



## Spatial patterns of ponderosa pine regeneration in high-severity burn patches



Suzanne M. Owen<sup>a,b,\*</sup>, Carolyn H. Sieg<sup>a</sup>, Andrew J. Sánchez Meador<sup>b</sup>, Peter Z. Fulé<sup>b</sup>, José M. Iniguez<sup>a</sup>, L. Scott Baggett<sup>c</sup>, Paula J. Fornwalt<sup>c</sup>, Michael A. Battaglia<sup>c</sup>

<sup>a</sup> USDA Forest Service: Rocky Mountain Research Station, 2500 S. Pine Knoll Drive, Flagstaff, AZ 86001, United States

<sup>b</sup> School of Forestry, Northern Arizona University, PO Box 15018, Flagstaff, AZ 86011, United States

<sup>c</sup> USDA Forest Service: Rocky Mountain Research Station, 240 W Prospect Rd, Fort Collins, CO 80526, United States

### ARTICLE INFO

#### Keywords:

*Pinus ponderosa*  
Fire severity  
Forest resilience  
Spatial heterogeneity  
Gambel oak (*Quercus gambelii*)  
Arizona

### ABSTRACT

Contemporary wildfires in southwestern US ponderosa pine forests can leave uncharacteristically large patches of tree mortality, raising concerns about the lack of seed-producing trees, which can prevent or significantly delay ponderosa pine regeneration. We established 4-ha plots in high-severity burn patches in two Arizona wildfires, the 2000 Pumpkin and 2002 Rodeo-Chediski Fires, to determine if: (1) distance from forest edge influences the density and spatial patterns of regenerating ponderosa pine and sprouting tree species, (2) interactions with re-sprouting trees affect spatial patterns of ponderosa pine regeneration, and (3) distance from forest edge and species competition affect regenerating ponderosa pine height. Plots were located in high-severity burn patches (defined as 100% tree mortality) and either adjacent to residual live forest edges (edge plots), or > 200 m from any residual live trees (interior plots). We found higher ponderosa pine regeneration densities in the edge plots (13–154 (median = 69) stems ha<sup>-1</sup>) than the interior plots (12–124 (median = 29) stems ha<sup>-1</sup>) on both wildfires, but no differences in spatial patterns between edge and interior plots. Ponderosa pine regeneration displayed patterns of small-scale spatial aggregation in all plots, except one edge and one interior plot on the Pumpkin Fire, which displayed random distributions. These patterns suggest both short- and long-distance dispersal play important roles in ponderosa pine regeneration in high-severity burn patches. Sprouting trees dominated tree regeneration on the Rodeo-Chediski Fire, but they were spatially independent of ponderosa pine and did not influence ponderosa pine height. Regenerating ponderosa pine height was positively correlated with neighboring ponderosa pine densities and height, suggesting that intraspecific facilitation or similar habitat preferences occur in high-severity burn patches. Collectively, these results indicate that ponderosa pines are re-establishing with heterogeneous spatial patterns in large high-severity burn patches, but often with low densities. Also, ponderosa pine regeneration could be more strongly influenced by intraspecific facilitation than interspecific competition from dense sprouting species. Future forest spatial patterns and composition are still unclear, but at this stage of development, these heterogeneous patches, characterized by drought-tolerant sprouting species or low pine densities, could be more resilient to climate change and severe wildfires than the overly-dense ponderosa pine forests that were present before the wildfires.

### 1. Introduction

Over the past three decades, wildfires in southwestern US ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests have increased in size and severity, leaving large, contiguous patches of tree mortality (often  $\geq 100$  ha) (Dillon et al., 2011; Poling, 2016). Increases in fire size and severity are attributed to the accumulation of abnormally high canopy and surface fuel loads from over 100 years of fire exclusion

(Fulé et al., 1997, 2009; Moore et al., 2004), warmer and drier climate conditions, and longer fire seasons (Dillon et al., 2011; Jolly et al., 2015; Reilly et al., 2017). High-severity wildfires are in stark contrast to the low- to moderate-severity wildfires that dominated the historical fire regime in ponderosa pine forests (Covington and Moore, 1994; Fulé et al., 1997; Moore et al., 2004). Consequently, there is concern for the future sustainability of ponderosa pine forests in large burn patches that kill seed-producing trees, which can prevent or significantly delay post-

\* Corresponding author at: USDA Forest Service: Rocky Mountain Research Station, 2500 S. Pine Knoll Drive, Flagstaff, AZ 86001, United States.

E-mail addresses: [smowen@fs.fed.us](mailto:smowen@fs.fed.us) (S.M. Owen), [csieg@fs.fed.us](mailto:csieg@fs.fed.us) (C.H. Sieg), [andrew.sanchezmeador@nau.edu](mailto:andrew.sanchezmeador@nau.edu) (A.J. Sánchez Meador), [pete.fule@nau.edu](mailto:pete.fule@nau.edu) (P.Z. Fulé), [jiniguez@fs.fed.us](mailto:jiniguez@fs.fed.us) (J.M. Iniguez), [lsbaggett@fs.fed.us](mailto:lsbaggett@fs.fed.us) (L.S. Baggett), [pfornwalt@fs.fed.us](mailto:pfornwalt@fs.fed.us) (P.J. Fornwalt), [mbattaglia@fs.fed.us](mailto:mbattaglia@fs.fed.us) (M.A. Battaglia).

<http://dx.doi.org/10.1016/j.foreco.2017.09.005>

Received 6 July 2017; Received in revised form 21 August 2017; Accepted 1 September 2017  
0378-1127/ Published by Elsevier B.V.

fire pine regeneration (Stephens et al., 2013).

Because ponderosa pines evolved under fire regimes dominated by low- to moderate-severity wildfires, they are poorly adapted to regenerate in large patches of high-severity fire (He et al., 2012). Ponderosa pines do not sprout or have serotinous cones, and do not maintain long-lived soil seedbanks; therefore regeneration is dispersal-limited in large patches of high-severity fire and is dependent on surviving seed-sources or residual live trees (Oliver and Ryker, 1990; Chambers et al., 2016; Kemp et al., 2016). Ponderosa pine seeds are morphologically adapted for wind dispersal but their relatively large seeds rarely travel farther than 30 m from seed sources (Oliver and Ryker, 1990), which limits regeneration in the center of large, high-severity burn patches, often > 200 m from seed sources (Chambers et al., 2016). Ponderosa pine seed can also be animal dispersed, and long-distance dispersal by birds may be important for regeneration in the interiors of high-severity burn patches (Li and Wilson, 1998; Lesser and Jackson, 2013; Pesendorfer et al., 2016). However, poor ponderosa pine seed crops, seed predation, and drought can all limit tree regeneration (Pearson, 1950; Larson and Schubert, 1970).

Consistent with the above limitations, a body of research documented low ponderosa pine regeneration densities in large high-severity burn patches (Lentile et al., 2005; Savage and Mast, 2005; Roccaforte et al., 2012; Savage et al., 2013), and declining regeneration with increasing distance from residual live trees (Haire and McGarigal, 2010; Chambers et al., 2016; Rother and Veblen, 2016). For example, regeneration in Arizona and New Mexico ranged from 11 to 26 stems  $\text{ha}^{-1}$  > 200 m from forest edges in large patches of high-severity fire (Haire and McGarigal, 2010). The strongest predictor of conifer regeneration in high-severity burn patches in the Colorado Front Range was distance from surviving forest, but regeneration also declined with elevation and on more xeric sites (Chambers et al., 2016; Rother and Veblen, 2016). Less is known about how the spatial arrangement of regenerating ponderosa pines in large high-severity burn patches will differ near forest edges compared to the interior of burn patches (e.g. if there are aggregated, random or uniform spatial arrangements). Regeneration spatial patterns should be considered when planning restoration treatments, or to better predict the spatial structure of forest development (Larson and Churchill, 2012; Donato et al., 2012). Ponderosa pine regeneration could be aggregated near the edges of high-severity burn patches due to a clustering of dense pine seeds that fall relatively close to parent trees, better growing conditions, or from rodent seed caches (Oliver and Ryker, 1990; Li and Wilson, 1998; Vander Wall, 2003). Regeneration spatial patterns could also be influenced by competition with sprouting trees to capture new post-fire growing spaces (Fulé and Covington, 1998).

A potential trajectory in large high-severity burn patches in ponderosa pine-dominated forests is a dominance by sprouting tree species (Fulé and Covington, 1998; Barton, 2005; Savage and Mast, 2005; Strom and Fulé, 2007; Coppoletta et al., 2016). Following high-severity fires, sprouting species have regeneration strategies that allow them to quickly recover (Bond and Midgley, 2001; Keeley et al., 2011). High-severity burn patches could potentially exclude tree species establishing from seed and favor a dominance of sprouting species for decades to centuries after high-severity fires (Iniguez et al., 2009). This pattern has been observed in some southwestern ponderosa pine forests (Savage and Mast, 2005; Strom and Fulé, 2007) and in forests that are taxonomically related to ponderosa pine with similar adaptations to frequent fire (*P. arizonica*, *P. durangensis*, *P. engelmannii* and *P. nigra*) (McCune, 1988; Fulé and Covington, 1998; Martín-Alcón and Coll, 2016). However, it is unclear whether or not regenerating ponderosa pines in large, high-severity burn patches will exhibit random associations, attraction (implying facilitation or similar habitat preferences) or repulsion (implying a negative interaction like competition, or different habitat preferences) with sprouting tree species (Luo et al., 2012).

Competition with other species and proximity to forest edges can also affect regenerating ponderosa pine height (Li and Wilson, 1998;

Comeau et al., 1993; Nelson and Bragg, 2016), which could play an important role in site dominance and survival after subsequent fires (Bailey and Covington, 2002; Battaglia et al., 2009; Schwinning and Kelly, 2013). Variation in regeneration height across recovering high-severity burn patches could be driven by variability in seedling age, or proximity to forest edges and/or competition with sprouting species. Hypothetically, regenerating ponderosa pines may grow faster and establish sooner near unburned forest edges than the far interior of burn patches because of protection from wind and shade (Oliver and Ryker, 1990; Li and Wilson, 1998), available microbial symbionts (Nara, 2006; Teste et al., 2009), and nearby seed sources (Bonnet et al., 2005). Post-wildfire tree regeneration height can also be driven by competition for light, water and nutrients with other regenerating species (Comeau et al., 1993; Schwinning and Kelly, 2013).

