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Mixed-Severity Fire Fosters Heterogeneous Spatial Patterns of Conifer Regeneration in a Dry Conifer Forest

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Received: 25 November 2017; Accepted: 17 January 2018; Published: 20 January 2018

Abstract: We examined spatial patterns of post-fire regenerating conifers in a Colorado, USA, dry conifer forest 11–12 years following the reintroduction of mixed-severity fire. We mapped and measured all post-fire regenerating conifers, as well as all other post-fire regenerating trees and all residual (i.e., surviving) trees, in three 4-ha plots following the 2002 Hayman Fire. Residual tree density ranged from 167 to 197 trees ha^{-1} (TPH), and these trees were clustered at distances up to 30 m. Post-fire regenerating conifers, which ranged in density from 241 to 1036 TPH, were also clustered at distances up to at least 30 m. Moreover, residual tree locations drove post-fire regenerating conifer locations, with the two showing a pattern of repulsion. Topography and post-fire sprouting tree species locations further drove post-fire conifer regeneration locations. These results provide a foundation for anticipating how the reintroduction of mixed-severity fire may affect long-term forest structure, and also yield insights into how historical mixed-severity fire may have regulated the spatially heterogeneous conditions commonly described for pre-settlement dry conifer forests of Colorado and elsewhere.

Keywords: forest recovery; wildfire effects; stem maps; resilient ecosystems; Pike National Forest; Hayman Fire

1. Introduction

Historically, many dry conifer forests of western North America were regulated by a relatively frequent mixed-severity fire regime [1–3]. Individual fires were typically dominated by low- and moderate-severity effects where many overstory trees survived, but also contained small patches of high-severity effects where most or all overstory trees were killed. These fires also acted as a control on tree recruitment [4,5], thereby resulting in a variety of tree densities and tree size and age distributions [5,6]. The clustered spatial pattern commonly associated with historical dry conifer stands—where well-defined groups of trees and individual trees were interspersed in a matrix of treeless openings is further attributed to the relatively frequent historical fire regime [7–9]. This heterogeneity in historical forest structure is thought to be more resilient to drought and subsequent wildfires [1], yet little is known regarding the process responsible for this spatial structure. Although we know that historically dry conifer forests had a clustered spatial structure, we do not fully understand whether this pattern was a function of fire-caused mortality, post-fire regeneration, or both.

After nearly a century of fire exclusion, wildfire activity in western North American dry conifer forests has increased [9–12]. Many of these recent wildfires contain uncharacteristically large high-severity burn patches, attributed to higher forest density and homogeneity as a result of fire exclusion, as well as livestock grazing [13], logging [14–16], and a warmer and drier climate [9,11]. However, recent wildfires also commonly include areas that burned with mixed-severity fire—that is, areas that are a more heterogeneous combination of low-, moderate-, and high-severity patches [17–19]. In mixed-severity portions of recent wildfires where high-severity patches are small, fires more closely align with the historical fire regime [6,20], and therefore may represent a reintroduction of the dominant historical processes. As a result, recent fires may provide an opportunity to better understand how mixed-severity fires shape tree spatial patterns and subsequent regeneration.

Post-fire forest recovery research in ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) dominated dry conifer forests has been primarily aimed at examining regeneration following recent high-severity fire. In the interiors of large high-severity patches, regeneration tends to be sparse, suggesting that forest recovery may be delayed or may not occur at all [21–26]. Along the edges of high-severity patches, regeneration tends to be concentrated in areas near surviving trees, as most species in dry conifer forests rely on seed production from live trees to regenerate [25–29]. Regeneration is also commonly concentrated in more mesic sites, such as areas at higher elevations or with more northerly aspects, and in the vicinity of nurse structures such as downed logs and other regenerating trees [24–31].

In contrast, little is known about regeneration following recent mixed-severity fire. Some research suggests that recent mixed-severity fire effects are effectively enhancing forest structure, improving drought resilience, and reducing the probability of high severity fire in subsequent fires [32,33]. It is therefore reasonable to expect that the re-introduction of mixed-severity fire is likely to have benefits to post-fire forest structure and function. Moreover, tree spatial patterns are important because they influence forest dynamics including tree establishment, competition, mortality and even fire behavior [7]. Although essential for understanding how fire shapes ponderosa pine forests, the forest structure created by mixed-severity fire and its effect on subsequent regeneration has rarely been explored in a spatial context. It is therefore unclear how the re-introduction of mixed-severity fire will influence the residual forest structure and subsequent forest development in ponderosa pine-dominated forests.

