showed that no exit from the envelope was detected in > 80% of plots across the entire range of tested distances (Fig. A.6). Among some analyzed plots, a small positive correlation was detected for height growth up to about 2 m distance. However, overall there was not a strong, consistent response pattern for height or diameter growth rate and inter-tree distance among all analyzed plots (See Fig. A.5).

4. Discussion

As far as we know, our study is one of the first to investigate spatial patterning and growth rates of juvenile trees in active-fire mixed-conifer forests at fine spatial scales. We found high regeneration densities relative to traditional reforestation stocking goals, likely due to abundant overstory seed production and frequent fire providing mineral soil beds that encourage establishment and emergence (Larson and Churchill, 2012; Welch et al., 2016). The majority of regenerating stems, regardless of species, were found in clumps. Stems were more likely to occur in clumps in sites that experienced their most recent fire greater than 10 years before data collection, suggesting that infilling is continuing within clumps long after the most recent fire, even as some expected thinning out of stems is occurring at older age classes. Increasing tree densities within a clump (i.e., 'local crowding') was associated with reduced growth rates, suggesting that competition reduces seedling growth at high densities. However, unexpectedly, our selected mixed-effects models indicated that being in a clump had a positive effect on both stem diameter growth and, to an even greater extent, stem height growth compared to growth rates for trees growing as individuals. This result held even at the moderate to high densities we observed across a relatively wide age range (1–20 years), and especially for seedlings less than 10 years old. There was no significant difference in diameter growth rates between clump sizes, suggesting that membership in a clump of any size is associated with increased growth compared to individual seedlings.

There were several limitations to this study that may have influenced our results. First, exact annual growth rates of regenerating trees could not be directly measured as we only visited sampling sites once, so we used average growth from estimated ages. As most of our sampling was completed in areas that prohibit destructive sampling, we also could not directly measure age. However, off-site calibration of our whorl count age estimation using ring counts from juvenile trees in neighboring forests indicated that our estimates for the species included in our growth modeling were consistent. Second, it is possible that some of the variation in growth rates could be attributed to differences in resources and site conditions not directly measured in this study (Shive et al., 2018). However, we believe that our hierarchical modeling approach should at least partially account for plot-by-plot variation in growth conditions, including overstory tree conditions (see Table A.3 for variance components of random effects for selected models).

Finally, a significant challenge for this study was in the delineation of the "zone of influence" of the regenerating trees for identification of clumps and clump size. ICO analyses for adult trees have typically created a competition zone buffer based on crown width (Lydersen et al., 2013; Ng et al., 2020). However, due to the small stature of the seedlings and saplings we studied, and their position in the forest understory where competition for shallow below-ground resources is of critical importance (Gray et al., 2005), we believe that an approximation of root spread was a reasonable proxy for determining a neighborhood of putative seedling interactions. However, given the complexity that goes into determining actual horizontal root spread in very young trees (including very small roots and/or possible mycorrhizal interactions), calculating specific allometric values for each tree based on diameter or height was prohibitive. As such, we believe our estimates of approximate root extent by seedling size were a reasonable approach to roughly defining clump membership.

4.1. Natural regeneration patterns in sampled sites

Consistent with other studies of post-fire regeneration in these forests, we found highly heterogeneous regeneration densities among and within sites across topographic variables, fire histories, and shrub conditions (Welch et al., 2016). Our average TPH estimates (calculated mean stocking value across sites and height classes: 1074 TPH) were also comparable to mean regeneration stocking estimates from other post-fire regeneration sampling efforts in this area (i.e. Welch et al., 2016) when including all stems greater than 10 cm in height (Welch et al., 2016). Across the range of topographic variables and fire histories that we sampled, white fir was the primary species driving stocking estimates among regenerating stems, similar to findings from other mixed-conifer regeneration studies (Crotteau et al., 2013; Gray et al., 2005). *Abies* species may dominate during post-fire regeneration for a range of reasons, including pre-fire forest composition, post-fire weather conditions, shrub competition, as well as the volume of seed produced by adult trees (Tubbesing et al., 2020; Zald et al., 2008; Zald et al., 2022). We found a steady decrease in the stocking numbers of total trees at increasing tree height intervals (Fig. 3). The increased resource requirements of taller trees may explain this thinning (Pommerening and Sánchez Meador, 2018).

The higher stocking rates we observed in areas that had experienced more recent fire might also be rooted in the dynamics of frequent-fire forests. Frequent, low-intensity fires may generate patches of bare-mineral soil, constantly renewing available substrate for seed germination and establishment (Larson and Churchill, 2012, Stephens and Fry, 2005, White, 1985). Though we observed a significant drop in net recruitment of small (<25 cm) juvenile trees in older-fire stands compared to recent fire sites (Fig. 4), our results suggest that some ongoing recruitment and infill is happening in areas with less recent fire, and that total regeneration post-fire does not just belong to a single cohort of post-fire cohort trees. The continued recruitment of younger seedlings several years after fire may contribute to the formation of a mosaic structure of uneven-aged patches, consistent with the historic structure of frequent-fire forests (Sánchez Meador et al., 2011).

4.2. Juvenile tree spatial patterns: Clump size and composition

Over 50% of regenerating trees across species were identified as being a member of a clump, consistent with Keyes et al. (2007), who found that the majority of establishing ponderosa pine seedlings in their study were found in clumps both at emergence and for two seasons following. Though white fir was the species most likely to be found in a clump (and the species that dominated clumps of any size), all clump sizes greater than the smallest category (2–5 trees) averaged more than one species within a clump. Our diversity analysis on clumps indicated that diversity and evenness indices tended to increase as clump size

increased. However, once clumps reached the "extreme clump" size category (>50 trees), diversity and evenness metrics decreased and were not distinct from those of medium clumps. This suggests that dense thickets of shade-tolerant white fir (the species that constituted approximately 78% of extreme clump membership) may preclude meaningful establishment by other species.

