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Clustering and growth patterns for natural regeneration in Sierra Nevada mixed-conifer forests with a restored fire regime

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Clustering and growth patterns for natural regeneration in Sierra Nevada mixed-conifer forests with a restored fire regime

By

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I. Abstract

Many, dry western conifer forests were historically adapted to high frequency, low-to-moderate severity fires but are increasingly susceptible to large, stand-replacing wildfires due to dramatically altered stand conditions, as well as the effects of climate change. The historic spatial patterns of fire adapted forests: individual trees, clusters of trees, and openings (ICO), have displayed heightened resistance and resilience to fire. How this pattern develops, however, is not well understood and could help inform reforestation practices better designed to increase fire resistance in young stands. We investigated growth and spatial patterns among regenerating tree species in mixed-conifer forests with restored fire regimes in California's Sierra Nevada. We collected and analyzed spatial patterning and growth rate data at 429 plots in eight different sites in old-growth, mixed-conifer forests with two to five low to moderate severity fires within the last 60 years. We compared average stocking rates of regenerating stems across species, shrub conditions, size classes, and fire histories. We also examined the effects of site fire history and topography on spatial patterning, and the effects of clustering, local density and adjacent shrubs on tree growth. We found very high seedling regeneration rates especially among white fir. The majority (75%) of sampled seedlings were within clusters. Our modeling results indicate that although increased crowding within clusters predictably had a negative impact on growth, growth rates within clusters were significantly higher than growth rates for individual trees. Although high shrub cover was found to negatively impact small seedlings (<137 cm tall), it was associated with increased growth and stocking rates among the oldest (>15 Years) and tallest (> 137 cm) seedlings, respectively. Our results suggest that clustered patterns of natural tree recruitment, as well as proximity of older clustered seedlings to shrub cover in active-fire forests may favor the establishment and growth of regenerating conifer stems. Our findings indicate

there may be a benefit to establishment and early growth of seedlings in clusters possibly due to their modification of the surface microclimate and their density keeping shrubs 'at bay'. While our study focused only on the early stages (<30 years old) of regeneration, our results are at odds with common reforestation strategies favoring regularly, widely spaced plantings and aggressive shrub reduction. Our research suggests we need a better understanding of how heterogeneity in seedling, shrub and gap patterns may enhance the resilience of regenerating stands as they mature.

1. Introduction

Prior to European settlement many western U.S. forests, 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, more homogeneous stands susceptible to high-severity wildfires (Stephens et al., 2016). While increases in surface and ladder fuels are known to increase fire intensity, recent research has shown that highly heterogeneous tree spatial patterns characterized by individual trees (I), small clumps (C), and openings (O) (hereafter ICO) (Lydersen et al., 2013; Kane et al., 2019) can result in greater stand resilience because it slows fire spread and decreases the potential for crown fires (Larson and Churchill, 2012). This spatial heterogeneity of frequent-fire forests may also have important ecosystem effects including 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; Stevens et al., 2016). Much recent attention has been focused on restoring fire- resistant and -resilient western forests through reinstating historic fire regimes and strategically lowering the fuel load, often through density-reduction using thinning or controlled burns (Larson and Churchill, 2012; Stephens, 2017; North et al., 2009). However, less attention has been paid to strategies that restore ICO patterns though heterogeneity of tree density and patch sizes, though such spatial patterns may be important for maintaining or regenerating forest structure after fire (Kemp et al., 2015).

With millions of hectares of forest now burning in Western North American forests each year (Hoover and Hanson, 2021), it is increasingly important to investigate both stand conditions and management practices that promote the development of fire- resilient forests "from the

ground up" --- i.e. through forest regeneration (Stevens-Rumann and Morgan, 2019; North et al., 2019). Many current reforestation practices use a regularly-spaced planting pattern focused on regenerating pines at relatively high densities to help shade out competing vegetation, particularly shrubs that vigorously germinate and re-sprout after high-intensity fire and are thought to suppress tree recruitment (Coppolleta et al., 2016). This planting pattern, however, is prone for several decades after planting to burning at high severity and, in the absence of natural recruitment, can produce regularly-spaced mature pine plantations. Despite these drawbacks to traditional reforestation practices, there is a surprising lack of research on alternative planting patterns. It has been suggested that planting patterns that promote spatial heterogeneity may create more variable fuel loads, limiting crown fire potential, and creating fuel breaks in openings (North et al 2019).

Skepticism surrounding alternative planting strategies focuses on the greater difficulty in designing and implementing irregular planting patterns, as well as uncertainty of what levels of clumping and species composition may optimize growth or other beneficial ecosystem traits such as fire resistance and carbon sequestration potential. Clumped plantings may lead to increased competition among seedlings, resulting in slower growth rates and stand recovery (North et al., 2019). However, empirical or observational studies of alternative plantings or natural regeneration spatial and growth patterns are limited. As manipulative experiments investigating the effects of clustered patterning on growth rates can be time consuming and costly to implement, a complementary approach to investigating these alternative patterns is to analyze *in situ* growth and regeneration dynamics in areas with a restored frequent fire regime and the resilient ICO patterns this disturbance regime fosters.

1.2 Project Objectives

Initial surveys of our sampling areas found a high degree of clustering (i.e. stems growing within a neighborhood of potential influence) in regenerating conifer seedlings; a contrasting pattern from regularly spaced individual seedlings typical of many western U.S. reforestation projects. In response, a focus of our study was comparing growth rates of clustered trees with individual trees and comparing trees in clusters of different sizes and densities. We sought to quantify the establishment, growth, and spatial pattern of regenerating conifers in old-growth, mixed-conifer forests with restored fire regimes. Specifically, we focused on the following questions:

1) What are the regeneration patterns in active fire forests (i.e., relative percentage of seedlings growing as individuals and in clumps by species) and how do they vary with seedling age, site fire history, and topographic variables?

2) What are the relationships between clustering pattern (i.e. individual vs. clustered patterning, and relative cluster size and density) and growth rates of seedlings within and across sites, and how does this vary across species and seedling age?

3) How does site fire history (i.e., fire frequency and time since last fire) and competing shrubs affect seedling growth and clustering patterns?

2. Methods

2.1 Study Sites

Study sites were selected among old-growth (not previously logged) stands in Yosemite National Park and Kings Canyon National Park, located between 600 and 2,100 m in elevation (Figure 1). Study areas were primarily in mixed-conifer and ponderosa pine forest types.