The goal of this study was to better understand spatial patterns of ponderosa pine regeneration, as well as interactions with sprouting species and regeneration height in contiguous, high-severity burn patches. In order to develop spatially explicit data on post-wildfire tree regeneration, we selected high severity burn patches in two wildfires (the 2000 Pumpkin and 2002 Rodeo-Chediski Fires) and recorded the spatial location of regenerating trees in 4-ha plots located either adjacent to the forest edge (edge plots) or > 200 m from residual live trees (interior plots). We tested the following hypotheses: H<sub>1</sub>: Higher ponderosa pine regeneration densities and aggregated spatial patterns will be found near forest edges; whereas lower densities and random spatial patterns will be found farther from residual live trees; H<sub>2</sub>: Ponderosa pine and sprouting species will display a spatial pattern of repulsion; and H<sub>3</sub>: Height of ponderosa pine regeneration will be greater near residual live trees and with less inter- and intra-specific competition.

## 2. Methods

### 2.1. Study sites and plots

We investigated the patterns of ponderosa pine regeneration in large high-severity burn patches in two large Arizona wildfires: the 2000 Pumpkin and 2002 Rodeo-Chediski Fires (Fig. 1). These fires were chosen from all 10 to 15 year old Arizona wildfires because they had extensive patches of high-severity fire (we define high-severity as 100% tree mortality) with no post-fire logging, planting, or subsequent fires. We collected data in 2013 on the Pumpkin Fire (13 years post-fire) and in 2014 and 2015 (12–13 years post-fire) on the Rodeo-Chediski Fire.

The Pumpkin Fire burned approximately 6500 ha, including 1400 ha of high-severity burned area, on the Kaibab and Coconino National Forests (<http://www.mtbs.gov/>). The average 15 year post-fire annual precipitation was 57.7 cm and the average temperature was 7.2 °C (Prism Climate Group: <http://prism.oregonstate.edu/>). The elevation ranged from 2350 to 2600 m on our plots. The soils are derived from basalt and study plots are located on soil conditions ranging from moderately deep cobbly clay loam to shallow gravelly sandy loam (Web Soil Survey: <http://websoilsurvey.nrcs.usda.gov>. Accessed 10/5/16).

The Rodeo-Chediski Fire burned 189,651 ha, including 68,409 ha of high-severity burn area, on the White Mountain Apache lands and the Apache-Sitgreaves National Forest (<http://www.mtbs.gov/>). Our plots were on the Apache-Sitgreaves National Forest, from 2000 to 2350 m elevation. The average 12-year post-fire annual precipitation was 54.5 cm and the average yearly temperature was 10.7 °C (Prism Climate Group: <http://prism.oregonstate.edu/>). The soils are derived from sandstone and limestone and are deeper than those at the Pumpkin Fire.

The pre-fire vegetation was dominated by ponderosa pine on both fires, as evidenced by extensive ponderosa pine snags and downed logs burned in the severely-burned areas of the fire, nearby unburned ponderosa pine forest, and dendrochronological reconstructions of forest structure in 1879 near both wildfires (Rodman et al., 2016, 2017). Other common species included grasses such as Arizona fescue (*Festuca*

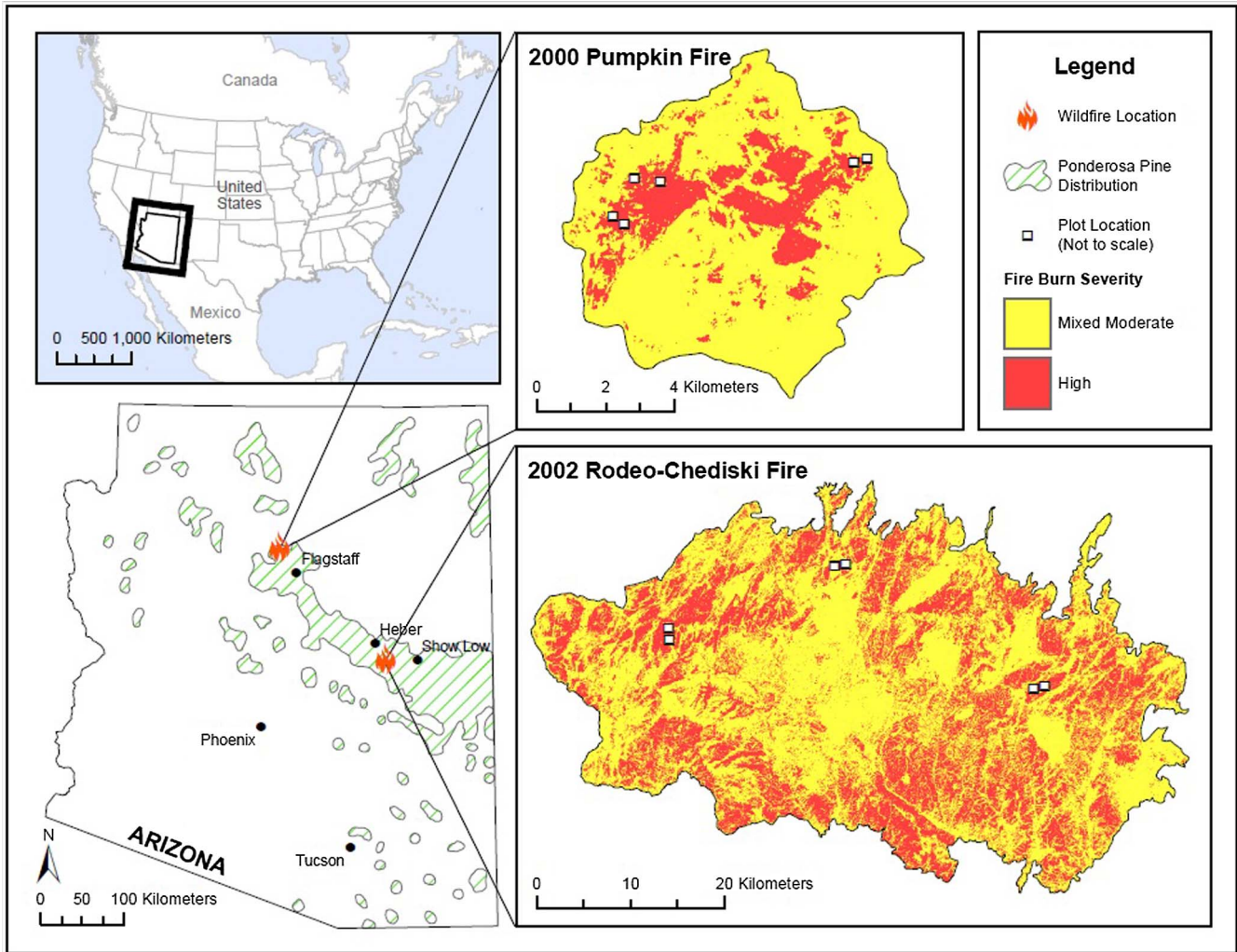


Fig. 1. Location of 4-ha research plots within the high-severity burned area of the 2000 Pumpkin Fire and the 2002 Rodeo-Chediski Fire in Arizona, USA. Study plots are not to scale.

*arizonica* Vasey) and mountain muhly (*Muhlenbergia montana* (Nutt.) Hitchc.), forbs, and shrubs such as Fendler's ceanothus (*Ceanothus fendleri* A.) on the Pumpkin Fire, and Fendler's ceanothus, Gambel oak (*Quercus gambelii* Nutt.) and alligator juniper (*Juniperus deppeana* Steud.), on the Rodeo-Chediski Fire.

We used Monitoring Trends in Burn Severity (MTBS, 2014) maps with field validation to identify all high-severity burn patches > 10 ha in the Pumpkin and Rodeo-Chediski Fires. We used ArcGIS 10.1 (ESRI, 2012) to randomly select three high-severity burn patches per wildfire, within which we established one 4-ha (200 × 200 m) “edge” plot and one 4-ha “interior” plot, for a total of six 4-ha plots per wildfire. Edge plots were established in high-severity burn patches adjacent to residual live trees, and interior plots were established where no surviving trees were found within at least 200 m from the plot boundaries (Fig. 1). From observation, most residual tree edges had high densities, e.g., 250–1000 trees/ha with very little understory vegetation. Plots were at least 30 m away from any roads and from another plot. Edge plot perimeters ranged from 2 to 220 m from residual live trees, and interior plot perimeters ranging from 203 to 455 m from residual live trees. This design allowed us to measure large areas, but does not capture regeneration in between plots, and the partial overlap of distance from residual live trees may limit a true separation between plot types.

## 2.2. Determining regeneration density and spatial patterns

To test the hypothesis that ponderosa pine regeneration densities and aggregation will be higher in edge than interior plots, we recorded the spatial location of all regenerating trees ( $\geq 10$  cm in height). We established reference points with a GPS (Trimble GeoXH with Terrasync, accurate to  $\pm 20$  cm) within each plot and used a range-finder (Laser Technologies Inc. TruePulse 360-B, accurate to  $\pm 38$  cm distance and  $\pm 1^\circ$  azimuth) to mark the geographic location of regenerating trees from each reference point. We verified that regeneration establishment dates were post-fire by whorl-counting and determining pith age on a subset of 46 regenerating ponderosa pines from both wildfires. Regenerating ponderosa pines were from multiple cohorts ranging from 2 to 9 years post-fire on the Pumpkin Fire and 5–13 years post-fire on the Rodeo-Chediski Fire. The two wildfires were treated as separate case-studies because of differences in soil types and pre-fire understory vegetation, and because post-fire regeneration in the Rodeo-Chediski Fire was dominated by sprouting species.

We tested for differences in ponderosa pine regeneration density between edge and interior plots on each fire with a measure of “intensity” that accounts for spatially explicit patterns, using mppm (model fitted to multiple point patterns) with the spatstat package in R v.3.4.1 (R development Core Team, 2016), as described by Baddeley et al. (2015). Intensity is measured as stems per  $m^2$  and can vary across each plot with an inhomogeneous process; therefore density is intensity integrated over a larger area. We assumed a Poisson spatial point



distribution because we were interested in evaluating overall location-dependent density for this analysis and not patterns of inhomogeneity within plots. We considered the three plots within each edge or interior location as replicates. The model results were interpreted similarly to a typical Analysis of Variance (ANOVA) that evaluates the null hypothesis that the treatment level effects of location are simultaneously zero by generating t-statistics and associated p-values (Bell and Grunwald, 2004). Juniper species on the Pumpkin Fire were excluded from this model because some plots did not contain juniper regeneration. We also tested for differences in stem density in each individual plot with distance from forest edge by using a Thomas process (kppm: cluster process model) model that evaluates Poisson-distributed parent clusters with offspring distributed as bivariate normal (Baddeley et al., 2015). The null hypothesis tests the conditional slope being equal to zero where the response is the log-intensity, and significance is determined by a Z-statistic and associated p-value (Baddeley et al., 2015). For these plot-level assessments, we accounted for other covariates such as Beer's aspect (Beers et al., 1966), elevation, percent slope, and topographic position index (TPI) (Jenness, 2006), each measured at 10-m resolution. We did not find any consistent patterns for these covariates across edge and interior plots on either fire.