4.3. Likelihood of clumping

Our logistic clumping model results indicate that regenerating stems in sites with older fires (longer time-since-fire) are more likely to be found in clumps, and that likelihood of clumping further increases with tree age and (slightly) with increasing number of fires. This infilling of stands with time is consistent with other regeneration studies where dense regeneration occurred at suitable sites after nine years of post-fire development (Berkey et al., 2021). As we expected, likelihood of clumping differed with changes in topographic variables such as slope and aspect, echoing the results of our post hoc summary statistics on clumping and topography patterns (Fig. A.2). Our model predicted that clumping likelihood was greater in sites with flatter slopes (<15%), supporting other conifer spatial pattern analyses that found similar trends between flatter valley floors and steeper mid-slope or ridgetop sites in larger (>20 cm dbh) trees (Ng et al., 2020). Though we were initially surprised that our model predicted increased likelihood of clumping on southwest facing slopes, given that the harsher environmental conditions might support lower tree density in general, Elliott and Kipfmueller (2010), also found similar clumping patterns on subalpine south-facing slopes. This could indicate that abiotic extremes may contribute to increased stress-mediated facilitation in trees clumped in habitable microsites.

4.4. The effects of shrub cover

One of the most surprising findings from our growth rate model was that percent shrub cover in a two-meter radius surrounding regenerating stems did not have a significant negative effect on juvenile tree growth rates. This finding was consistent across all of our models. Some studies have shown shrubs to be a strong competitor with young seedlings in areas with low soil-moisture, at least until they develop a deeper root structure (e.g., Plamboeck et al., 2008), but other studies have found that shrubs may facilitate survival and growth in young seedlings under arid or otherwise abiotically stressful conditions (Gómez-Aparicio et al., 2004; Sthultz et al., 2007) and even provide mechanical protection and ameliorate climatic extremes (Keyes et al., 2009; Gray et al., 2005). Though high shrub cover has been found to reduce growth of young stems in evenly-spaced ponderosa pine plantations (Finley and Zhang, 2019; McDonald and Fiddler, 1989; McDonald and Fiddler, 2007; Oliver, 1979), we are not aware of studies comparing growth rates in highly clumped regenerating stands. One possible explanation is that in frequent-fire forests that naturally develop clumped regeneration, clumps of trees may prevent complete encroachment by shrubs, in contrast to conditions in regularly spaced plantations where shrubs can effectively surround and 'swallow' a single gridded seedling.

Estimated coefficients for shrub cover in our models were not consistent across models. Shrub cover was associated with higher growth rates in our height growth model comparing individual trees to all clump sizes, but did not have a significant effect in our diameter growth model. Though we did not find evidence supporting a significant relationship between increasing tree age and high shrub cover in our modeling, our stocking estimates were consistently higher among the tallest height classes (trees > 137 cm in height) in high shrub cover plots (>50% cover) across all major species (Table A2, Fig. A.1).

The faster height growth rates found among regenerating stems in increasing shrub cover, as well as higher stocking densities among taller stems in high shrub cover conditions (Fig. A1), may simply indicate superior microsite conditions for both shrubs and trees. Given sufficient

microsite conditions, locations with high shrub cover might also select to some degree for juvenile trees that grow taller faster (i.e., those that can outpace the shrub layer), whereas locations with low shrub cover might not necessitate resource competition to the same degree, thereby permitting survival of juvenile trees with greater variation in height growth rates.

Alternatively, the spatial variability of seedling clumps within large shrub patches may create greater heterogeneity and discontinuity in fuel conditions across the landscape. This in turn could have resulted in greater heterogeneity in burn intensities as fire moved through the stand and potentially have allowed entire patches of seedlings to survive the most recent fire. It is also possible that depending on the burn weather conditions, shrubs might retain high moisture content from recent rain, contributing to reduced fire intensity and preventing complete consumption of regenerating trees that are buffered within shrub patches (Knapp et al., 2007; Lutz et al., 2017; North et al., 2019; Pellizzaro et al., 2007). If this is the case, it is possible that shrubs could be an important factor contributing to increased resistance to fire even among young regenerating patches, at least shortly after a precipitation event.

4.5. Clumping and growth rates

Our selected statistical models detected a robust positive association of clumping with higher rates of both diameter growth and height growth but did not reveal any significant differences among clump sizes (See Figs. 6, A.4, and Table A.2.). This suggests that clumping may be beneficial for juvenile trees in this range of fire ages (<30 years) in frequent-fire, naturally-regenerating stands. The idea that clumping may be beneficial for tree regeneration may seem counter-intuitive, as competition has long been considered one of the most basic tenets driving succession dynamics in plant community ecology (Pommerening and Sánchez Meador, 2018). Our results are not in conflict with this classical view of competition: we found that higher density or "crowding" of stems was negatively correlated with growth (Pommerening and Sánchez Meador, 2018). This apparent mismatch could indicate that the "spread" of seedlings within a cluster, or available growing space for each stem is important, and that, while proximity to other regenerating stems may provide facilitative benefits, too high of densities could negatively impact growth. Our models found that the competitive pressures exerted by multiple close neighbors outweighed the benefits of clump membership at densities approximating 7 stems per meter, a relatively high value especially compared with traditional planting practices where seedlings are often spaced anywhere from 8 to 15 feet apart (Stewart, 2020). However, actual thresholds at which competition may outweigh facilitation certainly vary based both on individual tree resource requirements (conditional on tree species, size, age etc.) as well as site conditions.

Though our mixed models found strong evidence of a positive relationship between clustering and growth rates, our mark correlation analysis of growth rates did not detect a consistent significant correlation among growth rates of proximal trees in the majority of analyzed plots. However, among plots where significant correlations were detected, height growth was generally positively correlated at distances less than 2 m, echoing the results of our mixed models analyses.