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 to support statistical analysis.
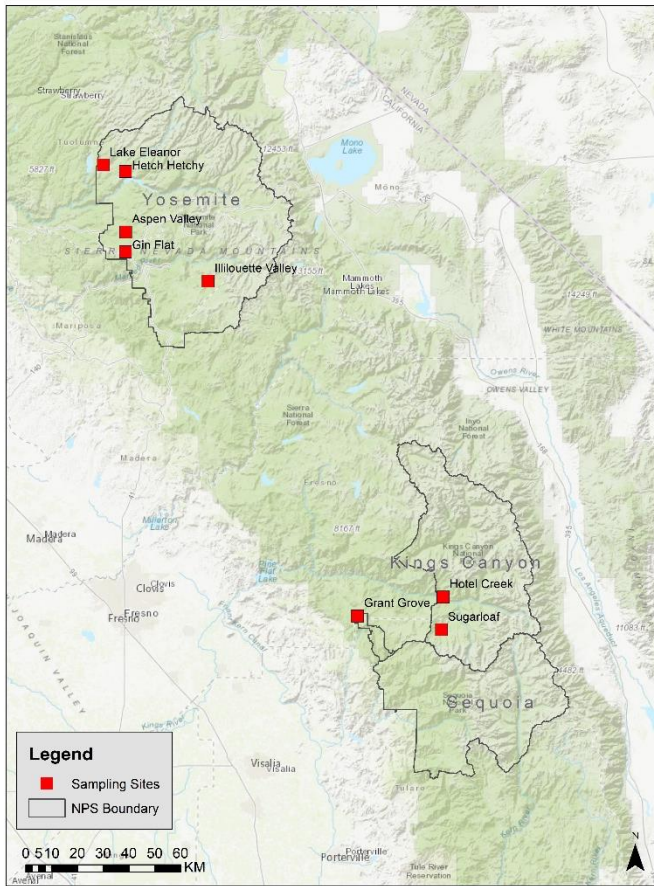

Figure 1. Map of study sites sampled in 2019 and 2020

All sites are currently managed to let natural ignition wildfires burn without suppression and have been since the late 1960s and early 1970s (Lydersen and North, 2012). Sites were selected based on a criterion of having at least two fires in the past 60 years, with the most recent fire having occurred in the past 20 years (from 2018). These criteria were used to select sites that approximate the historical range of variation in fire return interval for the dominant forest types (Barrett et al. 2010) and an earlier study suggesting that two burns may drive forest stands to approach pre-suppression structure (Lydersen and North 2012). To determine burn severity, we used CALFIRE burn perimeter and severity datasets, and selected sites that had only burned at low to moderate severity. In

addition, we further filtered sites using CalVeg GIS database map identification as "Mixed-Conifer" or "Ponderosa Pine" forest types.

2.2 Data Collection

Eight sites in Yosemite and Kings Canyon National Parks were sampled over two summer field seasons. Each site had one or more sampling areas, where sampling areas were classified by both the number of fires the site had experienced and time since last fire since these factors can affect the biotic community (McLauchlan et al., 2020). In total, this categorization resulted in 26 unique "fire history" sampling areas for our analysis to help determine what relationship may exist between number of burns, time since burn, and site regeneration patterns. Depending on the size and shape of the identified sampling area, plots were located either in a grid-based pattern with a random starting point and azimuth, or randomly distributed within the sampling area based on randomly generated azimuths.

Within each sampling area, plots consisted of variable-width circular plots to examine spatial patterns and density of seedlings. We adjusted and recorded the size of the sampling area using the following criteria to efficiently census regeneration, which was often either sparse or highly concentrated. Circle plot size was determined by seedling density. Plot sizes were chosen to include a minimum of 20 seedlings with larger plot diameters implemented at gradations (1 m, 2m, 4 m, 5.64 m, 8m, 12.6m) until at least 20 seedlings were recorded or the maximum plot radius (12.6m) was reached. Within each plot, species, height, diameter, condition (live or dead) and relative location to plot center (azimuth and distance) was recorded for every seedling/sapling >10 cm tall and less than 5 cm diameter at breast height (DBH) for all conifers

and oak species. Age of each regenerating stem was approximated using visual whorl counts (Hättenschwiler and Smith 1999). All crew members were trained in whorl counts and age estimates were calibrated using a destructive sampling of different species and sizes of seedlings from outside the sample areas. Additionally, for each individual regenerating stem and clump, the percentage shrub cover and dominant species within a 2m radius was recorded to estimate shrub cover effects on growth rate and spatial patterning. Site-level information including aspect, slope, shape (concave, flat, convex), and exact location were recorded at each plot.

Belt transects were sampled between circular plots or at randomly selected azimuths out from circular plots, with belt width varying to account for tree density. The belt width began at 4m and shrunk by half for every 12 trees measured down to a minimum width of 1m. For every stem within the transect width, species, height, ground diameter, and approximate age were recorded, as well as percentage shrub cover within a 2m radius. Aspect and slope were measured either from field measurements or extrapolated from a 1 m digital elevation model and categorized by cardinal direction and relative steepness: Flat (1-15%), Moderate (15-35%, and Steep (>35%) slopes. Any changes in either variable was recorded along the transect to capture topographical variation across the sampling area.

Field crews sampled 216 circular plots and 213 transect plots, collecting data on over 10,000 trees. Each individual tree location was entered into a spatial data frame, resulting in a complete stem map for all regeneration within sampled circular plots.
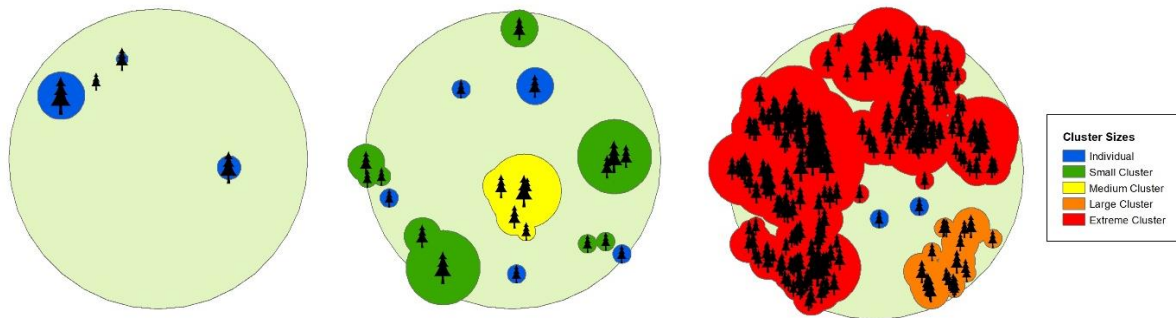
2.3 Cluster Pattern Detection

Figure 2. Example plots featuring different clustering patterns and identified buffers ranging from very sparse with a few individual trees to highly clustered, dense patterning

Because an important aspect of this study was to determine the impact of non-homogeneous spatial patterns (i.e. clumping) on seedling growth and mortality, trees were identified as either individuals or members of clusters. To assess whether each individual stem was a member of a cluster, circular horizontal buffers were assigned outward from the base of each tree with buffer diameter determined by height (0.25 m for trees 10-50 cm, 0.50 m for 50-100, 1.0 m for trees 100-137, and 2.0 m for trees >137 cm) to approximate a "neighborhood" of influence based on estimated lateral root spread. 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 clustering analysis, though not at the scale of regenerating trees and seedlings. (Lydersen et al., 2013; Plotkin et al., 2002; Ng et al., 2020; Meador et al., 2011). The lateral root spread of seedlings varies significantly across species and individuals and may be highly dependent on environmental and microsite conditions (Stein 1978). However, 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 (Stein, 1978; Casper and Jackson, 1997). To further test the robustness of our cluster analysis assumptions, all analyses pertaining to our cluster

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identification schema were subsequently run with a range of defined buffer sizes (all buffers 25% larger, 25% smaller, all buffers set to 0.5 m, and all buffers set equal to stem height with a maximum buffer diameter of 2m) to determine how our results might vary with different buffer sizes.