To compare regeneration spatial patterns between edge and interior plots, we used the *spatstat* package (Baddeley et al., 2015) in R v.3.4.1. We first used a Monte Carlo method to test the hypothesis that the points exhibited Complete Spatial Randomness (CSR) on each plot. We used the inhomogeneous Ripley's K(r) function (Baddeley et al., 2015) for all plots, unless they exhibited homogeneous patterns within the plot, where we used the traditional form of the Ripley's K(r) function (Ripley, 1976, 1977, 1979). To determine whether regeneration was distributed in a uniform, random or aggregated fashion, we used Ripley's K(r) function or the inhomogeneous Ripley's K(r) function for all plots. These tests compare the distances of all pairs of points, the null hypothesis being that all points are randomly distributed (Ripley, 1976). The variance was stabilized to simplify visual interpretations by using the L(r)-r transformation (Besag, 1977). Interpretation of point pattern analysis results were limited to lag distances of 0–100 m (half the shortest plot dimension; *sensu* Dixon, 2002) to minimize the influence of unobserved points near observed points close to the plot edge (Boots and Getis, 1988). Significant aggregation or uniformity was determined by comparing observed L(r)-r transformation values to a 95% confidence envelope based on 999 permutations of simulated complete spatial randomness (Upton and Fingleton, 1985). We quantified patch sizes from the lag distance and value of L(r) at the highest point of separation from CSR (Boyden et al., 2005; Sánchez Meador et al., 2009).

### 2.3. Determining species interactions and predictors of regeneration height

To test the hypothesis that pine and sprouting species will display a spatial pattern of repulsion, we performed Ripley's bivariate  $K_{12}(r)$ -r analysis (Lotwick and Silverman, 1982) on each plot, also using the *spatstat* package in R v.3.4.1. For this analysis, we pooled spatial locations of the sprouting species, Gambel oak and alligator juniper, as "sprouters" on the Rodeo-Chediski Fire, and we also tested individual effects of each sprouter species on ponderosa pine spatial patterns. We analyzed ponderosa pine regeneration as an event occurring a posteriori populations of sprouting species (holding the location of sprouting species constant) instead of randomizing the location of all species, assuming that most sprouting species established soon after the wild-fires, whereas ponderosa pine establishment likely occurred later (Harrington, 1989; Haire and McGarigal, 2010). We used the Ripley's  $K_{12}(r)$  bivariate function transformed form,  $L_{12}(r)$ -r, proposed by Besag (1977) to calculate the distances between points from different populations and formed confidence envelopes by holding the locations of the sprouting species constant while simulating ponderosa pine locations. Interpretation of analysis results were limited to lag distances

of 0–50 m (one-quarter the shortest plot dimension) to describe relationships between two or more point patterns (e.g., pine regeneration and established oak), to minimize the influence of unobserved points near observed points close to the plot edge, and to maximize comparisons to similar studies reporting bivariate patterns in pine regeneration (e.g., Sánchez Meador and Moore, 2010). A 95% confidence envelope was created by 999 Monte Carlo simulations of the independent point processes null hypothesis (Goreaud and Pélissier, 2003), to evaluate deviations from the null hypothesis. In our case, the null hypothesis was that the location of ponderosa pine and sprouting species was produced from two independent spatial point processes. The alternative hypothesis was that the position of ponderosa pine seedlings was dependent on the location of sprouting species;  $L_{12}(r)$ -r values  $> 0$  indicate a positive dependence between species, and  $L_{12}(r)$ -r values  $< 0$  indicate repulsion between species (Goreaud and Pélissier, 2003).

To test the hypothesis that ponderosa pine regeneration height will be greater near residual live trees and with less interspecific competition, we measured the heights of all stem-mapped regeneration, and we derived the distance from each regenerating ponderosa pine to the nearest residual live ponderosa pine tree and the density of regeneration within 1 m of each regenerating pine. We determined the distance from each regenerating ponderosa pine to the nearest residual live ponderosa pine tree using imagery (Google Earth<sup>®</sup>, 2016) and field validation, including trees found along the forest edge, as well as single trees within the interior of the burned patches. We used the Proximity-Near tool in ArcGIS to determine the closest mature trees from all regeneration. We defined amount of competition as the density of neighbors within a fixed radius of 1 m around each regenerating ponderosa pine. Density and height of neighboring ponderosa pines (intraspecific competition) and sprouting species (interspecific competition) were determined within the 1-m buffer around each regenerating ponderosa pine. We used a generalized linear mixed model (GLMM) with a log-link function and Gaussian distribution to test the effects of closest residual ponderosa pine tree and the density and height of intra- and interspecific neighbors on ponderosa pine height, and we included plot as a random effect in the model. All GLMM analyses were completed in SAS 9.4 (SAS PROC GLIMMIX<sup>®</sup>, 2017). We tested the effect of Gambel oak and alligator juniper density on ponderosa pine height separately to understand the influence of each species.

## 3. Results

### 3.1. Regeneration density and spatial patterns

Regenerating ponderosa pine densities were lower in the interior plots than edge plots on the Pumpkin Fire ( $t = -8.6$ ;  $p < 0.01$ ; Fig. 2A), supporting part of our first hypothesis. All plots exhibited inhomogeneous point processes, except one interior plot (interior 2) on the Pumpkin Fire (Appendix A). At a plot level, pine density significantly decreased with distance from forest edge in two out of the three edge plots (three edge plots:  $p = 0.01, 0.05, 1.0$ ), and density did not differ with distance in any of the interior plots ( $p = 1.0$  in all three interior plots; Appendix B). Ponderosa pine densities were highly variable on both edge and interior plots (edge plots: 13, 51.3, 153.8 stems  $ha^{-1}$ ; interior plots: 15.2, 31.2, 12 stems  $ha^{-1}$ ) (Fig. 2A). Other tree species made up a small portion of the total regeneration. We documented an average of 15.2 quaking aspen (*Populus tremuloides* Michx.) stems  $ha^{-1}$  in the interior plots and 9.1 stems  $ha^{-1}$  in the edge plots. We found an average of 6 juniper stems  $ha^{-1}$  in the edge plots and 4.8 juniper stems  $ha^{-1}$  in the interior plots. These were likely alligator juniper or Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), but we could not identify juveniles to species. We found an average of  $< 1$  Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stem  $ha^{-1}$  in the interior plots, and Douglas-fir was not observed in the edge plots. Both edge and interior plots on the Pumpkin fire were dominated by understory herbaceous plants.

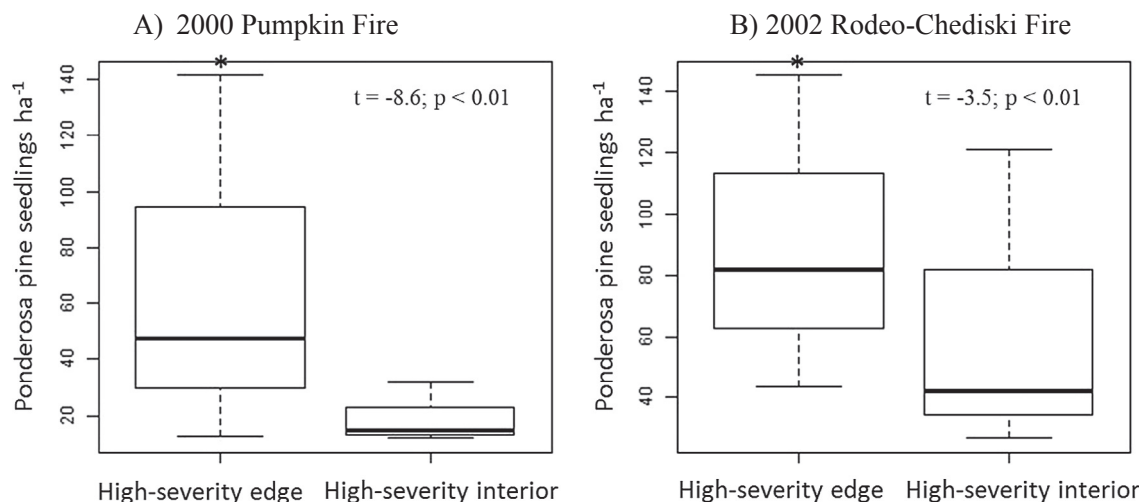


Fig. 2. Ponderosa pine regeneration densities (stems  $\text{ha}^{-1}$ ) were lower in interior plots than edge plots in large high-severity burn patches for both (A) the 2000 Pumpkin Fire and (B) the 2002 Rodeo-Chediski Fire. The central boxes span the first to the third quartile, a center line represents the median, and the “whiskers” above and below the box represent the minimum and maximum values.

On the Rodeo-Chediski Fire, ponderosa pine regeneration densities were also lower in the interior plots than the edge plots ( $t = -3.5$ ;  $p < 0.01$ ; Fig. 2B). All plots exhibited inhomogeneous point processes (Appendix A). At a plot level, ponderosa pine densities decreased significantly with distance from forest edge in two out of the three edge plots (three edge plots:  $p = 0.01, < 0.01, 1.0$ ), and one interior plot ( $p = 0.05$ ). Ponderosa pine densities were not correlated with distance from forest edge in one interior plot ( $p = 1.0$ ), and density actually increased ( $p = 0.01$ ) with distance in one interior plot (Appendix B). Ponderosa pine density was highly variable on edge and interior plots (edge plots: 148.5, 86.3, 45.8 stems  $\text{ha}^{-1}$ ; interior plots: 44.5, 27.3, 124.0 stems  $\text{ha}^{-1}$ ). One interior plot located 220–420 m from any residual live trees unexpectedly had almost 3 times higher regeneration densities than a nearby edge plot (interior and edge plots 3). Both edge and interior plots on the Rodeo-Chediski Fire were dominated by sprouting species. We documented an average of 969 Gambel oak stems  $\text{ha}^{-1}$  (58, 415.8, and 2,433.8 stems  $\text{ha}^{-1}$ ) on the edge plots and 453 Gambel oak stems  $\text{ha}^{-1}$  (246, 8.3, and 1,104.5 stems  $\text{ha}^{-1}$ ) on the interior plots. We found an average of 330 alligator juniper stems  $\text{ha}^{-1}$  (14.3, 519, 457.5 stems  $\text{ha}^{-1}$ ) on the edge plots and 464 alligator juniper stems  $\text{ha}^{-1}$  (77, 291.8, 94.8 stems  $\text{ha}^{-1}$ ) on the interior plots. The relationship between ponderosa pine vs. sprouter density was not consistent. The edge plot with the highest density of sprouting species had the least ponderosa pine regeneration. However, the interior plot with the highest density of sprouting species had the most ponderosa pine regeneration.