The objective of this research is to evaluate spatial patterns of post-fire conifer regeneration following mixed-severity burning in the 2002 Hayman Fire, Colorado, USA. Specifically, we aim to (1) describe the post-fire forest structure created by the re-introduction of mixed-severity fire; (2) examine the relationship between the residual forest and post-fire conifer regeneration; and (3) determine how abiotic and biotic factors influence post-fire conifer regeneration density (trees m^{-2}). We hypothesized that (1) trees in the residual forest will be clustered, creating openings and opportunities for conifer regeneration; (2) post-fire residual conifers and regeneration will show repulsion, reflecting the preference for high light environments in regenerating conifers; and (3) post-fire regenerating conifer density will not be limited by distance from residual conifers, but by interactions with sprouting trees and by topography. That is, we expect regenerating conifers to be concentrated in more mesic areas, similar to patterns found in high-severity areas [26]. Understanding the characteristics of ponderosa pine-dominated forest and requirements for seed production, germination, and establishment, we expect topography and burn severity to be important drivers of regeneration density [25]. Characterizing these patterns of tree regeneration following wildfire is critical for understanding the drivers of the clustered spatial patterns observed in historical dry conifer forests, and anticipating longer-term stand structure and intertwined ecological properties and processes such as potential fire behavior and understory plant community composition and productivity.

2. Materials and Methods

2.1. Study Area

The Hayman Fire provides an ideal landscape for examining the post-fire forest structure created by mixed-severity fire and subsequent conifer regeneration. This 52,000 ha fire is the largest known wildfire in Colorado (USA) within the last century, making it of considerable interest to land managers, policy makers, researchers, and the public [34]. Located ~60 km southwest of Denver, the Hayman Fire was ignited on 8 June 2002 (Figure 1) in an area that receives 511 mm of precipitation year^{-1} and has a mean annual temperature of 6 °C [35]. The fire predominantly burned through stands of overly dense and homogeneous ponderosa pine-dominated forest from which the historical mixed-severity fire regime had been excluded for about a century [34,36,37]. A large portion of the Hayman Fire burned with high-severity (43%; Monitoring Trends in Burn Severity; [38], much of it in a single day with extreme weather conditions [39]. Low- and moderate-severity burning occurred on 34% and 22% of area, respectively, typically under less extreme weather conditions [39]. Additional information on fire behavior, fire weather, and fire effects can be found in The Hayman Fire Case Study [34].

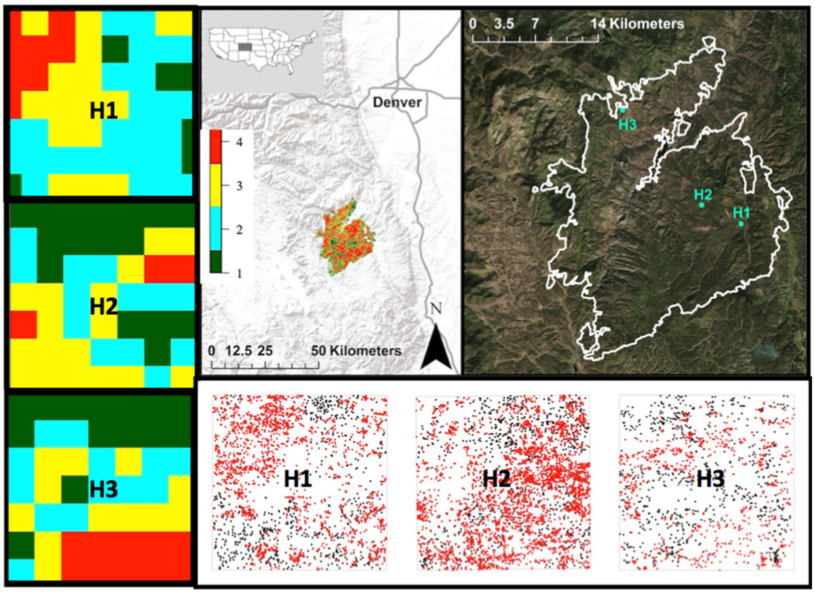

Figure 1. The Hayman Fire and plot (H1, H2, and H3) locations in the Colorado Front Range, USA. Within each plot, residual trees (black points) are shown relative to post-fire regeneration (red points) (bottom row). Esri basemap layers: the World Terrain Reference shows the Hayman Fire in relation to Denver and World Imagery denotes topography and forest cover in relation to plot locations within the fire. Monitoring trends in Burn Severity (MTBS) shows the mixed-severity fire effect in the Hayman Fire. Thematic burn severity classes include unchanged (green), low- (cyan), moderate- (yellow), and high- (red) severity (left side; scale is 4 ha).