Buffer polygons were subsequently spatially dissolved based on overlap, and individual trees within each clump polygon were summed inclusively to determine the number of trees in each clump. Trees were assigned either Individual or Clumped status based on the absence or presence of an overlapping "neighborhood" buffer centered on each stem. Clumped trees were additionally assigned categories based on the number of trees in their member cluster to determine the effect of clump size on growth metrics (Kane et al., 2019). Categories assigned were: small cluster (2-4 trees), medium cluster (6-14 trees), large cluster (15-49 trees), or extreme cluster (>50 trees)

2.4 Analysis and Modeling

Following data entry and post-collection processing, all statistical analyses were performed in R software V.3.6.3 (R Core Team 2020) unless otherwise noted.

First, we calculated summary statistics of the data to assess patterns of regeneration establishment and clustering across species and site variables. Regeneration counts were averaged by plot, species, height, topographic category, and fire history to obtain average stocking densities through estimates of trees per hectare (TPH) (Welch et al., 2016). Estimated TPH values were grouped in different height categories as a proxy for estimating stocking at different seedling ages.

Tree counts by species and cluster type were evaluated across topographic and specific site fire history to characterize establishment, clumping patterns, and density across the study area. We used grouped trees by individual clusters and cluster sizes to obtain average number of species, average height, and standard deviation of height in clusters of each category as a way of characterizing the patterns we observed in clusters of different sizes, and to examine the species, height, and age dynamics within individual clusters. To compare diversity across cluster sizes, we measured within-cluster diversity and evenness using Shannon's Diversity Index and Pielou's evenness metric in the Vegan R package (Okansen et al., 2019). Post-hoc ANOVA comparison of calculated metrics by cluster size using Tukey's Honest Significant Difference Test (HSD) was made to determine if a significant difference could be detected.

Mean annual diameter growth rates were calculated by dividing the stem diameter at ground level of each stem by the estimated age of the seedling. Average growth rates were calculated by species, cluster status (if the tree was identified as an individual or member of a cluster of any size), and age group. Post-hoc ANOVA comparison of calculated metrics by cluster size using Tukey's Significant Difference Test (HSD) was made to test differences in growth rates between clustered and individual trees across species and age classes.

2.4.2 Modeling effect of topographic variables and fire history on regeneration clustering pattern

We fit generalized linear mixed-effects models (GLMMs) using the glmer function in the lme4 R package (Bates et al., 2015) on cluster data and individual tree data, to evaluate the influence of topographic variables and fire histories on cluster patterning. We first applied a binomial logistic distribution GLMM on individual tree data to assess probabilities of a regenerating stem being a member of a cluster or an individual. For our logistic clustering

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model, sampling site was applied as a random variable and predictor variables included the number of fires for each site, a categorical variable to indicate when the most recent fire was (Recent :<10 years or Older:>10 years), slope category (flat, moderate, or steep, aspect category (SW or non-SW) and scaled continuous variables for elevation and tree age. Models were evaluated and selected based on calculated Akaike's Information Criterion (AIC) scores.

2.4.3 Modeling effect of clustering 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 clustering pattern and specific fire site history affected annual growth rates of regenerating seedlings. For all our hierarchical growth rate models, "Plot" was entered as a random variable to partially account for plot and site-level variables affecting growth and spatial patterning that were not captured during data collection. Mean annual stem growth was calculated for each seedling based on estimated age and measured ground diameter, and used as a response variable for our models. Scaled continuous variables for seedling age, and cluster density, and categorical variables for seedling species and cluster type (individual tree, small cluster, medium cluster, large cluster, and extreme cluster) were included as predictor variables. Cluster density for clustered seedlings was calculated by dividing the number of stems in each cluster by the area of the cluster (calculated from the polygon of intersecting tree buffers) to obtain a "stems per meter" metric. For individual stems, distance to nearest neighbor was used as a radius for calculating a neighborhood area. A "stem per meter" metric for use in our model density variable was then obtained by dividing 1 by the calculated neighborhood area. Our outcome variable of mean annual growth rate was calculated by dividing the measured stem diameter with the estimated age of the seedling.

Models were evaluated and selected based on calculated AIC scores. Using our model selection criteria, we developed and selected two models to describe annual mean growth rate patterns among regenerating seedlings. Our first model looked at growth rates with our clustering predictor variable a binomial categorical variable identifying seedlings only as a member of a cluster or as an individual. Our other model was developed specifically to look at differences between cluster sizes and looked only at clustered trees with a categorical variable identifying what size cluster the regenerating stem was a member of (small [2-5], medium [5-15], large [15-50], or extreme [>50]).

3.Results

3.1 Seedling Inventory and Stocking Density

Stocking estimates of regenerating stems were very high compared to mean regeneration stocking estimates from other mixed conifer reference sites when including all seedlings greater than 10 cm in height (Safford and Stevens 2017). Trees per hectare estimates declined with increasing the height threshold. Regenerating white fir (ABCO) stems were the principal driver of these high counts across sites and height classes.

Estimated Trees Per Hectare Values by Height Class

	Age Estimates for Height		Species TPH Estimates						
	Mean(Median)	Range	ABCO	CADE	PIJE	PILA	PIPO	QUKE	TotalTPH
All Regene >10 cm	7 (6)	1-38	5,120	725	448	488	193	67	7,714
10-25 cm	3 (3)	1-33	3,421	411	210	310	40	35	4,765
25-75 cm	8 (8)	2-30	1,226	212	115	83	121	12	2,011
75-137 cm	13 (13)	4-35	284	19	41	10	9	5	404
>137 cm	18 (18)	5-44	39	15	23	7	0	21	181

Figure 3. Table showing TPH values by size class and species with adjacent graph showing proportion of each species by size class

The distribution of stocking density by height class differed between sites with the most recent fire occurring less than (Recent) or greater than 10 years (Old) ago (Figure 4). Regeneration densities were slightly, though non-significantly (P-value >.05) higher in areas with more recent fires, especially of recent regeneration (stems 10-25 cm in height), and among white fir and incense cedar seedlings.

Stocking density estimates in plots with high shrub cover (>50%) were lower for shorter stems, but significantly higher among stems >137 cm in height (p value <.001 per Tukey HSD). See Figure 6, and supplemental for more information and figures relating to these findings.
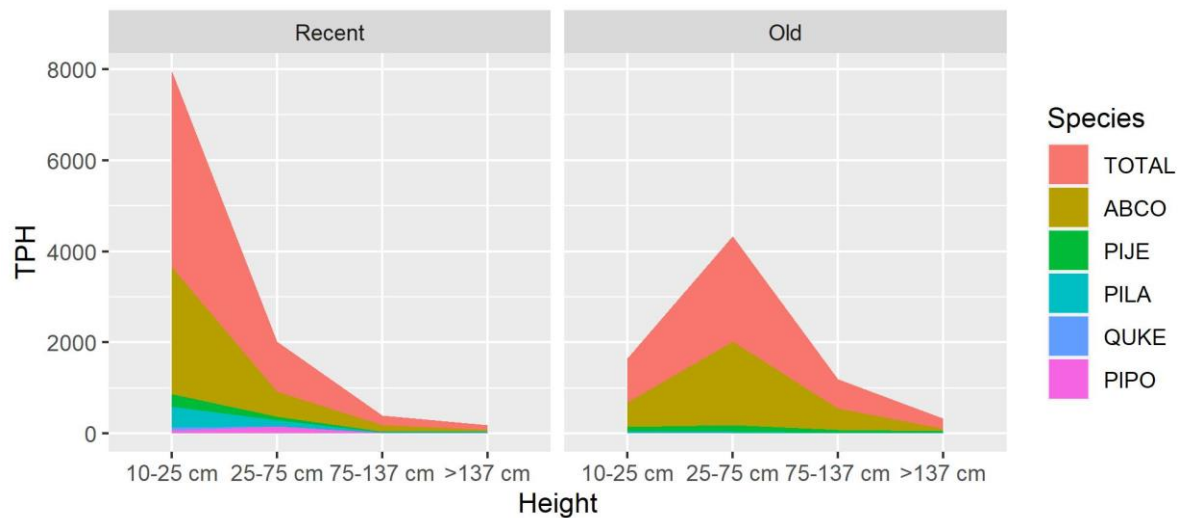
Figure 4. Stocking Density Estimates in old and recent fire sites. Differences in stocking levels between sizes classes are clear as a "shifting peak" can be observed moving from the smallest to a more intermediate height class as time since fire increases.