Contrary to our hypothesis, we did not observe differences in ponderosa pine spatial patterns between edge and interior plots on the Pumpkin Fire (Fig. 3, Table 1, Appendix C). Ponderosa pine regeneration exhibited significant small-scale aggregation in two edge and two interior plots from approximately 1 to 22 m lag distance, and had uniform and/or random spatial patterns at larger scales (Fig. 3, Table 1, Appendix C). Ponderosa pine regeneration did not fall outside complete spatial randomness in one edge and in one interior plot (Fig. 3, Table 1, Appendix C). Regeneration that displayed aggregation had patch sizes ranging from 0.001 to 0.045 ha on one edge and one interior plot (edge 2, interior 1) (Table 1, Appendix C). Aspen regeneration was significantly aggregated on 5 of the 6 plots at varying lag distances (from 1 to 10 m up to 1 to 75 m) and displayed spatial randomness at other distances (from 59 to 100 up to 1 to 100 m) on the Pumpkin Fire (Appendices D and E).

We also did not observe differences in ponderosa pine spatial patterns between edge and interior plots on the Rodeo-Chediski Fire

(Fig. 3, Table 1, Appendix C). Pine regeneration exhibited significant small-scale aggregation from 1 to 35 m lag distances, and had uniform and/or random spatial patterns at larger scales on all plots (Fig. 3, Table 1, Appendix C). Average patch sizes ranged from 0.001 to 0.031 ha, with the highest density on 2 interior plots (Table 1, Appendix C). Furthermore, Gambel oak and alligator juniper were also significantly aggregated in all edge and interior plots at varying distances, except Gambel oak displayed a random distribution in one interior plot (Fig. 4, Appendix F). Gambel oak and alligator juniper also had varying patch sizes, and on some plots the patch was almost as large as the 4-ha plot due to such high densities (Fig. 4, Appendix E).

### 3.2. Ponderosa pine species interactions and regeneration height

Populations of ponderosa pine and sprouting species were spatially independent, contrary to our second hypothesis (Fig. 5). Ponderosa pine and quaking aspen populations were spatially independent on all edge and interior plots on the Pumpkin Fire. Ponderosa pine and pooled sprouting species (alligator juniper and Gambel oak) were spatially independent on all edge and interior plots on the Rodeo-Chediski Fire (Fig. 5), and when sprouting species were analyzed separately, ponderosa pine and individual populations of alligator juniper and Gambel oak were spatially independent on all plots (Appendix F). There was a trend for more repulsion between pine and alligator juniper on plots when juniper regeneration was dense, and attraction with Gambel oak, but there were no statistically significant patterns (Appendix F).

Contrary to our third hypothesis, regenerating pine height was not greater near residual live trees or with less interspecific competition, and model differences were driven by density and similar heights of intraspecific neighbors. Distance from residual live trees did not explain variation in regenerating ponderosa pine heights on either wildfire (Pumpkin Fire:  $F = 1.40$ ,  $p = 0.24$ ; Rodeo-Chediski Fire:  $F = 0.22$ ,  $p = 0.64$ ; Appendix G). The Pumpkin Fire had too few sprouting neighbors within 1-m radius of regenerating ponderosa pines for the model; therefore only intraspecific neighbors were included for neighborhood density and height variables. Neighborhood intraspecific density ( $F = 4.73$ ,  $p = 0.03$ ) and height ( $F = 9.21$ ,  $p < 0.01$ ) were both positively correlated with ponderosa pine height on the Pumpkin Fire (Fig. 6A, Appendix H). Neighborhood intraspecific density ( $F = 45.47$ ,  $p < 0.01$ ) and height ( $F = 171.13$ ,  $p < 0.01$ ) were also both positively correlated with ponderosa pine height on the Rodeo-Chediski Fire, but the heights of neighboring sprouting species were not significant predictors of ponderosa pine height (Fig. 6B, Appendix H).

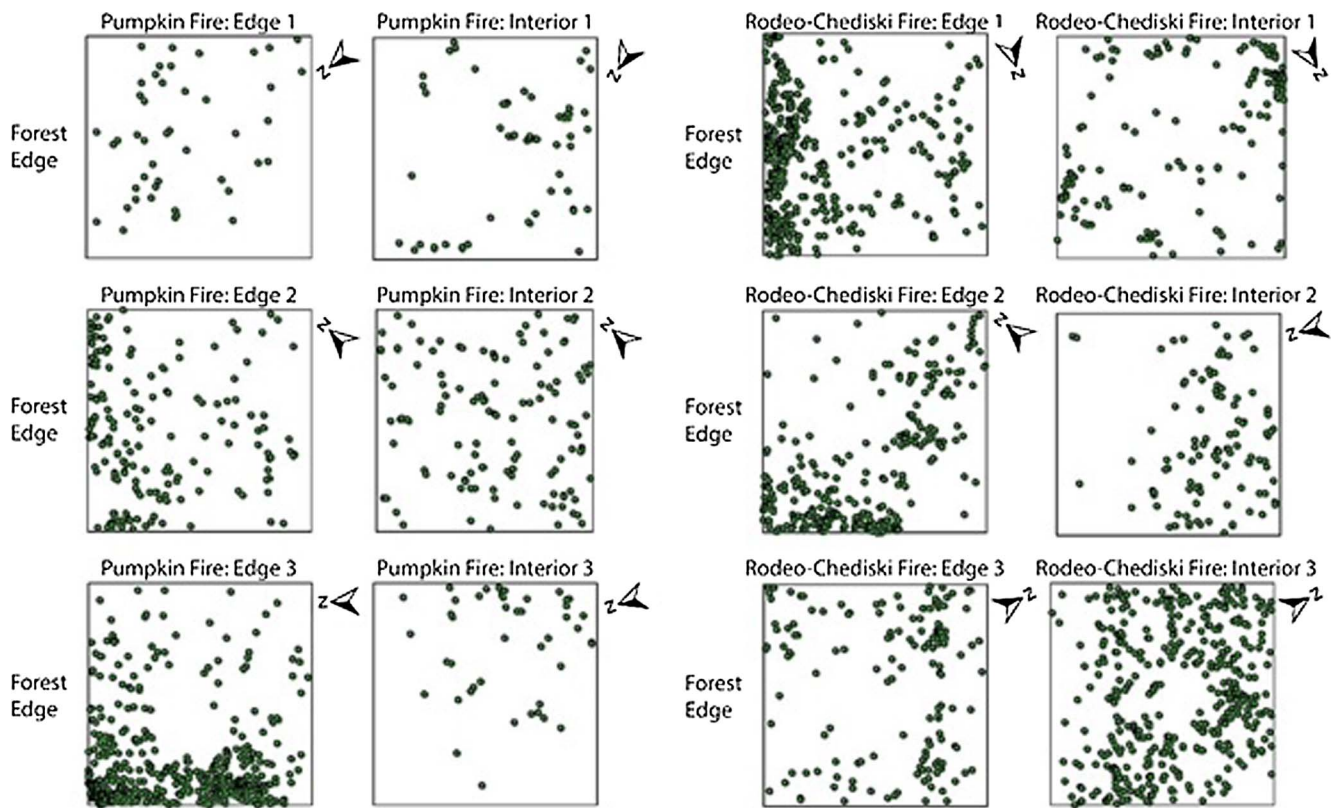


Fig. 3. Stem maps of ponderosa pine regeneration 13 years after the Pumpkin Fire and 12–13 years after the Rodeo-Chediski Fire in 3 edge plots along residual live ponderosa pine trees and 3 plots > 200 m from any residual live ponderosa pine trees (interior). Plots are rotated for this figure (north arrows are correct) to line up forest edges for ease of interpretation, but actual plot locations occur at varying distances from residual live forest edges and other plots.

Table 1

Lag distances and average patch sizes (determined by the lag distance and maximum deviation from complete spatial randomness (CSR)) for ponderosa pine regeneration with spatial aggregation, uniform, or CSR distributions from univariate Ripley's K, corresponding to the stem maps shown in Fig. 3. Individual Ripley's K outputs are shown in Appendix C.

	Lag distance (m)			Patch size (ha)
	Aggregation	Uniform	Random	
<i>Pumpkin Fire plots</i>				
Edge 1			1–100	
Edge 2	1–15	57–100	16–56	0.001
Edge 3	1–10	23–100	11–22	0.008
Interior 1	1–22	61–100	23–60	0.031
Interior 2	5–16		17–100	0.045
Interior 3			1–100	
<i>Rodeo-Chediski Fire plots</i>				
Edge 1	1–20	21–100		0.001
Edge 2	1–30	31–100		0.008
Edge 3	1–35	51–100	36–50	0.031
Interior 1	1–30	40–100	31–39	0.008
Interior 2	1–18	40–100	19–39	0.002
Interior 3	1–30	51–100	31–50	0.031

Neighboring Gambel oak ( $F = 1.90$ ,  $p = 0.17$ ) and alligator juniper density ( $F = 3.33$ ,  $p = 0.07$ ) were also not significant predictors of ponderosa pine height (Appendix H).

#### 4. Discussion

Our study found that pine densities were lower in the interiors of high-severity burn patches than near forest edges, consistent with previous studies (Haire and McGarigal, 2010; Chambers et al., 2016).