The ponderosa pine-dominated forests burned by the Hayman Fire were variable in overstory tree density and composition [37]. Tree density was greater at higher elevations, on northerly slopes, and in draws, where moisture was more available. Douglas-fir (*Pseudotsuga menziesii* Franco) tended to be more abundant in these more moist locales, often becoming codominant with ponderosa pine. Quaking aspen (*Populus tremuloides* Michx.), blue spruce (*Picea pungens* Engelm.) and lodgepole pine (*Pinus contorta* Douglas ex Loudon), also became more common as elevation increased and as aspect became more northerly. Understory plant communities prior to the fire were dominated by graminoids and forbs (e.g., common yarrow (*Achillea millefolium* L.), white sagebrush (*Artemisia ludoviciana* Nutt.), Ross' sedge (*Carex rossii* Boott), and mountain muhly (*Muhlenbergia montana* (Nutt.) Hitchc.) [40].

Relatively short-statured shrubs were also present (e.g., kinnikinnick (*Arctostaphylos uva-ursi* (L.) Spreng.) and alderleaf mountain mahogany (*Cercocarpus montanus* Raf.).

2.2. Study Design

We established 4-ha plots (n = 3) within the Hayman Fire perimeter in 2013 and 2014 (Figure 1). Plot locations were determined by first using ArcGIS 10.1 (Esri, Redlands, CA, USA) to identify suitable large-scale (~15 to 35 ha) study sites. Suitable sites were areas that burned with a heterogeneous mosaic of severities (as indicated by the MTBS burn severity product and ArcGIS' aerial imagery basemap), that were on US Forest Service land that were accessible (i.e., within 2–3 km of a road), and not impacted by post-fire logging or planting activities. Once suitable sites were identified, points were randomly generated in ArcGIS, and one point was randomly selected. We then established a plot corner at that point, with the plot oriented to keep the plot within the study site or to avoid undesirable features within the plot (i.e., roads, streams, large rock outcroppings, and areas heavily utilized by the public). All plots contained mixed-severity fire effects, verified by MTBS burn severity, which included elements of low and moderate severity fire, and small portions of high severity that occupied no more than 1 ha within the plot (Figure 1). Post-fire regeneration was measured 12–14 years following wildfire to allow enough time for regeneration to occur.

Within each plot, we mapped all live trees >15 cm tall (Figure 1). A rangefinder (Laser Technologies Inc. TruPulse 360-B) was used in combination with a Trimble global positioning system (GeoXH with Terrasync, accurate to ±20 cm; Trimble Navigation Limited, Sunnyvale, CA, USA) to record the location of every living tree with high accuracy (±38 cm) [30]. In addition to location, we recorded diameter at breast height (DBH), tree height, and species for each overstory tree (i.e., >1.4 m tall), and we recorded tree height, species, and whether germination occurred pre- or post-fire for each regenerating tree (i.e., >15 cm tall and <1.4 m tall). We refer to regeneration that established pre-fire as advanced regeneration and all regeneration that established after the fire as post-fire regeneration. It is important to note that in some portions of the plots we encountered dense clumps of regenerating trees, making it time-consuming to map each one individually. For clumps where regenerating trees were similar in species, height, and age, we mapped the center point of the clump and we recorded the clump radius and the number of regenerating trees in the clump, in addition to recording species, average height, and pre- or post-fire germination status. The radius of the clumps ranged from 0.5 to 4 m, with most being 1 m or less.

2.3. Residual Forest Structure

Forest structure has two principal dimensions: the types, number and sizes of individual structural elements (e.g., individual trees); and their arrangement in space [7,41]. Here, residual forest structure refers to remnant surviving trees and does not include dead standing or downed trees. We described non-spatial aspects of forest structure using tree density (trees per hectare; TPH), diameter at breast height (DBH), tree height, basal area (BA), and quadratic mean diameter (QMD) [42,43]. To estimate canopy cover of the residual forest, we used a crown radius of 3 m for all overstory trees [8]. We measured the nearest neighbor distance for each tree and the distance to the nearest tree for each 1 m pixel within the plot using the R package spatstat [44,45]. We also used spatial quantitative descriptions of forest stand structure that describe three structural characteristics: positioning, mixture, and differentiation [46] (Table 1).

Table 1. Non-spatial and spatial measures of forest structure used to evaluate study objectives and hypotheses.