3.2 Clustering Patterns

Altering the sizes of the assigned buffers did somewhat impact our parameter coefficient estimates, as well as the percentage of trees in each cluster category. However, the trends in our results remained generally consistent: across all buffer sizes, the majority of sampled trees were found to be a member of a cluster, our clustering probability model found that age and increasing time since fire increased likelihood of clustering, and being a member of a cluster was positively

associated with growth. Given these results we opted to present the values and estimates calculated from our original tiered buffering scheme, though further empirical research to better elucidate a seedling's exact neighborhood of potential influence is needed.

3.2.1 Cluster Membership Across Species

The majority of regenerating stems across plots, fire histories, and species were found in clusters, defined here as all groupings of greater than one regenerating stem with intersecting buffers. Exact breakdown of cluster membership varied by species, with white fir having the largest percentage of trees in clusters (85% of all sampled trees), and black oak having the largest percentage of individual trees (45% of all sampled trees). White fir made up the plurality of all species across cluster types, and among extreme clusters (>35 trees) it accounted for 78% of all seedlings (Table A.2). Pines collectively accounted for 43% of individual trees. Jeffrey pine made up a sizable proportion of trees across individual-large clusters (all between 19-25%), and less than one percent were in extreme clusters.

3.2.2 Patterns within clusters analysis by cluster type

Significant differences were detected across cluster types by our applied metrics. Large cluster averages had significantly higher ($p < .001$) average number of species (2.9), average height (68 cm), and standard deviation of height (43) within the cluster, when compared to all other cluster types. Small clusters had the lowest values in all three categories.

Calculated diversity and evenness index values averaged by cluster size, per Shannon's Diversity Index, were significantly higher in large clusters than either medium or small clusters. Although the average values of both metrics for extreme clusters was smaller than for large and medium clusters, it was not significantly distinct from small, medium, or large clusters.
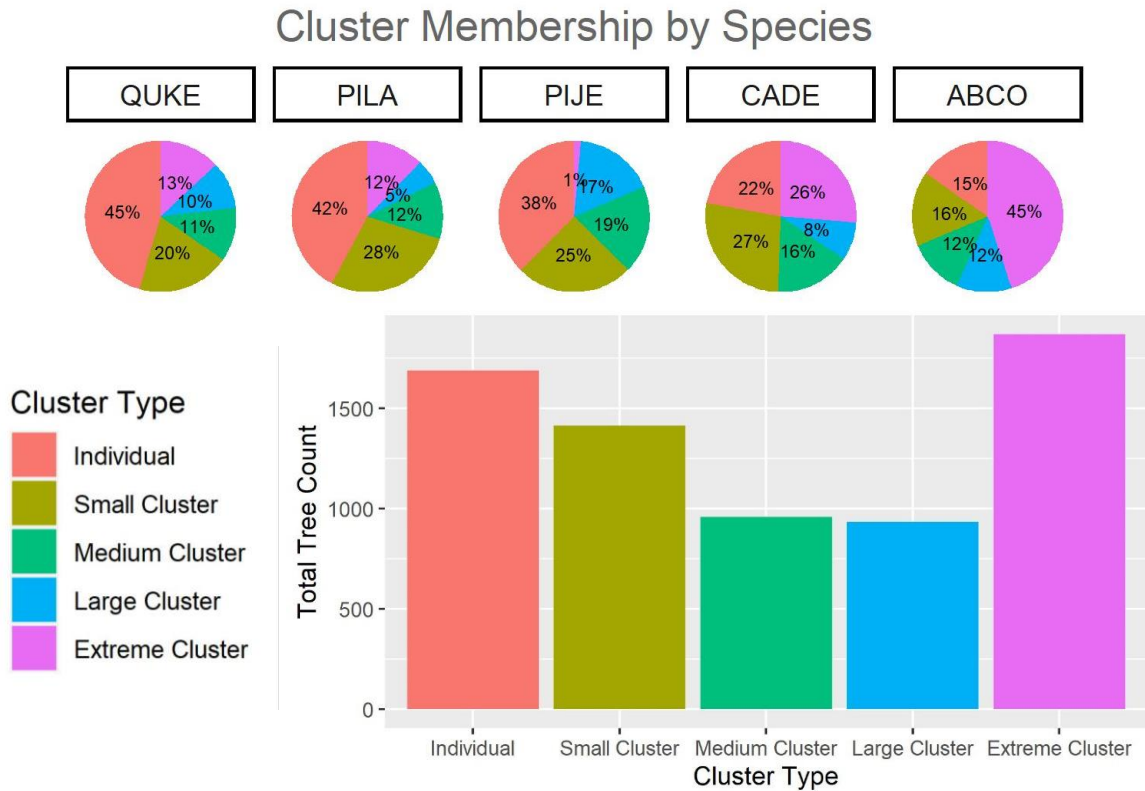

Figure 5. Cluster membership overall and by species. The majority of stems of all species were found in clusters of some kind.

3.2.3 Modeling of Clustering across Topographic Patterns and Fire: Logistic Model

Predicted bootstrapped probability estimates (n=500) generated from an expanded grid combination of all predictor variable values from our binomial mixed model indicated that regenerating stems in sites which had experienced their most recent fire >10 years prior were