Seed dispersal from forest edges, protection from wind and sun, and favorable soil conditions near forest edges likely led to higher ponderosa pine densities than in the interior plots (Teste et al., 2009; Haire and McGarigal, 2010; Reynolds et al., 2013; Chambers et al., 2016; Kemp et al., 2016). It may take longer for regeneration to occur within the interiors than the edges of burn patches due to dispersal by wind or birds vs. high seed pressure from nearby residual trees. Low ponderosa pine regeneration densities in both plot types, and a dominance of either understory herbaceous plants or sprouting trees, could be due to a lack of adequate ponderosa pine seed-sources, slow recovery, or unfavorable post-fire habitat or climate conditions for ponderosa pine regeneration (Pearson, 1950; Larson and Schubert, 1970; Haire and McGarigal, 2010). These results could also be from superior regeneration strategies from herbaceous or sprouting species that allowed them to quickly recover in these large, treeless patches (Bond and Midgley, 2001; Battaglia et al., 2002). We investigated potential differences in regeneration densities from topography and aspect and found no consistent patterns, although two Colorado studies found reduced pine regeneration on lower elevations and more southerly aspects (Chambers et al., 2016; Rother and Veblen, 2016).

Even though pine densities were lower in interior than edge plots, regenerating ponderosa pines were nonetheless found over 300 m from any residual live tree in all interior plots, suggesting long-distance dispersal may be an important mechanism for regeneration in the interior of burn patches (Haire and McGarigal, 2010; Lesser and Jackson, 2013). Similar to our findings, post-fire ponderosa pine regeneration has been found > 200 m from residual live trees (Bonnet et al., 2005; Haire and McGarigal, 2010), and even up to > 10 km away from parent trees, likely from scatter-hoarding by corvids and other birds (Lesser and Jackson, 2013; Pesendorfer et al., 2016). Long-distance dispersal of seeds can have a critical effect on species survival and increase genetic diversity in patchy landscapes (Ozawa et al., 2013). Long-distance



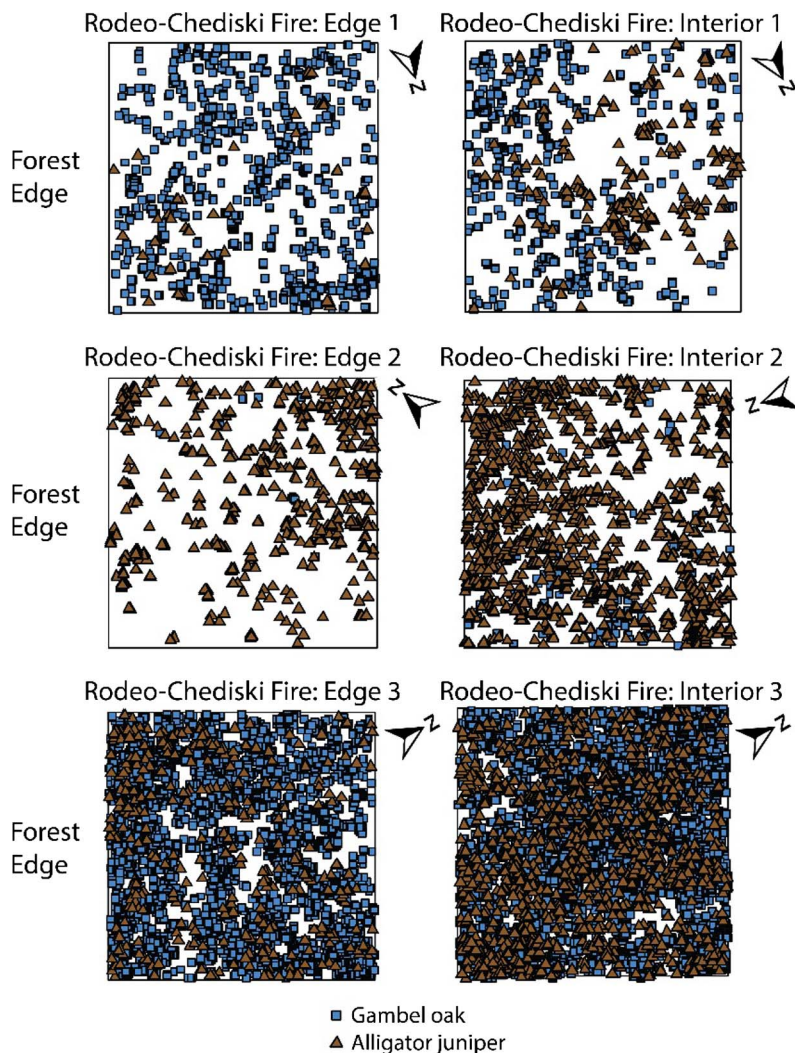


Fig. 4. Stem maps of Gambel oak (blue squares) and alligator juniper (brown triangles) regeneration 12–13 years after the Rodeo-Chediski Fire in 3 plots along the forest edges (edge), and 3 plots > 200 m from any live residual ponderosa pine tree (interior).

dispersal likely contributed to the heterogeneous spatial patterns of regenerating ponderosa pine in the interior plots as well.

We did not observe differences in the spatial patterns of regenerating ponderosa pine between plot types as expected, suggesting factors other than proximity to forest edges, such as animal seed dispersal or favorable microhabitat contributed to small-scale ponderosa pine aggregation in both edge and interior plots (Oliver and Ryker, 1990; Lesser and Jackson, 2013; Pesendorfer et al., 2016). Ponderosa pine regeneration was spatially aggregated at scales similar to those found in managed ponderosa pine stands in Arizona and Montana (Fajardo et al., 2006; Sánchez Meador and Moore, 2010). Small-scale spatial aggregation in the edge plots may have been from rodents because they usually cache ponderosa pine seeds within 30 m of seed-source trees (Vander Wall, 2003); whereas birds may have contributed to seedling aggregation in the interior plots because they can cache seeds > 10 km away from parent trees (Lesser and Jackson, 2013). Aggregated ponderosa pine regeneration could occur in pockets of preferred microhabitat, such as favorable soil conditions or near logs or stumps that provide extra moisture or wind protection (Oliver and Ryker, 1990; Teste et al., 2009; Sánchez Meador and Moore, 2010; Castro et al., 2011). Southwest prevailing winds can also influence the spatial location of seed dispersal, but we did not observe regeneration aggregating along this direction. Post-fire ponderosa pine can regenerate in clumps, as well as by remotely dispersed individuals, depending on seed sources and competition with sprouting species (Haire and McGarigal, 2010).

We expected a spatial pattern of repulsion between ponderosa pine and sprouting species because competition with sprouters influenced seedling regeneration in other studies (Fulé and Covington, 1998; Higgins et al., 2008). We observed a dominance of sprouting tree species on the Rodeo-Chediski Fire, a pattern similarly found by other studies (Barton, 2005; Savage and Mast, 2005; Strom and Fulé, 2007; Coppoletta et al., 2016). Even though sprouting species were found at high densities, we found spatial independence between ponderosa pine and sprouting species on all of our plots, suggesting that sprouting species did not repulse nor attract pine regeneration. Regenerating ponderosa pine had a random association with the locations of Gambel oak trees in northern Arizona under different harvesting regimes (Sánchez Meador and Moore, 2010). Perhaps interspecific competition or facilitation is not always a strong driver of pine regeneration and survival. There is evidence that ponderosa pine can establish beneath oaks and eventually overtop them as they mature, which can sometimes lead to decreases in sprouting species (McDonald, 1990; Vankat, 2013).

Interspecific competition and distance from forest edges did not influence ponderosa pine growth as expected. Ponderosa pine regeneration height in large high-severity burn patches could be the result of seedling age, microsite conditions, herbivory or facilitation (Fajardo and McIntire, 2011; Waring and Goodrich, 2012; Smith et al., 2016), rather than distance from forest edge or competition. A limitation of this study was not knowing the age of each pine seedling. We attributed differences in regenerating ponderosa heights between the two wildfires (2–3X taller on the Rodeo-Chediski Fire) to differences in

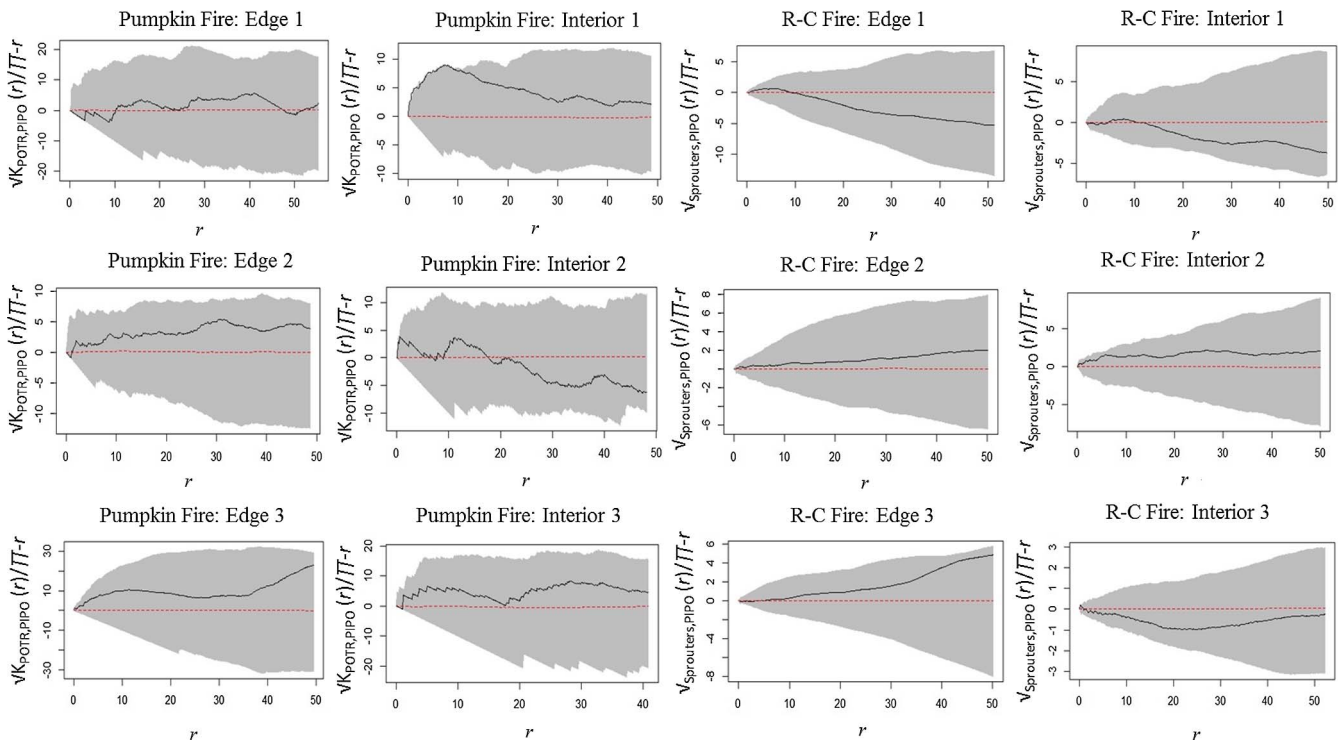


Fig. 5. Ripley's  $K_{12}(t)$  bivariate statistic is shown for the comparison of ponderosa pine regeneration to sprouting species locations (quaking aspen (POTR) in the Pumpkin Fire and alligator juniper and Gambel oak (sprouters) in the Rodeo-Chediski Fire) in three edge plots and three interior plots. The x-axis ( $r$ ) is the lag distance, and the y-axis is the square root, variance-stabilizing transformation of Ripley's  $K$ . The red line (values = 0) is the expectation under complete spatial randomness and the shaded areas are the 95% confidence limits. Values that fall outside of the confidence interval are significant; values  $> 0$  indicate attraction and values  $< 0$  indicate repulsion between ponderosa pine and sprouting species.