The focus of our study was on mostly young, smaller trees, where the full effects of competition and crowding may yet to be felt. Past studies on the influence of seedling spacing (though in regular gridded planting patterns) have noted a "cross-over" effect in certain species where denser plantings may initially display increased height growth, but this effect can reverse at some point between 6 and 10 years (Pienaar and Shiver, 1993; Scott et al., 1998). These results, however, have not been consistently observed across experiments, and most studies measuring growth of regularly-spaced planted seedlings over time have found increased height with increased spacing (Antón-Fernández et al., 2011). Our data focused on growth rates of clumped seedlings suggest proximity to other seedlings may provide benefits for young (<20 years old)

trees that outweigh the negative impacts of crowding at moderate and even high densities of several stems per square meter. Our results suggest that the number of trees within a clump (clump size) does not hinder growth of regenerating young seedlings compared to individual seedling growth rates. Although we were not directly investigating mechanisms driving establishment and growth rates of seedlings in clumps, we suspect that the highly heterogeneous structure of clumped stems may be providing some facilitation, possibly through modification of microclimate that favors regenerating trees (Calder and St. Clair, 2012; Elliott and Kipfmueller, 2010). It is also possible that ectomycorrhizal networks (MNs) may be another driver of the regeneration and growth patterns we observed in our study, and that clumped trees tap into an established MN, providing a competitive advantage over individual trees. It has been shown that MNs influence establishment and growth of seedlings, and that connection to MNs from overstory trees may positively impact seedling establishment especially under abiotically stressful conditions (Bingham and Simard, 2011; Booth and Hoeksema, 2010). Other seedling establishment studies focusing on mortality have also found that natural recruitment often begins in large, clumped groups, and although clumps often shrink in size as seedlings age, they are not eliminated (Keyes et al., 2007; Vander wall, 1992). More research is needed within Sierra Nevada mixed-conifer forests to better evaluate these scenarios and understand the dynamics of MN networks and microclimate modification on seedling growth and spatial patterning.

5. Management implications

Tree spatial patterns, as a critical component of resistance and resilience to fire, are a priority for fire management in the Western U.S. and elsewhere (Addington et al., 2018, Churchill et al., 2013, Larson and Churchill, 2012; North et al., 2019, Reynolds et al., 2013). Though there is increasing evidence that spatially heterogeneous patterns among mature trees (characterized by ICO) are more resistant and resilient to fire (Koontz et al., 2020; Lydersen et al., 2013; Stephens et al., 2016), most reforestation practices use regularly spaced rows of planted seedlings. Strictly mimicking the clump patterns we found in future reforestation planting would be labor intensive and a waste of expensive nursery seedlings. Silviculture's focus has often been on how to achieve a desired stand condition in altered environments, such as current forests with less frequent and more intense fire patterns. Our results point to the value of structural heterogeneity in regenerating stands, benefiting tree seedling growth and diversity, and fire resistance and resilience. Though we did not find strong evidence across our analyses that clumping significantly impedes growth rates of juvenile trees in this study (a key hesitation in planting or encouraging clumped growth patterns in reforested areas), it may be that many of the trees sampled during our study were simply too young or small to fully experience the brunt of resource competition. However, even if growth rates may suffer to some extent as trees age, naturally clumped growth patterns may have other desirable managerial implications for some stands, including prevention of full encroachment by shrubs and potential mediation of fire-induced mortality. Supporting variable seedling, shrub, and opening conditions in regenerating stands may enable and perpetuate heterogeneous burn and natural recruitment patterns, further reinforcing stand resilience to fire over time (North et al., 2019).

Although we did not directly test potential best management practices for increasing fire resilience in regenerating mixed-conifer forests, our unexpected findings of positive effects of clumping and shrub cover on seedling and sapling growth rates merits further investigation. Future planting studies focused on spatial patterning of regenerating trees over time may help distinguish how facilitation and/or competition dynamics change as stands mature, and how site factors and species composition influence these dynamics. The spatial patterns of vegetation observed in fire-restored forests, particularly the mix of tree clumps, shrub patches, and openings, may offer some guidance on creating the heterogeneity associated with greater fire resilience in young regenerating stands. Additional empirical and observational analyses of alternative plantings strategies or natural regeneration spatial and growth patterns are needed to better understand how clumping patterns affect growth, mortality, and ultimately forest resilience to fire.

6. Conclusions

The predicted impacts of climate change, such as increasing temperatures and more variable precipitation patterns, are likely to exacerbate forest susceptibility to wildfire as high-severity, stand replacing fires become more prevalent (Vose et al., 2012). Changing climate and disturbance conditions are also accelerating forest loss due to type conversion (Coop et al., 2020) and new approaches are needed that can build resilience even in young, developing plantations. Management strategies to promote and restore fire resilient stands are of key interest to land managers, especially in forests not intended for high-yield timber production (where regular-spaced planting may fulfill desired economic and efficiency objectives). As underscored by Berkey et al. (2021), mixed-conifer forests are complex ecosystems without a single successional trajectory. Investigating patterns of seedling establishment in areas with restored fire regimes will help fill a critical knowledge gap regarding how regeneration patterns vary with environmental variables and fire regime. Our findings suggest field trials and more experimentation in seedling and sapling spatial patterns are warranted to better understand how fire resilient conditions can be fostered in regenerating forests.

CRediT authorship contribution statement

Hannah M. Fertel: Methodology, Investigation, Formal analysis, Software, Resources, Data curation, Visualization, Writing – original draft, Writing – review & editing, Project administration. **Malcolm P. North:** Conceptualization, Methodology, Supervision, Writing – original draft, Writing – review & editing, Funding acquisition. **Andrew M. Latimer:** Conceptualization, Methodology, Funding acquisition, Writing – review & editing. **Jan Ng:** Writing – review & editing.