significantly more likely to be in clusters than those in younger fires across species, slope
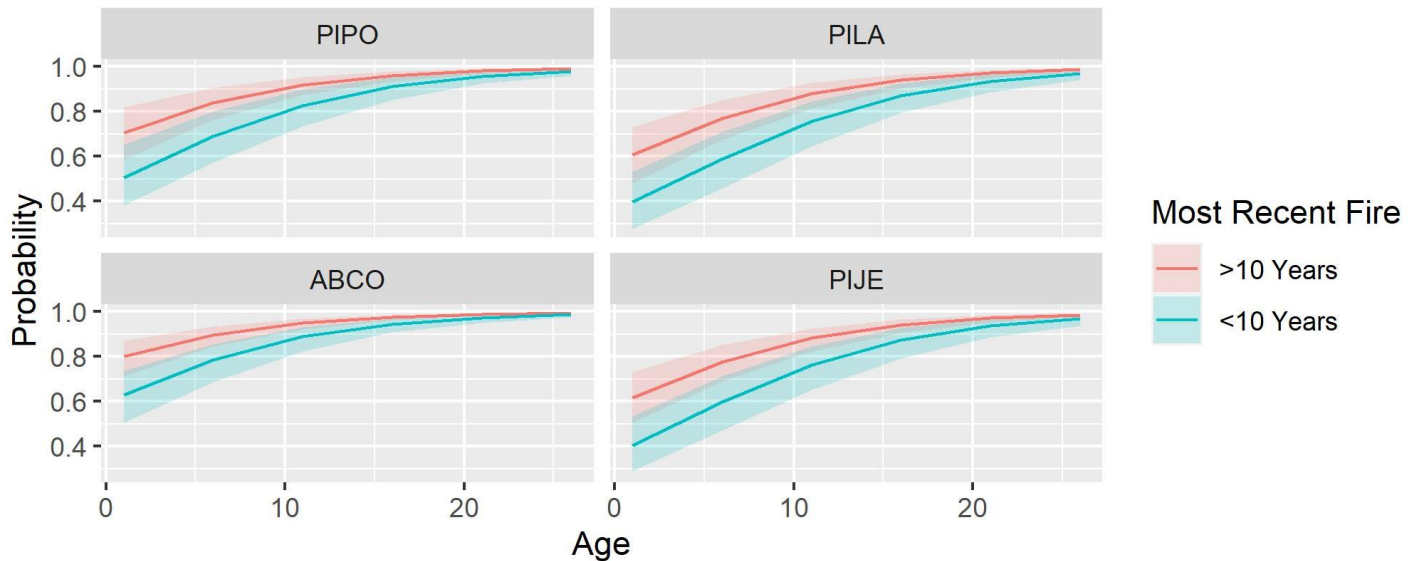
categories, and aspect categories (Figure 6).

Figure 6. Predicted bootstrapped probability estimates of a seedling being a member of a cluster across seedling ages by tree species. The probability of clustering is increased in sites that experienced fires less recently and increases as trees age.

Predicted estimates also showed that the likelihood of clustering increases significantly as

seedlings age. Among the species included in the analysis, white fir was the most likely to be

growing in a cluster (mean estimates >50% across age range 1-30).

3.3 Growth Rates by Clustering Type

Trees in clusters grew significantly faster in diameter across stems of all ages for white

fir, Jeffrey pine, and ponderosa pine (all Tukey's HSD, $P<0.05$) (Figure 7). A comparison across

different age categories (Ages 1-5, 6-11, 12-19, and >20) between white fir and yellow pines

(Jeffrey and ponderosa pine grouped together for comparison) revealed that growth rate averages

among clustered trees were significantly greater ($P<0.05$) for yellow pines ages 1-5 and 6-11, as

well as for white fir ages 1-5. Older age groups in yellow pine did not demonstrate significant

mean growth differences. White fir exhibited a negative significant difference between mean

growth rates of clustered and individual trees for stems aged 12-19 (Table A.2.).

Selected models indicated that individuals had grown in diameter significantly slower than all cluster types over all species. In our model examining different cluster types (small, medium, large, and extreme clusters) there were not significant detectable differences between cluster types on growth rates.

In our first model, shrub cover was not significantly related to differences in growth rates between clustered and individual trees. However, our selected model for clustered trees revealed a statistically significant interaction between age and shrub cover suggesting that although shrubs were negatively correlated with growth rates in younger (1–10-year-old) seedlings, they were positively correlated with growth rates in older (Age >10) seedlings (Figure 8). The estimated coefficient for our predictive variable measuring seedling density or crowding within clusters was significantly negative.
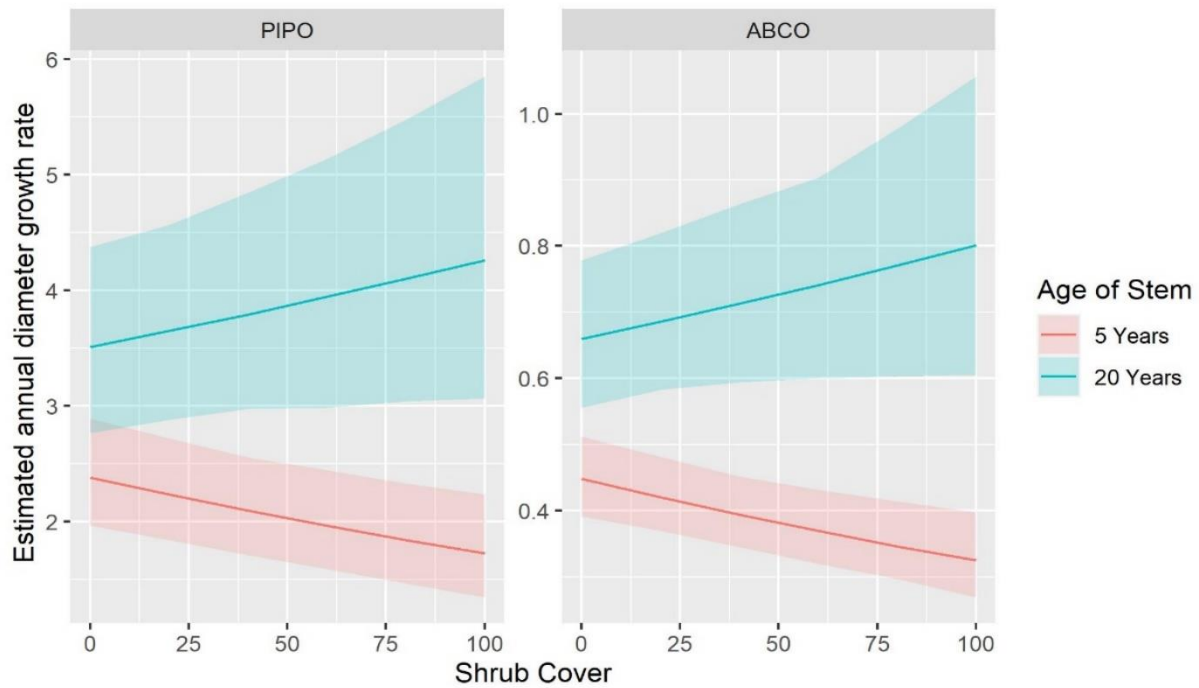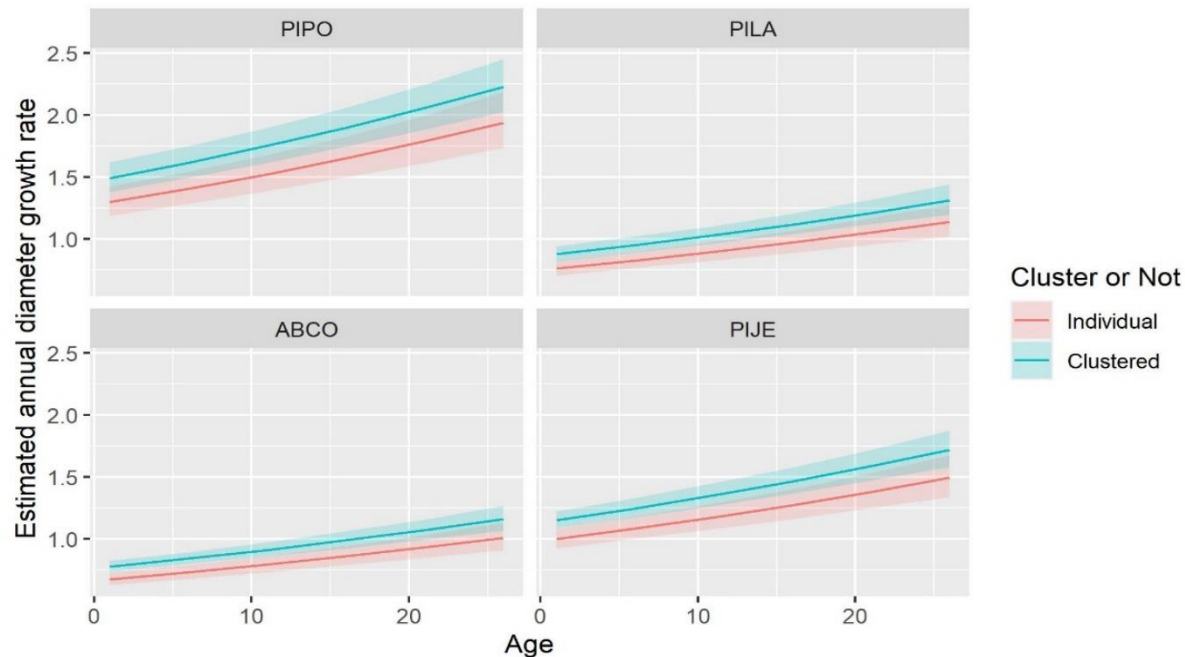