temperature, moisture, soil nutrients, or herbivore or insect damage (Pubhlick et al., 2012, 2013). The positive correlation between ponderosa pine height and neighboring ponderosa pine heights and densities, suggests that similar ages established together or similar environmental conditions influenced establishment and growth (Oliver and Ryker, 1990). It is also possible that facilitation could be a stronger process than intraspecific competition, a pattern observed by Fajardo and McIntire (2011), and led to greater height and ultimately survival. Rapid height growth may also allow regenerating ponderosa pines to survive a subsequent fire (Bailey and Covington, 2002; Battaglia et al., 2009). Approximately half of the ponderosa pine regeneration on the Rodeo-Chediski Fire and a fourth on the Pumpkin Fire had heights  $> 1.4$  m, with a measurable diameter at breast height (DBH). Ponderosa pine seedlings can be more fire-resistant at 3 m height (Bailey and Covington, 2002), and those  $\sim 2$  m tall are predicted to require  $> 2$  m tall flame length to cause mortality (Battaglia et al., 2009).

If established post-fire ponderosa pines survive and regeneration

continues to occur on these high-severity burn patches, some tree cover will be regained, even if below historical densities. Historical ponderosa pine densities ranged from 49 to 115 trees  $\text{ha}^{-1}$  in areas near the Pumpkin and Rodeo-Chediski Fires, determined by dendrochronological reconstructions of forest structure in 1879 (Rodman et al., 2016, 2017). Four out of our twelve plots fell within this range, and others were just below based on a projected 44% survival rate of seedlings to mature trees from the 5th to 50th year after planting in northern Arizona (DeWald and Mahalovich, 2008; Ouzts et al., 2015). Pine regeneration is potentially faced with additional challenges such as fire, drought, herbivory, disease, and further competition with neighboring species that could reduce survival rates (Huffman et al., 2012; Waring and Goodrich, 2012; Savage et al., 2013; Rother and Vebler, 2016). However, most regenerating pines have already made it through the high-mortality stage, within the first few years of germination (Pearson, 1950), and new seedlings on our study sites are still establishing. The small subset of aged post-fire ponderosa pines (data

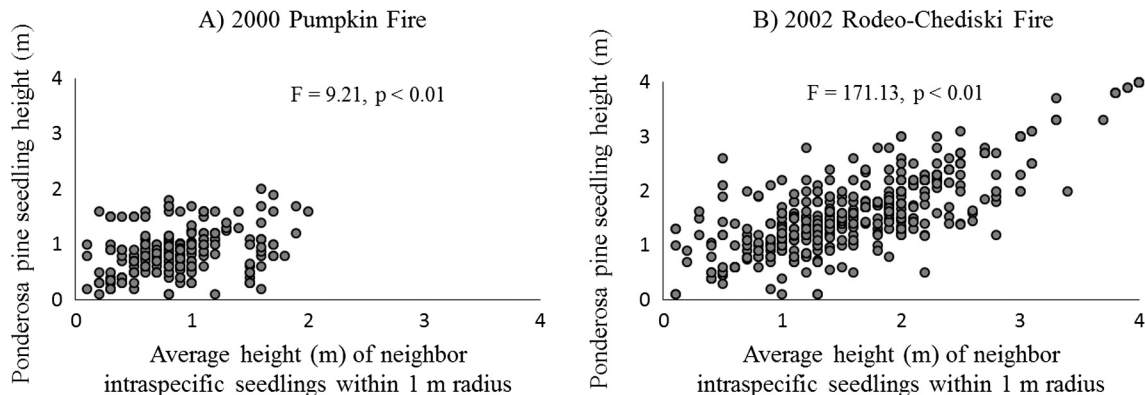


Fig. 6. Regenerating ponderosa pine height was significantly correlated with the average height of neighboring intraspecific ponderosa pine regeneration in both the A) Pumpkin Fire and B) Rodeo-Chediski Fire.



not shown) revealed an age range of 2–13 years-old, suggesting that regeneration is episodic in this area and not necessarily concentrated in the first few years after the fires, similar to findings by [Haire and McGarigal \(2010\)](#). We did not observe any pine seedlings or saplings that were producing cones on our plots; in the future, such reproduction may become a localized seed-source and serve to fill in treeless gaps, assuming seedlings survive and reproduce.

Historical ponderosa pine forests also had patterns of structural heterogeneity at multiple spatial scales ([Mast and Wolf, 2004](#); [Reynolds et al., 2013](#); [Rodman et al., 2016](#)), including trees of different size and age classes and an open structure over large portions of the landscape ([Sánchez Meador et al., 2011](#)). Regenerating ponderosa pines on our study sites already exhibit some patterns of spatial and structural (variable seedling ages and heights) heterogeneity, but with reduced average patch sizes. Regenerating ponderosa pine patch sizes from our plots averaged  $\geq 3$  X smaller than reported historical regeneration patch sizes (averaging 0.01 ha) across northern Arizona (reviewed in [Stephens and Fry, 2005](#)). Ponderosa pine regeneration patch sizes varied across the burned landscape, and the stem-maps revealed openings, widely-spaced single seedlings, and seedling aggregation, similar to the mosaic of fire-frequent forests described by [Larson and Churchill \(2012\)](#). However, it is unclear if regeneration on our study sites will emulate historical spatial patterns because drier conditions, increased wildfire activity and widespread conifer loss are forecasted to increase in the coming decades ([McDowell et al., 2016](#); [Abatzoglou and Williams, 2016](#)).

#### 4.1. Conclusions and management implications

Both spatial and non-spatial information on post-fire regeneration are vital for future management plans. By contrasting the edge and interiors of burn patches, we found that 12+ years post-fire, in high-severity burn patches, ponderosa pine regeneration had similar heterogeneous spatial patterns and interactions with neighboring species, yet lower densities in the interior patches. Intraspecific facilitation and more time could eventually lead to higher ponderosa pine densities. However, given the predictions for warming climates and increased wildfires ([McDowell et al., 2016](#); [Abatzoglou and Williams, 2016](#)), this heterogeneous stage of forest development, that includes native sprouting species could be more resilient to drought and high-severity fires than dense pine stands. Forest managers may need to adopt new objectives such as accepting forest types that could be more adapted to climate change and high-severity fires (including more drought-tolerant sprouting species). High-severity wildfires and climate change are predicted to favor sprouting species over ponderosa pine on the Rodeo-Chediski Fire ([Strom and Fulé, 2007](#); [Azpeleta Tarancón et al., 2014](#)). New vegetation types may be a future reality, especially since a combination of adequate moisture and fire-free periods are needed for the initiation of ponderosa pine regeneration and maintenance of pine-dominant forests ([Iniguez et al., 2016](#)). Future climate change is predicted to result in large-scale vegetation displacement and reorganization for some elevation zones in Arizona ([Flatley and Fulé, 2016](#)). Post-

## Appendix A

Results from Monte Carlo method to test for Complete Spatial Randomness (CSR) on each plot, indicating all plots exhibited inhomogeneous point processes, except for one plot on the Pumpkin Fire (Interior 2).

Pumpkin fire	$\chi^2$	p
Edge 1	36.3	0.05*
Edge 2	180.96	0.001*
Edge 3	1656.9	0.001*
Interior 1	56.51	0.004*
Interior 2	27.22	0.28
Interior 3	120.48	0.001*

wildfire non-forested patches or alternative vegetation types can also be areas of resilience to climate variability and resistance to subsequent fire within portions of the pine-dominant landscape ([Coop et al., 2016](#); [Schoennagel et al., 2017](#)).

We recommend that managers use an experimental/adaptive approach to reach goals of resilient landscapes and fire-adapted communities in light of the prediction of potential vegetation shifts and increased risk of high-severity wildfires in the future. Biotic and abiotic conditions vary greatly across western US ponderosa pine forests ([Oliver and Ryker, 1990](#)), and management treatments should adapt accordingly. There is value in experimenting with a variety of treatments by incorporating a before–after–control–impact (BACI) design; this approach is useful in controlling confounding factors, so that observed changes are likely due to management treatments ([Underwood, 1994](#)). Potential post-fire management strategies could include introducing fire (with seasonal variabilities), while regeneration is small if overly dense, or waiting for trees to reach greater heights to become more fire-resistant ([Bailey and Covington, 2002](#); [Battaglia et al., 2009](#)). If management goals are to restore ponderosa forests, planting pine seedlings in the interiors of high-severity burn patches could be an option ([Ouzts et al., 2015](#)). However, plantings should reflect the goal of spatial heterogeneity instead of uniformity, and should not be overly dense so that they increase future fire severity ([Thompson et al., 2007](#)). There are also advantages for a natural recovery processes, such as increased plant diversity and more resilient vegetation types ([Haire and McGarigal, 2010](#); [Fornwalt and Kaufmann, 2014](#); [Coop et al., 2016](#)).

Other management options revolve around reducing the potential for large high severity fires by increasing thinning and managed fire to maintain recently treated stands that resemble historical forests or thinning high density stands ([Fulé et al., 2012](#); [Stevens-Rumann et al., 2012](#); [Stephens et al., 2016](#); [Huffman et al., 2017](#)). Pre-wildfire thinning and prescribed fire treatments on the Rodeo-Chediski Fire reduced fire severity and significantly increased ponderosa pine regeneration, compared to untreated areas ([Shive et al., 2013](#)). Restoration efforts to reduce the risk of stand-replacing wildfires should include the goal of spatial heterogeneity to increase resilience to future climate and wild-fire conditions, as recommended by [Larson and Churchill \(2012\)](#), and long-term, permanent plots are essential for quantifying treatment success or ecosystem changes over time ([Sánchez Meador and Moore, 2010](#)).