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.

Appendix A

See Figs. A1–A6.
See Table A1–A6.
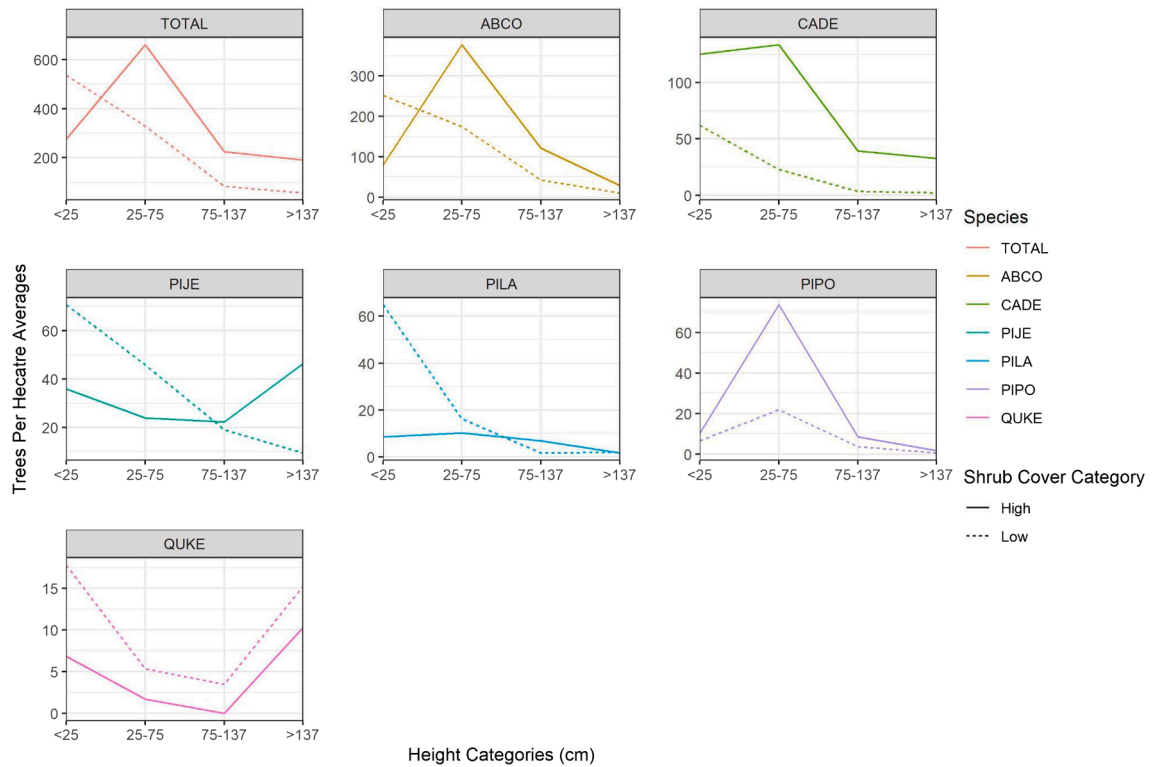
Fig. A1. Average stocking densities of juvenile tree species (individually and for all species combined) at high (≥50%) and low (<50%) shrub cover conditions across tree height classes.
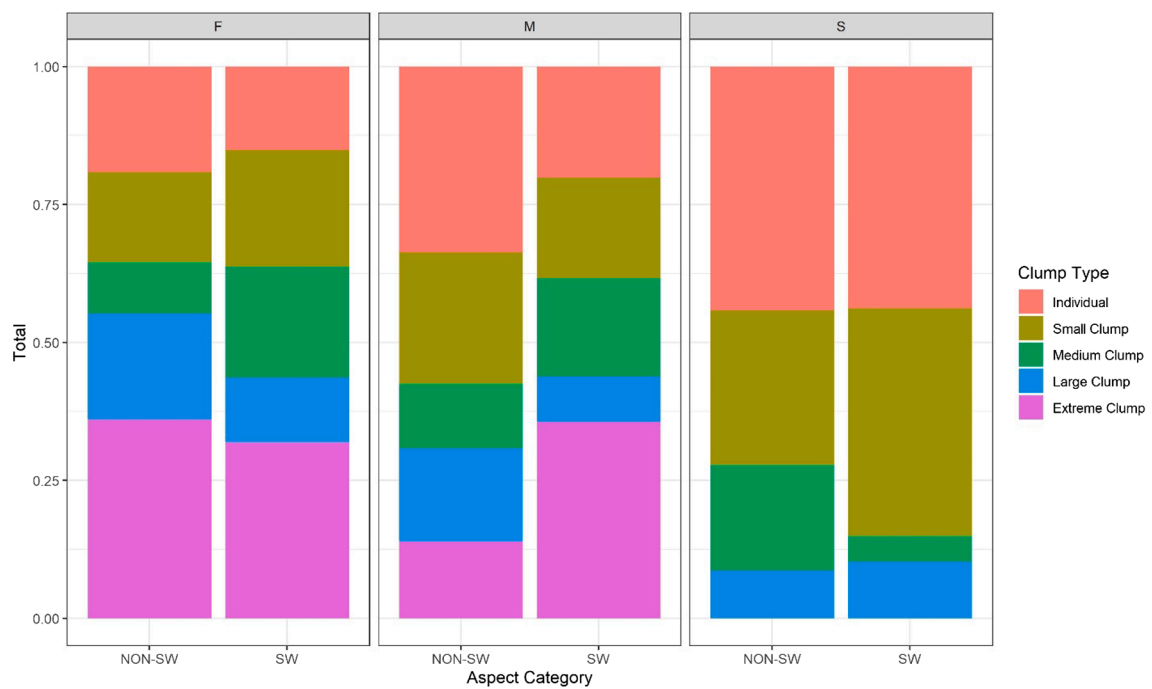
Fig. A2. Topographic breakdown of clump membership by slope category and aspect.
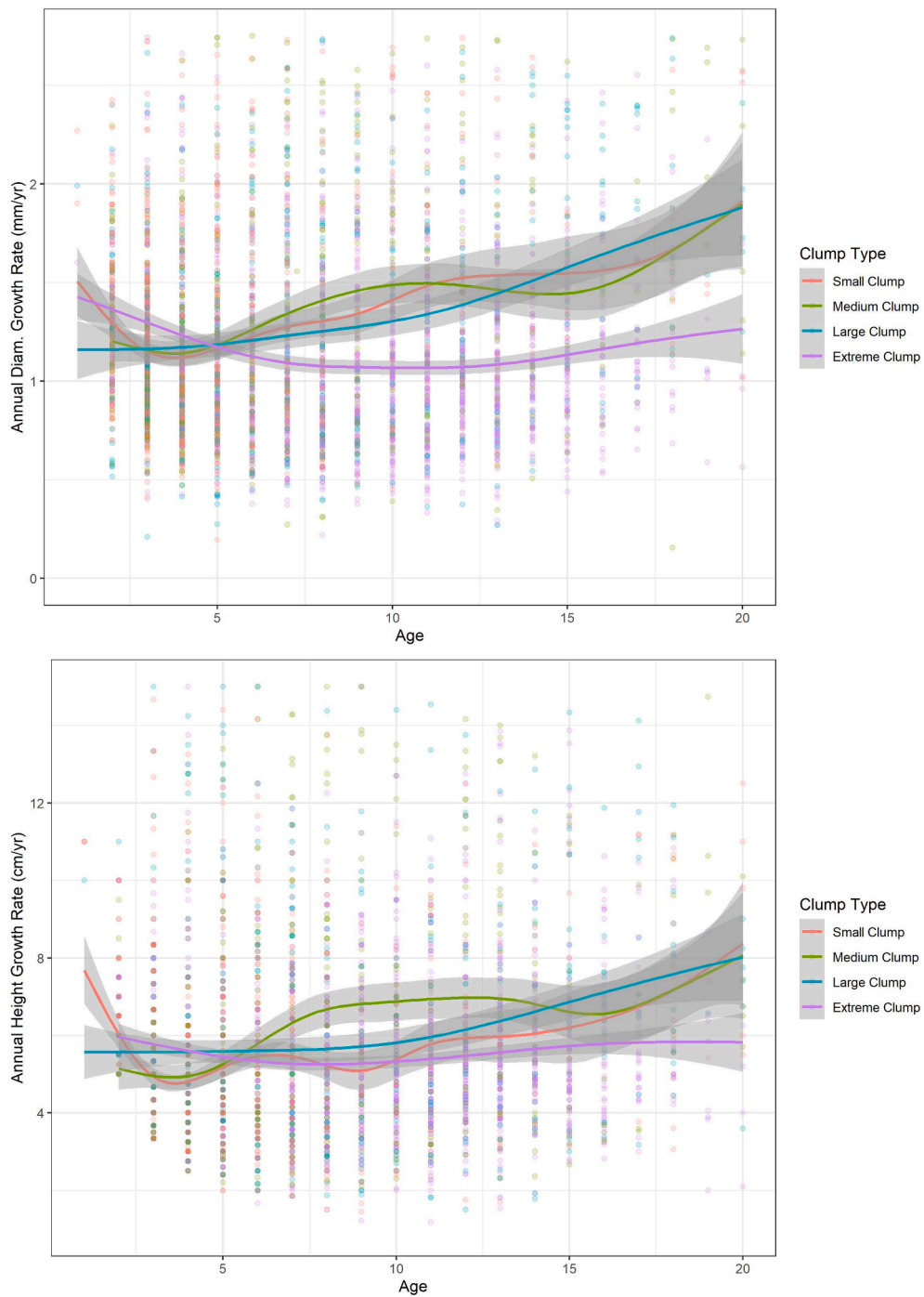
Fig. A3. Geometric -Smoothed figure showing estimated annual diameter growth rate(top) and height growth (bottom) across clumps (excluding individual trees) using collected field data. A clear lag in estimated diameter growth can be observed for trees