Figure 7 and 8. Binomial model with clustering as a binomial categorical predictor of diametric growth rate (Above). Predicted results from model looking only at clustered trees and containing an interaction between shrub cover and tree age (Below).

4. Discussion

4.1 Overview

    As far as we know, our study is the first to investigate spatial patterning and growth rates of regenerating seedlings in active-fire mixed-conifer forests at fine spatial scales. We found high regeneration rates relative to traditional reforestation stocking goals among seedlings across size classes, likely due to abundant overstory seed production in the year of the fire and frequent fire providing mineral soil seed beds that encourage emergence and establishment (Larson and Churchill, 2012; Welch et al., 2016). The majority of seedlings, regardless of species were found in clusters. Sites that experienced their most recent fire >10 years before sampling were more likely to have stems in clusters, indicating infilling is occurring within clusters, even as some expected thinning out of seedlings is occurring at older age classes. Increasing tree densities within a cluster (i.e., local 'crowding') was associated with reduced stem grow rates, suggesting competition. However, contrary to traditional silvicultural doctrine, our models indicated that clustering had a positive effect on stem diameter growth at moderate to high densities within the

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age range we extensively sampled (1-30 years). There was no significant difference in diameter growth rates between cluster sizes.

There were several limitations to this study that may have influenced our results. First, accurate annual growth rates of regenerating seedlings 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, age could not be directly measured. However, off-site calibration of our whorl count age estimation to seedling ring-counting suggest that our estimates were relatively accurate. 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. Finally, a significant challenge for this study was in the delineation of the "zone of influence" of the regenerating trees for identification of clusters and cluster size. ICO analyses for adult trees have typically created a competition zone buffer based on crown width as light is believed to be among the most limiting growth-resources (Ng et al., 2020; Lydersen et al., 2013). However, due to the small stature of the seedlings and saplings we studied, and their position in the forest understory where competition for below-ground resources is of critical importance (Gray et al., 2005), we believe that an approximation of root diameter based on height was a reasonable proxy for determining a neighborhood of putative seedling interactions.

4.2 Natural Regeneration Patterns in Sampled Sites

We found high rates of regeneration when averaged across sites, topographic variables, fire histories, and shrub conditions, although seedling density was highly heterogeneous across and within sites. These high regeneration estimates are consistent with other studies of post-fire

regeneration, which found regeneration rates peaked in areas that experienced low and moderate severity burns during their most recent fire (Welch et al., 2016; Crotteau et al., 2013).   Across the range of topographic variables and fire histories sampled, white fir was the primary species driving high stocking estimates among regenerating stems, similar to findings in 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, 2021; Zald et al., 2008). We also found a steady decrease in the stocking numbers of trees at increasing mean seedling height intervals. The increased resource requirements of taller trees may explain this thinning (Pommerening and Meador, 2018).

The high stocking regeneration rates we observed in active fire areas, and especially in areas that had experienced more recent fire, may be rooted in the dynamics of frequent fire systems. Returning frequent, low-intensity fire may generate patches of bare-mineral soil, constantly renewing available substrate for conifer seed germination and establishment (Larson and Churchill, 2012) Though we observed somewhat of a drop in net recruitment of small seedlings in older stands compared to recent fire sites, there were also relatively high seedling densities of the smallest size class for several species (533, 105, and 112 TPH for white fir, incense cedar, and Jeffrey pine, respectively). This suggests ongoing recruitment and infill is happening in areas with less recent fire, and that all regeneration post fire is not just part of a single post-fire cohort of seedlings. 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 (Meador et al., 2011).

4.3 Clusters: Size and Composition

Over 50% of regenerating seedlings across species were identified as being a member of a cluster, consistent with Keyes et al., (2007), who found that the majority of establishing ponderosa pine seedlings were found in clusters at emergence, and for two seasons following. Though white fir was the most likely species to be found in a cluster (and the species that dominated clusters of any size), all cluster sizes greater than the smallest category (2-5 trees) averaged more than one species within a cluster. Our diversity analysis on clusters indicated that diversity and evenness indices tended to increase as cluster size increased. However, once clusters reached the "extreme cluster" size category (>50 trees), diversity and evenness metrics decreased and were not distinct from those of medium clusters. This suggests that dense thickets of shade-tolerant white fir (the species that constituted ~ 78% of extreme cluster membership) may preclude meaningful establishment by other species.

Likelihood of Clustering

Our logistic clustering model results indicate that regenerating stems in sites with older fires are more likely to be found in clusters, and that likelihood of clustering further increases with tree age and slightly with an 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, clustering likelihood differed with topographic variables such as slope and aspect. Our model predicted that clustering 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 clustering on southwest facing slopes,

Elliot and Kipfmueller (2010), also found similar clustering patterns on sub-alpine south-facing slopes. This could indicate that abiotic extremes may contribute to increased stress-mediated facilitation in trees clustered in habitable microsites.

4.5 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 seedling growth rates. Many studies have found that high shrub cover negatively impacts seedling growth (add cites), but there is less information on shrub cover effects on early seedling establishment and survival (Tubbesing et al., 2021). Shrubs have been shown to be a strong competitor with young seedlings in areas with low soil-moisture, at least until they develop a deeper root structure (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 (Sthultz et al., 2007; Gomez-Aparicio et al., 2004) and even provide mechanical protection and ameliorate climactic 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 (Oliver, 1979; McDonald and Fiddler, 1989; McDonald and Fiddler, 2007), we are not aware of other studies comparing growth rates in highly clustered regenerating stands. One possibility to explain the dynamic we observed is that in frequent-fire forests naturally develop clumped regeneration, clusters of trees may prevent complete encroachment by shrubs unlike in regularly spaced plantations where shrubs can effectively surround and 'swallow' a single gridded seedling.

Shrub cover did have a significant effect in our second growth rate model examining only trees in clusters, and included an interaction between age and shrub cover for seedlings. The

coefficient estimate for shrub cover was negative for younger seedlings (<10 years old) but switched to a positive association with older (> 15 years), and likely taller, trees. Though we did not measure surrounding shrub height, this positive relationship may kick in once seedlings had emerged above the shrub canopy and no longer suffered from low-light conditions from the surrounding shrub cover (Oakley et al., 2006). This possible facilitation of older seedlings and saplings by shrubs is consistent with our calculated stocking estimates where TPH estimates were consistently higher among the tallest tree classes (trees >137 cm in height) in high shrub cover plots (>50% cover) across all major species.