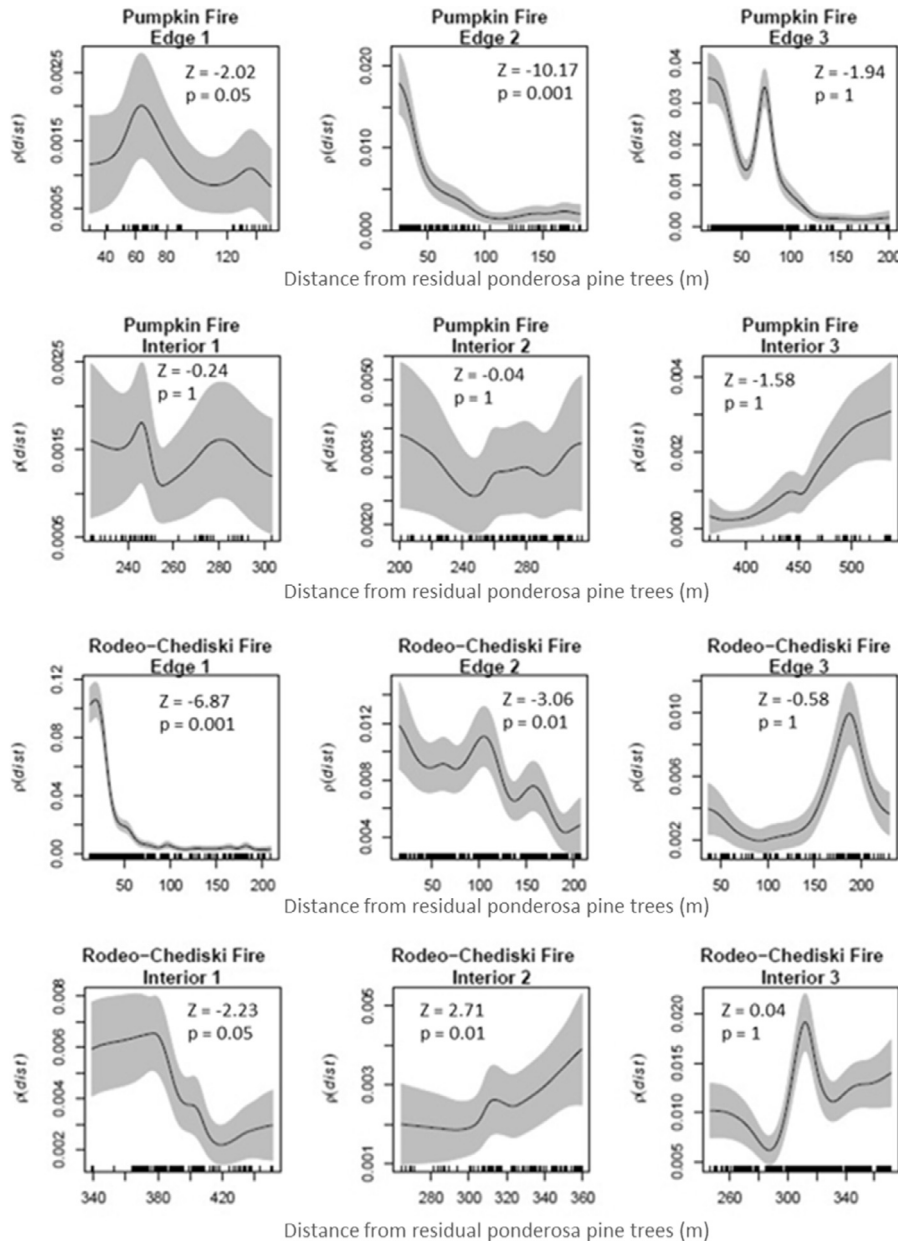
## Acknowledgements

We thank Scott Vojta, Jennifer Blanks, Patrick Cassidy, Spenser Biehler, Katie Gobble, Kimberly Istok, Thallita Mendes, Sam Ebright, Alec Soderberg, and Thomas Huck for helping with field data collection; Danna Muise for helping with ArcGIS and map development, and Chis Barrett, FS Enterprise team, for GIS support. This work was supported by the USDA FS Rocky Mountain Research Station, The National Fire Plan NFP-13-16-FWE-43, and Achievement Rewards for College Students (ARCS) Foundation.

Rodeo-Chediski fire	$\chi^2$	p
Edge 1	211.7	0.001*
Edge 2	1977	0.001*
Edge 3	561.14	0.001*
Interior 1	129.09	0.001*
Interior 2	88.67	0.001*
Interior 3	148.21	0.001*

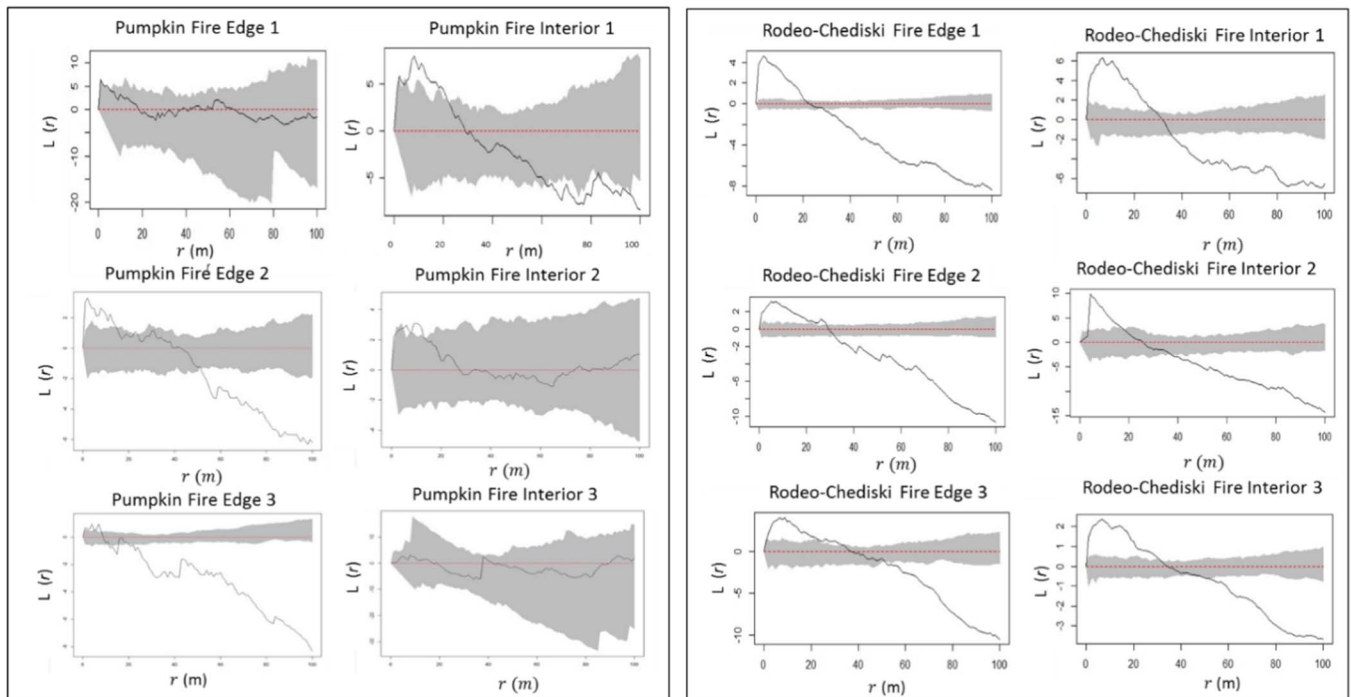
**Appendix B**

Results of the kppm model testing for differences in ponderosa pine stem intensity with distance from residual live trees. The x-axis illustrates distance from residual live trees (m), and the y-axis and the black lines near the x-axis indicate regenerating ponderosa pine intensity per m<sup>2</sup>. The scale differences between panels are due to differences in seedling locations along varying distances from residual live trees.



Appendix C

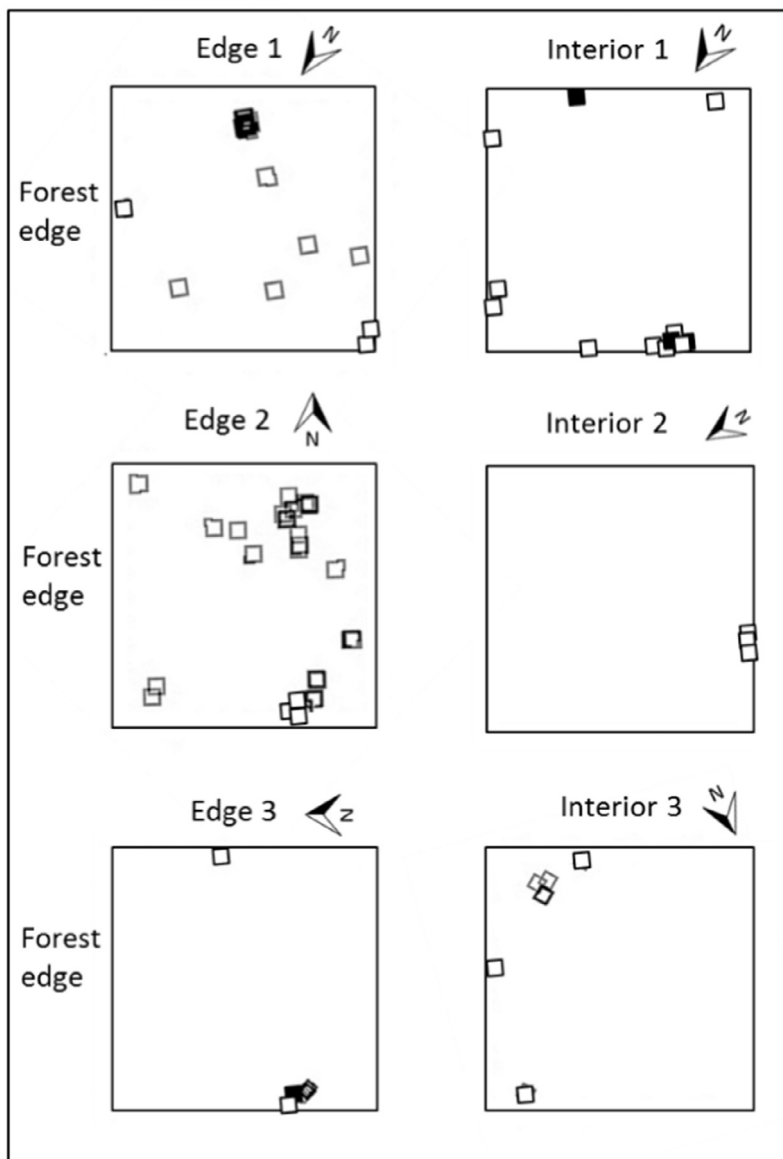
Results of the univariate Ripley’s K statistic (transformed as  $L(r)$  as lag distance) for ponderosa pine in each plot, corresponding to the stem maps shown in Fig. 3. The shaded area is the expectation under complete spatial randomness; values that fall outside of this are statistically significant; values  $> 0$  (red line) indicate aggregation and values  $< 0$  indicate uniform spatial distribution.