in extreme clumps after about 5 years in age, but the other cluster estimates showed no significant differentiation. Height growth rates display less significant differentiation among all size classes across ages.
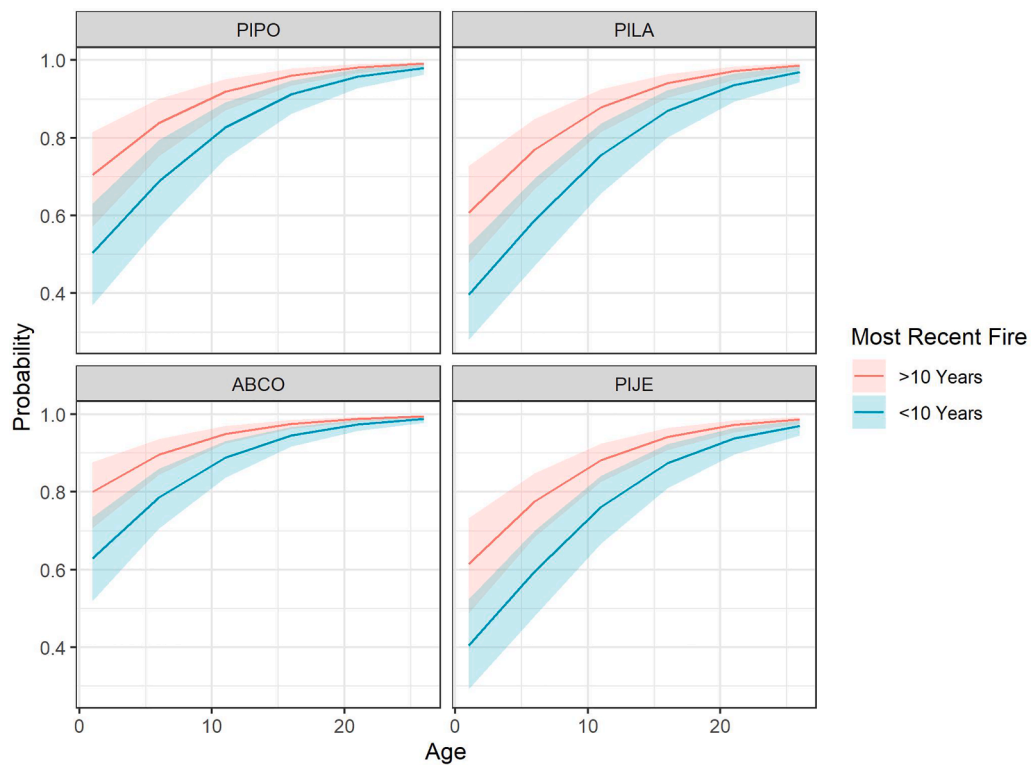
Fig. A4. Predicted bootstrapped probability estimates of a seedling being a member of a clump across seedling ages by tree species. The probability of clumping increased in sites that experienced fires less recently and as trees age.
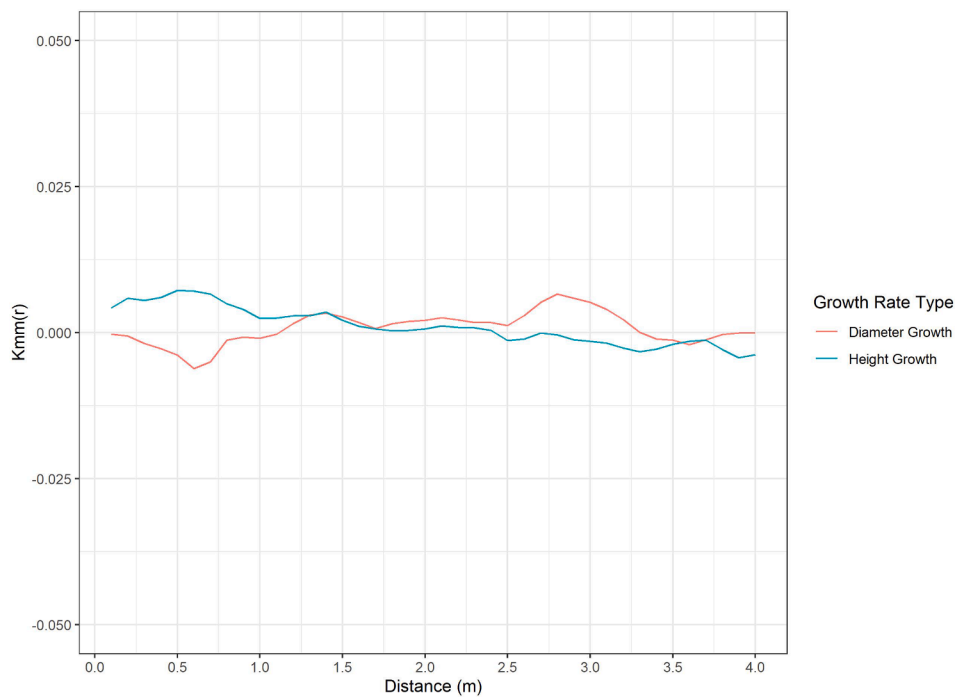
Fig. A5. Graph showing average differences in values of $k_{mm}(r)$, a measure of correlation, between the simulation envelope boundary and observed value at 0.1 m intervals across a distance gradient for plots analyzed