The faster growth rates found among seedlings in high shrub cover plots may simply indicate superior microsite conditions for both shrubs and trees. Alternatively, one possible explanation for this phenomenon is that the spatial variability of seedling clusters within large shrub patches may create greater heterogeneity in burn intensities and potentially allow patches of seedlings to survive the most recent fire. Additionally, depending on the burn weather conditions shrubs may have high moisture content from recent rain, reducing fire intensity and preventing complete incineration of regenerating seedlings that are buffered within shrub patches (North et al., 2019; Lutz et al., 2017; Pellizzaro et al., 2007; Zhou et al., 2005). If this is the case, it is possible that shrubs could be an important aspect of contributing to increased resistance to fire even among young regenerating patches.

4.6 Clustering and Growth Rates

Our models detected a robust positive association of clustering with higher rates of seedling growth but did not reveal any significant differences among cluster sizes. This suggests that clustering may be beneficial for conifer seedlings in this range of fire ages (<30 years) in frequent-fire, naturally regenerating stands. The idea that clustering may be beneficial for tree

regeneration may seem counter-intuitive, as competition has long been considered one of the most basic driving tenets of plant community ecology (Pommerening and Meador, 2018). Our results are not, however, in conflict with this classical view of competition: we found that higher density or "crowding" of seedlings was negatively correlated with growth (Pommerening and Meador, 2018). Model predictions estimated that clustered trees at the median seedling age in our sampling (6 years) fare better than individual trees growing at the smallest possible density (.0005 stems per meter) up to a density of about 7 stems per meter, indicating that proximity to other seedlings may provide benefits for individual regenerating trees that outweigh the negative impacts of crowding at moderate and even high densities, and that the number of trees within a cluster (cluster size) does not hinder growth of seedlings.

Although we were not directly investigating mechanisms driving establishment and growth rates of seedlings in clusters, we suspect that the highly heterogeneous structure of mostly clustered seedlings may be providing some facilitation, possibly through modification of microclimate that favors regenerating trees (Elliot and Kipfmueller 2010; Calder and St. Clair, 2012). Other seedling establishment studies focusing on mortality have also found that natural recruitment often begins in large, clustered groups, and although clusters often shrink in size, as seedlings age, they are not eliminated (Vander wall, 1992; Keyes et al., 2007). Strictly mimicking this pattern would be labor intensive and a profligate use of expensive nursery seedlings. Silviculture's focus has always been on how to achieve a desired stand condition in altered environments such as forests with less frequent and more intense fire patterns. Our results point to the value of structural heterogeneity in regenerating stands, both from the standpoint of growth, plant diversity, and fire resistance and resilience. The patterns 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 forests.

5. Management Implications

Tree spatial patterns are a critical component of resistance and resilience to fire, a management concern in the Western U.S., and elsewhere (Larson and Churchill, 2012, North et al., 2019). Though there is increasing evidence that spatially heterogeneous growth patterns among mature trees characterized by ICO are more resistant and resilient to fire (Stephens et al., 2016; Lydersen et al., 2013; Koontz et al., 2020), traditional reforestation practices continue to use regularly spaced rows of planted seedlings, which does not reflect the spatial patterns in areas with a more active fire regime (Lydersen et al., 2013). Though we did not find evidence that clustering impedes seedling growth rates in this study (a key hesitation in planting or encouraging clustered growth patterns in reforested areas), it is certainly possible 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, natural clustering 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 perpetuate heterogeneous burn and natural recruitment patterns, further reinforcing this resilience as the stand matures (North et al., 2019). The continued recruitment of young seedlings in stands with older fires also supports the idea that, particularly in natural tree regeneration, initial recruitment and establishment in stands after fire may be the biggest bottleneck to stand restoration (Davis et al., 2019; Stewart et al., 2021). Though the limits of this study cannot identify the best management practices for increasing fire resistance in regenerating

western forests, our unexpected findings of positive effects of clustering and shrub cover on seedling growth rates merits further investigation. 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 stand resilience to fire.

6. Conclusion

The predicted impacts of climate change, such as increasing temperatures and more variable precipitation patterns are likely to exacerbate forest susceptibility to wildfire and as such, high-severity, stand replacing fire is likely to remain a prevalent form of disturbance in western forests (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 resistant stands are of key interest to land managers, specifically in forestlands 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) and many others, 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 of how regeneration patterns vary with environmental variables and fire regime. Our findings suggest field trials and more experimentation in seedling spatial patterns is warranted to better understand how resilient forest conditions can be fostered in regenerating forests.

Acknowledgements

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Appendices

Appendix A

		ABCO				CADE				PIJE				PILA				PIPO				All Species			
Spec	10-25	25-75	75-137	>137	10-25	25-75	75-137	>137	10-25	25-75	75-137	>137	10-25	25-75	75-137	>137	10-25	25-75	75-137	75-137	All >10	10-25	25-75	75-137	>137
Plot Shrub Cover Conditions																									
Low Shrub	1944	1203	298	38	321	92	11	7	211	114	32	12	291	85	4	8	43	92	10	0	5574	3013	1713	387	127
High Shrub	177	601	277	56	341	337	90	69	102	80	136	114	20	19	8	3	6	35	3	2	3042	705	1212	555	439
Fire Age																									
Oldest	533	1836	469	50	105	122	28	18	112	142	75	37	25	23	5	0	0	0	1	0	4393	966	2311	634	228
Recent	2793	541	147	30	509	116	12	9	274	83	15	12	464	124	5	15	71	159	16	0	6071	4296	1101	210	104