**Appendix D**

Stem maps of aspen regeneration 13 years after the Pumpkin Fire in 3 plots along the forest edges, and 3 plots > 200 m from any live tree (Interior plots).



**Appendix E**

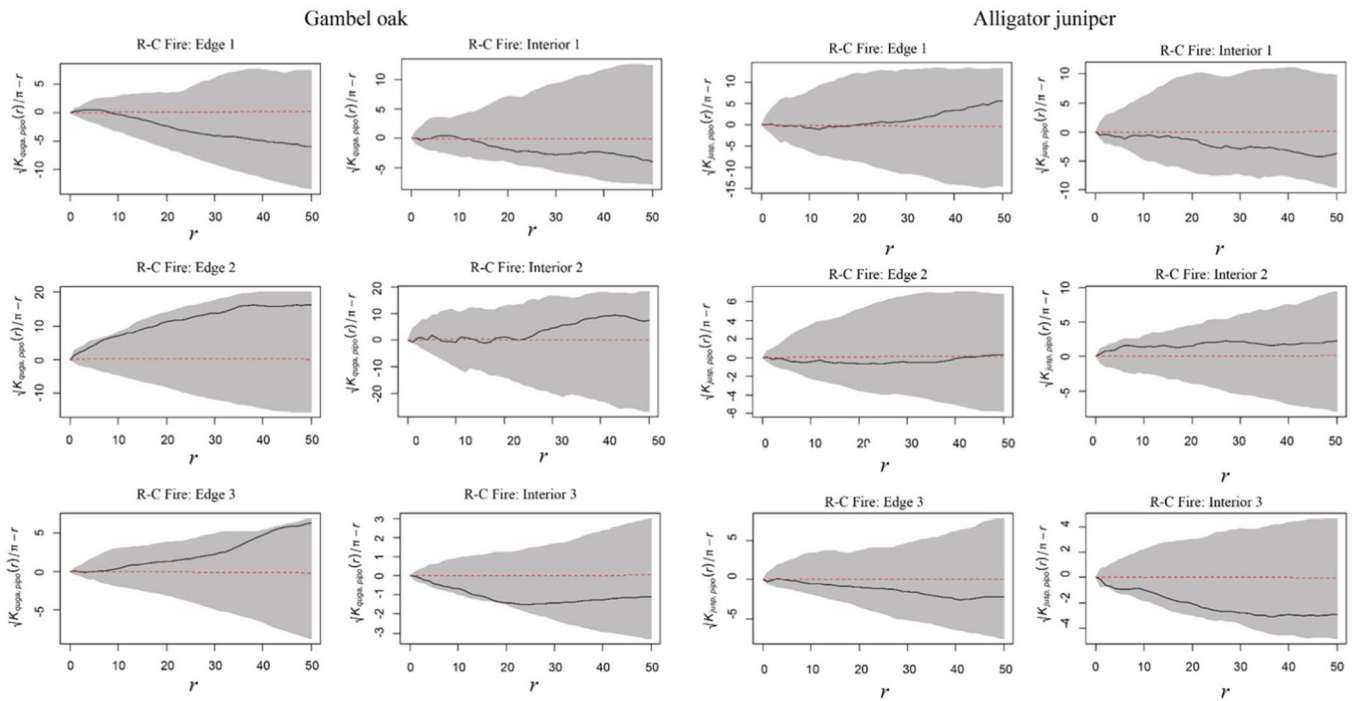
The lag distance for aspen stems on the Pumpkin Fire and Gambel oak and alligator juniper stems on the Rodeo-Chediski Fire with spatial aggregation, complete spatial randomness, or uniform spatial distribution from the univariate Ripley’s K, corresponding to the stem maps shown in Appendix D and Fig. 4. Values that fall outside the 95% confidence limits > 0 indicate aggregation and values < 0 indicate uniform spatial patterns, and values within the confidence limit are expected under complete spatial randomness.

Pumpkin fire	Lag distance (m)		
	Aggregation	Uniform	Random
Aspen			
Edge 1	1–60		61–100
Edge 2	1–75		76–100
Edge 3			1–100
Interior 1	1–58		59–100
Interior 2	1–15		16–100
Interior 3	1–10		11–100

Rodeo-Chediski fire		Lag distance (m)		
Gambel oak	Aggregation	Uniform	Random	
Edge 1	1–95		96–100	
Edge 2	1–35	40–100	36–39	
Edge 3	1–100			
Interior 1	1–100			
Interior 2			1–100	
Interior 3	1–100			
Alligator juniper	Aggregation	Uniform	Random	
Edge 1	1–15	80–100	16–79	
Edge 2	1–75		76–100	
Edge 3	1–100			
Interior 1	1–100			
Interior 2	1–100			
Interior 3	1–80		81–100	

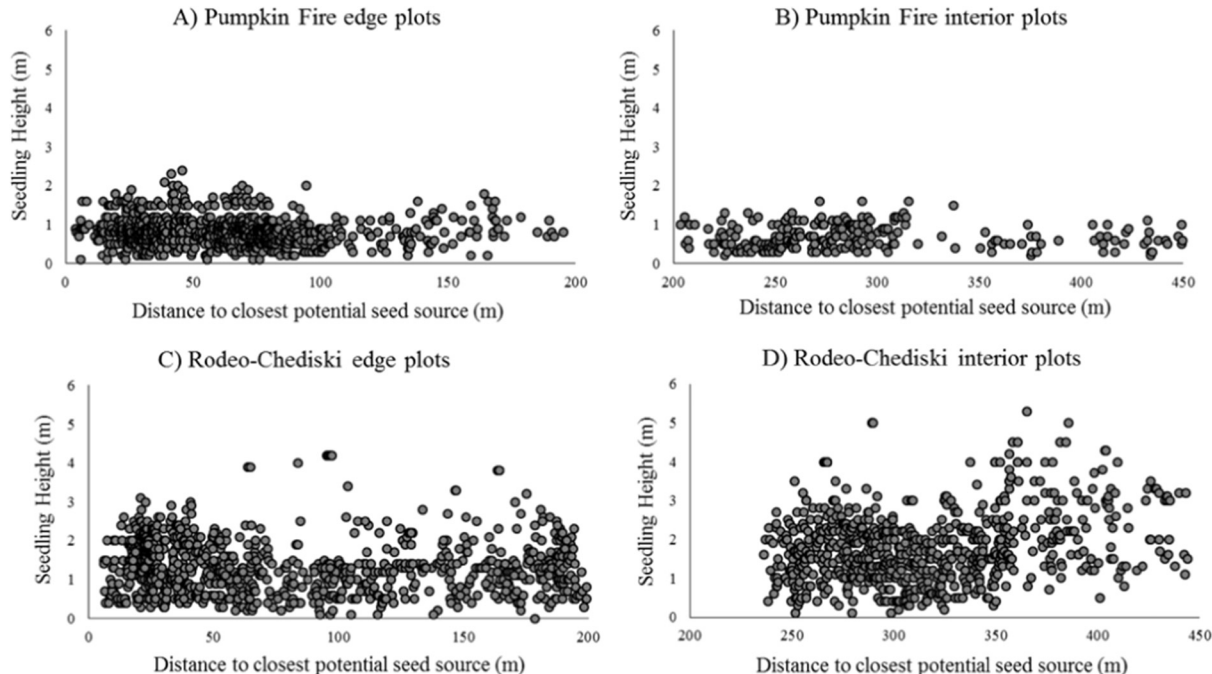
**Appendix F**

Ripley’s  $K_{12}(t)$  bivariate statistic is shown for the comparison of ponderosa pine regeneration to location of Gambel oak and alligator juniper in the Rodeo-Chediski Fire. The red line is the expectation under complete spatial randomness and the shaded areas are the 95% confidence limits. Values that fall outside of the confidence interval are significant; values > 0 indicate attraction and values < 0 indicate repulsion between ponderosa pine and sprouting species.



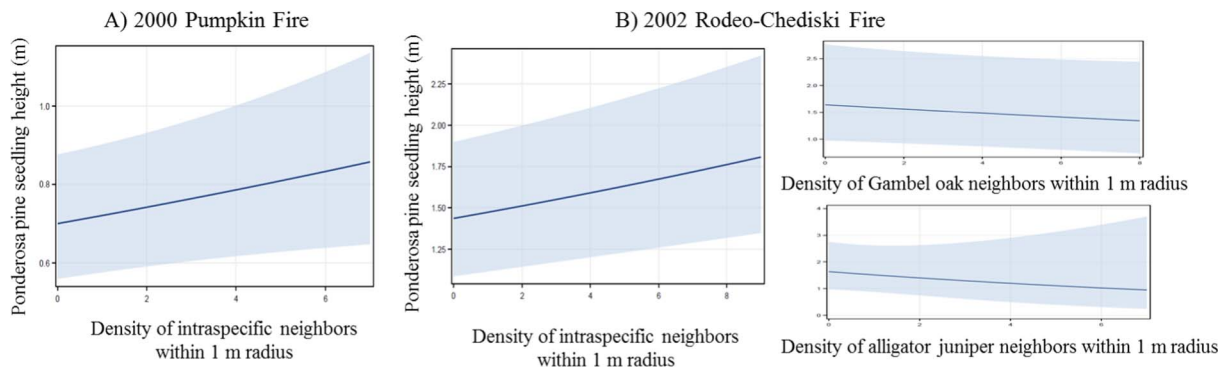
## Appendix G

Distance from residual live ponderosa pine trees (or potential seed sources) is not significantly correlated with regenerating ponderosa pine height on either wildfire.



## Appendix H

Ponderosa pine seedling height is positively correlated with the density of intraspecific neighbors within 1 m radius in the (A) Pumpkin Fire and the (B) Rodeo-Chediski Fire, but density of Gambel oak and alligator juniper are not significant predictors of ponderosa pine height in the Rodeo-Chediski Fire. Model fit with 95% confidence limits.



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