with the mark correlation function. In the majority of plots, significant correlations were not detected across the tested range of distances for diameter or height growth rates.
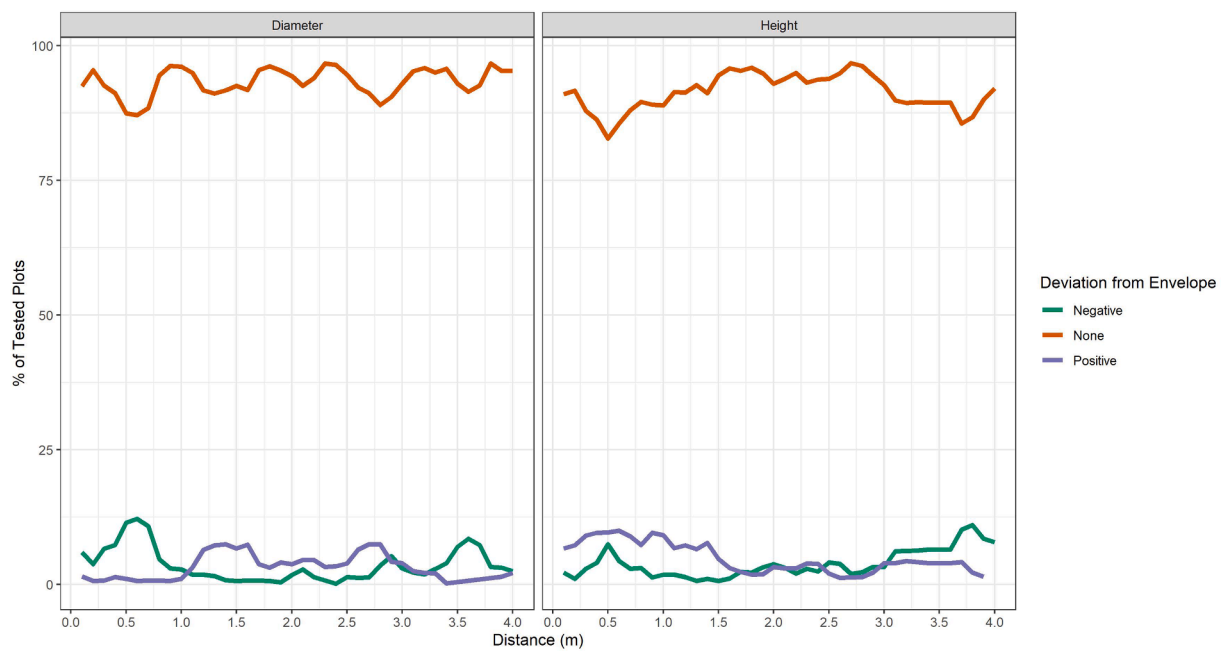
Fig. A6. Graph showing percentage of plots where positive correlations (observed value above simulation envelope), negative correlations (observed value below simulation envelope), or no correlation (observed value did not exit the simulation envelope) were detected for height and diameter growth rates across the range of tested distances for our mark correlation analyses. Across the range of tested distances, the vast majority of plots (>80%) a significant deviation from the significance envelope was not detected.