Estimated Trees Per Hectare Values For Different Fire Histories

Table A.1. Stocking density averages by species for different plot site conditions at increasing height intervals. High stocking numbers were driven by ABCO, especially among smaller and younger seedlings. Recent fires had higher numbers of seedlings in younger age classes. High shrub cover plots averaged lower numbers of small seedlings in the smaller size classes, but frequently had high stocking densities in the taller size classes (>75 cm).
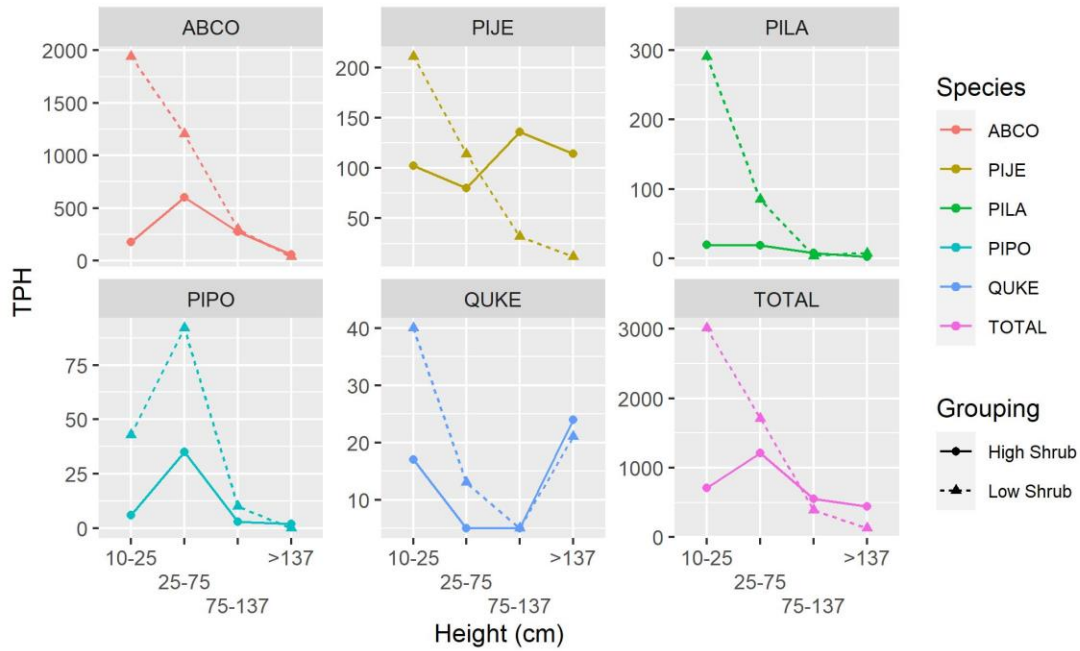
Figure A.1. Graphs showing average stocking densities of different species at high and low shrub conditions at increasing size classes.
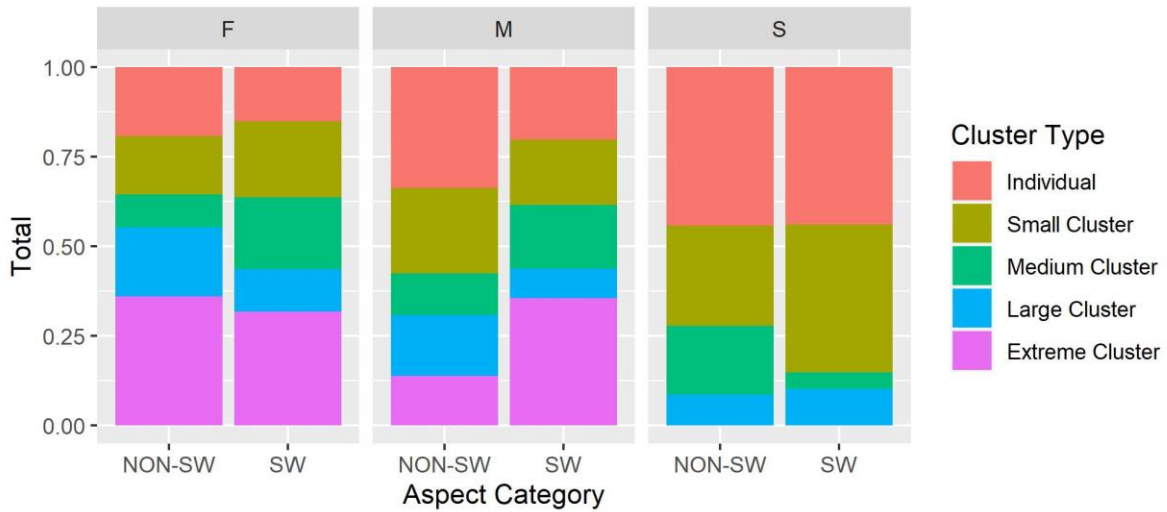

Figure A.2. Breakdown of tree cluster membership by slope(F=<15% , M=15-35% and S=>35%), aspect category, and cluster size category. A larger proportion of trees are found as individuals as slope increases. A larger percentage of trees were found in clusters on SW-facing slopes.

Species			Cluster Size		
	Individual	Small Cluster	Large Cluster	Medium Cluster	Extreme Cluster
ABCO	0.301	0.376	0.421	0.417	0.797
CADE	0.097	0.143	0.064	0.125	0.104
PIJE	0.247	0.197	0.203	0.217	0.009
PILA	0.127	0.102	0.029	0.065	0.034
PIPO	0.053	0.047	0.050	0.042	0.011
QUKE	0.085	0.045	0.034	0.038	0.022
Other	0.091	0.090	0.198	0.096	0.024

Table A.2. Breakdown of cluster membership by species showing the proportion of each cluster category made up by each species. White fir dominated across all cluster categories.

	Estimated differences between growth rates of clustered and individual trees									
	Overall		Age 1-5		Age 6-11		Age 12-19		Age >20	
Spec	Difference Estimate	P-Value Significance	Difference Estimate	P-Value Significance	Difference Estimate	P-Value Significance	Difference Estimate	P-Value Significance	Difference Estimate	P-Value Significance
ABCO	0.053	*	0.062	*	0.037	ns	−0.177	*	0.095	ns
YP	0.321	****	0.164	*	0.489	****	−0.196	ns	0.489	ns

Estimates are mean differences (mm/yr) between clustered and individual tree diameter growth rates. A positive value indicates a faster growth rate among clustered trees

* indicates P value <.05, ** indicates P value <.01, **** indicates P value < .0001, ns indicates non-significant value

Table A.3. Results of Tukey HSD tests for yellow pines (ponderosa and Jeffrey) and white firs by age category. Overall, clustering had a significantly positive effect, though significance varied among different age groups, and was not detectable among the oldest trees for either species.
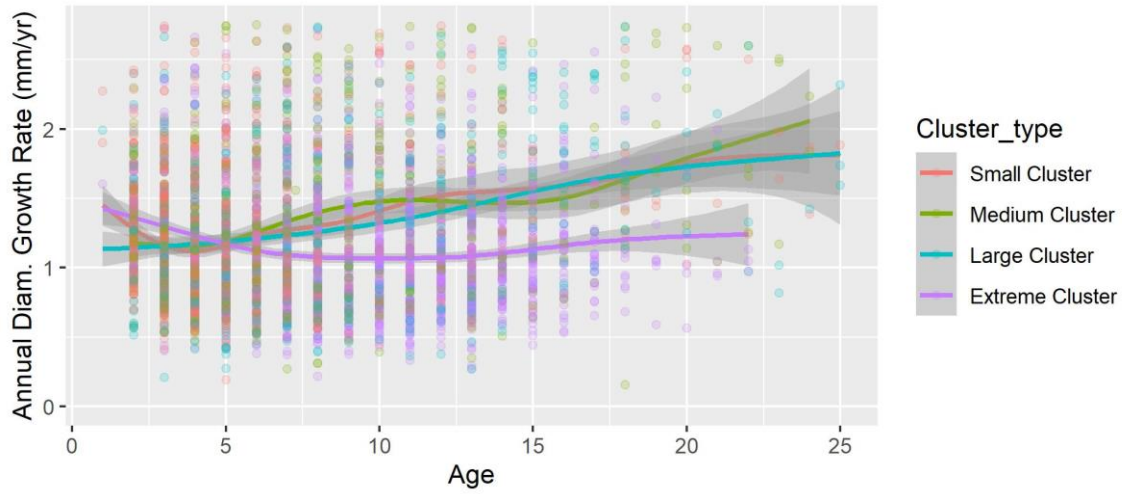
Figure A.3. Geometric -Smoothed figure showing estimated annual diametric growth rate across cluster sizes using collected field data. A clear lag in estimated diametric growth can be observed for trees in extreme clusters, but the other cluster estimates showed no significant differentiation.