Table A1

Results of Tukey HSD tests for yellow pine (ponderosa and Jeffrey combined) and white fir by age category. Overall, when looking at trees across all ages, and at trees in younger age groups (<12 years for yellow pine and < 5 years for white fir), clumping had a significantly positive effect. A significant difference was not detectable among older yellow pine seedlings and saplings (likely due to the extremely small sample size of Individual older trees), while a significantly negative effect of clumping on diameter growth was identified in white fir ages 12–19, indicating that the effect of clumping on growth may vary with species and might also change as a tree ages.

Estimated diameter growth rate differences between Clumped and Individual trees

Species	Overall			Age 1–5			Age 6–11			Age 12–19			Age > 20		
	Diff. Est.	P	n I|C	Diff. Est.	P	n I|C	Diff. Est.	P	n I|C	Diff. Est.	P	n I|C	Diff. Est.	P	n I|C
white fir	**0.053**	**0.03**	505|2810	**0.061**	**0.02**	302|929	0.037	0.42	142|1156	**−0.177**	**0.03**	55|653	0.53	0.76	6|72
yellow pine	**0.321**	**< 0.001**	505|866	**0.164**	**0.03**	353|457	**0.4894**	**<0.001**	132|273	−0.196	0.433	18|116	0.489	0.422	2|22

Estimates (Diff. Est.) are mean differences (mm/yr) between clumped and individual tree diameter growth rates. A positive value indicates a faster growth rate among clumped trees.
"C" indicates sample size of clumped trees, "I" indicates sample size of individual trees.
Bold font indicates a significant result ($\alpha = 0.05$)

Estimated height growth rate differences between clumped and individual trees

Species	Overall			Age 1–5			Age 6–11			Age 12–19			Age ≥20		
	Diff. Est.	P	I|C	Diff. Est.	P	I|C	Diff. Est.	P	I|C	Diff. Est.	P	I|C	Diff. Est.	P	I|C
white fir	**0.69**	**< 0.001**	505|2810	**0.248**	**0.04**	302|929	**1.024**	**<0.001**	142|1156	**0.824**	**0.007**	55|653	**3.531**	**<0.001**	6|72
yellow pine	**1.919**	**<0.001**	505|866	**0.923**	**<0.001**	353|457	**3.189**	**<0.001**	132|273	1.373	0.17	18|116	3.013	0.21	2|22

Estimates (Diff. Est.) are mean differences (cm/yr) between clumped and individual tree diameter growth rates. A positive value indicates a faster growth rate among Clumped trees.
Bold font indicates a significant result($\alpha =0.05$)

Table A2

Comparison of estimated model coefficients across different "neighborhood of influence" buffer sizes around stems. Only variables related to buffering schema were included in table.

| | | Model Coefficient Estimates Across Defined Buffer Sizes | | | | | | | | | | | | | | |
| | | Original Buffering Scheme | | | Buffers 75% of Original | | | Buffers 125% of Original Size | | | Buffers set at 0.5 M | | | Buffers = Stem Height (Max. 2 M) | | |
		Est.	SE	P Val.	Est.	SE	P Val.	Est.	SE	P Val.	Est.	SE	P Val.	Est.	SE	P Val.
Diameter Growth Rate Model	(Intercept)	−0.092	0.03	0.0011	**−0.056**	0.02	0.0234	**−0.122**	0.03	0.0001	**−0.086**	0.04	0.0371	−0.002	0.02	0.9800
	Small Clump	0.138	0.02	<0.0001	**0.137**	0.02	<0.0001	**0.128**	0.02	<0.0001	**0.067**	0.02	0.0009	**0.106**	0.02	<0.0001
	Medium Clump	0.147	0.02	<0.0001	**0.149**	0.02	<0.0001	**0.138**	0.02	<0.0001	0.017	0.02	0.4694	**0.127**	0.02	<0.0001
	Large Clump	0.131	0.02	<0.0001	**0.133**	0.03	<0.0001	**0.137**	0.03	<0.0001	0.032	0.03	0.3122	**0.111**	0.02	<0.0001
	Extreme Clump	0.118	0.04	0.0037	**0.126**	0.03	0.0003	**0.161**	0.04	0.0001	0.077	0.04	0.0570	0.029	0.04	0.4070
	Density	−0.196	0.02	<0.0001	**−0.137**	0.02	<0.0001	**−0.243**	0.03	<0.0001	**−0.298**	0.05	<0.0001	**−0.056**	0.01	<0.0001
Height Growth Rate Model	(Intercept)	**1.253**	0.027	<0.0001	**1.301**	0.023	<0.0001	**1.239**	0.029	<0.0001	**1.452**	0.039	<0.0001	**1.355**	0.022	<0.0001
	Small Clump	**0.183**	0.019	<0.0001	**0.184**	0.018	<0.0001	**0.156**	0.019	<0.0001	**0.043**	0.019	0.0240	**0.157**	0.017	<0.0001
	Medium Clump	**0.221**	0.021	<0.0001	**0.227**	0.020	<0.0001	**0.190**	0.021	<0.0001	0.021	0.022	0.3390	**0.211**	0.020	<0.0001
	Large Clump	**0.211**	0.023	<0.0001	**0.283**	0.026	<0.0001	**0.214**	0.024	<0.0001	−0.012	0.030	0.6990	**0.220**	0.022	<0.0001
	Extreme Clump	**0.332**	0.038	<0.0001	**0.333**	0.033	<0.0001	**0.330**	0.037	<0.0001	0.058	0.038	0.1300	**0.208**	0.033	0.0000
	Density	**−0.238**	0.021	<0.0001	**−0.161**	0.014	<0.0001	**−0.260**	0.025	<0.0001	−0.042	0.049	0.3900	**−0.069**	0.008	<0.0001
Clumping Probability Model	(Intercept)	**2.147**	0.247	<0.0001	**1.809**	0.239	<0.0001	**2.497**	0.261	<0.0001	**2.682**	0.250	<0.0001	**1.998**	0.219	<0.0001
	Recent Fire	**−0.855**	0.180	<0.0001	**−1.006**	0.169	<0.0001	**−0.858**	0.191	<0.0001	**−0.951**	0.202	<0.0001	**−0.872**	0.177	<0.0001
	scale(# of Fires)	**0.219**	0.063	0.0005	**0.199**	0.060	0.0009	**0.202**	0.066	0.0023	**0.208**	0.067	0.0019	**0.216**	0.063	0.0006
	M Slope	**−0.281**	0.090	0.0018	**−0.215**	0.084	0.0109	**−0.244**	0.096	0.0112	**−0.202**	0.100	0.0424	−0.104	0.087	0.2312
	S Slope	**−0.652**	0.134	<0.0001	**−0.524**	0.130	0.0001	**−0.596**	0.141	<0.0001	**−0.780**	0.145	<0.0001	**−0.415**	0.133	0.0018
	SW Aspect	**0.575**	0.085	<0.0001	**0.471**	0.079	<0.0001	**0.578**	0.091	<0.0001	**0.537**	0.097	<0.0001	**0.267**	0.081	0.0010
	PIJE	**−0.916**	0.093	<0.0001	**−0.848**	0.088	<0.0001	**−1.007**	0.098	<0.0001	**−1.283**	0.102	<0.0001	**−0.724**	0.091	<0.0001
	PILA	**−0.950**	0.114	<0.0001	**−0.894**	0.110	<0.0001	**−1.026**	0.120	<0.0001	**−1.207**	0.130	<0.0001	**−0.874**	0.111	<0.0001
	PIPO	**−0.515**	0.164	0.0018	**−0.498**	0.156	0.0014	**−0.592**	0.178	0.0009	**−0.809**	0.189	<0.0001	0.067	0.165	0.6851
	scale(Age)	**0.749**	0.058	<0.0001	**0.657**	0.051	<0.0001	**0.739**	0.063	<0.0001	0.082	0.049	0.0938	**0.994**	0.062	<0.0001
	Indicates Significant Result															

Table A3

Comparison table of random effects for selected mixed-effects models. σ^2 is the variance of the model's random effects, $\tau00$ is the between-subject variance, ICC is the intraclass correlation coefficient, Marginal R^2 is the variance explained only by the fixed effects, while the conditional R^2 includes both fixed and random effects. Marginal R^2 values show that while fixed effects in selected models account for the majority of explained variance, the addition of random effects improves the model fit in both types of models, though significantly more for growth rate models.

Mixed Model Random Effects	Cluster Likelihood	Diameter Growth	Height Growth
σ^2	3.29	0.12	0.1
$\tau00$	0.37	0.06	0.05
ICC	0.1	0.32	0.34
Observations	5196	5196	5196
Marginal R^2 / Conditional R^2	0.316 / 0.385	0.373 / 0.575	0.377 / 0.588

Table A4

Breakdown of clump membership by species showing the proportion of each cluster category made up by each species. White fir dominated across all clump categories.

Species	Clump Size Individual	Small Clump	Medium Clump	Large Clump	Extreme Clump
ABCO	0.301	0.376	0.417	0.421	0.797
CADE	0.097	0.143	0.125	0.064	0.104
PIJE	0.247	0.197	0.217	0.203	0.009
PILA	0.127	0.102	3065	0.029	0.034
PIPO	0.053	0.047	0.042	0.05	0.011
QUKE	0.085	0.045	0.038	0.034	0.022
Other	0.091	0.09	0.096	0.198	0.024

Table A5

Calculated diversity metrics by clump size. Large clumps had the highest estimated diversity values while small clumps had the lowest.

Diversity Metrics by Clump Size Clump Type	Ave. # Species	Shannon Diversity	Ave. Evenness
Small Clump	1.47	0.2841	0.3906
Medium Clump	2.23	0.5059	0.5295
Large Clump	2.91	0.6493	0.5733
Extreme Clump	2.31	0.5062	0.5231

Table A6

Results of Tukey HSD tests comparing calculated diversity metrics across clump sizes. Medium and large clumps were found to have a significantly higher value than small clumps, while other tested pairwise comparisons were not significant.

Estimated Difference in Average Diversity by Clump Size Clump Type 1	Clump Type 2	Diff. Estimate	Conf. low	Conf. high	P Value
Small	**Medium**	**0.139**	**0.026**	**0.252**	**0.009****
Small	**Large**	**0.183**	**0.000**	**0.365**	**0.0494***
Small	Extreme	0.133	−0.183	0.448	0.700
Medium	Large	0.044	−0.159	0.247	0.945
Medium	Extreme	−0.006	−0.334	0.321	1.000
Large	Extreme	−0.050	−0.408	0.307	0.984

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