Objectives	Approach		Inference	Scale	Hypotheses
Describe residual forest structure	Non-spatial Metric	Density, DBH, Height, QMD, Canopy Cover	Non-spatial attributes of the residual forest	Plot	
	Spatial Metric	Nearest Neighbor Distance, Distance to the Nearest Tree	Spatial attributes of trees in the residual forest	Within-plot	
	Spatial Metric (Positioning)	Clark and Evans Index (CEI)	Spatial pattern of the residual forest	Plot	1
	Spatial Analysis (Positioning)	Ripley's K Function	Spatial pattern of trees in the residual forest across distance scales	Within-plot	1
	Spatial Metric (Species Mixture)	Durchmischung Index (DMI)	Residual forest species associations	Plot	
	Spatial Metric (Differentiation)	Differenzierung Index (DZI)	Residual forest horizontal and vertical structural complexity	Plot	
Describe the relationship between the residual forest and post-fire conifer regeneration	Spatial Analysis (Positioning)	Ripley's K Function	Patterning of regenerating trees across distance scales	Within-plot	
	Spatial Analysis (Positioning)	Bivariate K Function	Attraction or repulsion between residual trees and regenerating trees	Within-plot	2
Drivers of post-fire conifer regeneration density	Spatial Analysis (Positioning)	Neyman–Scott Point-Process Model	Drivers of regeneration density	Within-plot	3

Positioning is the spatial distribution of points (i.e., trees) in an area. The Clark and Evans index (CEI) was used to characterize point patterns at the plot level as either random, regular, or clustered [46]. In a completely random pattern (CEI = 1), the position of any one point is independent of the position of all the other points. In a regular pattern (CEI > 1), points are farther away from their nearest neighbors than would be expected for a random pattern. Points are more likely to be found near other points in a clustered pattern (CEI < 1), and the average distance from any arbitrary point to its nearest-neighbor is less than expected in a completely random pattern. We also evaluated positioning with Ripley's K [7,8,47,48] using the R package spatstat [44,45]. The K function estimates spatial dependence between points of the same type (e.g., residual trees) across spatial scales by determining the expected number of points within a distance (r) from any randomly sampled point. For each plot, we evaluate deviations from complete spatial randomness (CSR) by comparing observed data with an inhomogeneous Poisson null model [49–51]. We used an inhomogeneous rather than a homogeneous Poisson process to account for non-constant density gradients in the data [52]. Points were randomly distributed under the inhomogeneous Poisson null model 999 times to test for departure from CSR. It is common to apply a correction for edge effects when calculating the K function. Using the correction = "best" setting in the package spatstat, the best available edge correction, "the isotropic correction" was applied. Observed patterns differ from CSR where the plot of K(r) falls outside the simulated envelope for a random pattern. A clustered point pattern is indicated by a K(r) above the envelope (i.e., more points present than would be expected under CSR) and regular spacing occurs where K(r) falls below the envelope (i.e., fewer points present than would be expected under CSR). Unlike the CEI, the K function describes characteristics of the point processes at many distance scales and uses spatial randomness as a benchmark to define spatial regularity and clustering [7]. Since clustering and regularity are characteristics of a pattern at a specific distance scale, point patterns can exhibit both clustering and regularity at the same time. For example, regeneration can be clustered at longer distances depending on how their parent trees are spaced, but regularly spaced at a small scale because they compete for resources. There is also evidence in some studies of clustering [53,54] and perhaps facilitation at small scales [29].

Mixture refers to spatial interspersion among species within an area and was quantified with the Durchmischung index (DMI) [46]. Ranging between 0 and 1, the DMI describes the degree to which species exist in homogeneous clusters, exhibit repulsion, or show attraction to other species. Strongly represented species or those that exist in homogeneous groups will result in low DMI values, whereas less frequent or regularly positioned species will have high DMI values (indicating that a species nearest neighbor is likely to be a different species) [46]. We calculated DMI on a plot level to understand the average degree of mixing between species in dry conifer forests and use the three nearest neighbors to calculate DMI for each plot [46]. Although we explored the effects of increasing the nearest neighbors up to six trees, results did not change so we report the DMI using the three nearest neighbors to aid comparisons with other studies [46].

Differentiation is a measure of the variation in tree height or DBH among neighboring trees (three nearest neighbors). We calculated the Differenzierung index (DZI) using total tree height (DZI_{TH}) and DBH (DZI_{DBH}) to measure vertical and horizontal structure, respectively. Ranging between 0 and 1, values from 0 to 0.2 represent low differentiation (similar height or DBH between neighboring trees), 0.2 to 0.4 moderate differentiation, 0.4 to 0.6 clear differentiation, 0.6 to 0.8 strong differentiation, and 0.8 to 1 very strong differentiation or heterogeneity between the three nearest neighbors [46]. Measuring horizontal and vertical variation is important for understanding the amount of within-plot variation among neighboring trees.

2.4. Post-Fire Regeneration

Similar to the residual trees, the spatial pattern of post-fire conifer regeneration was analyzed using Ripley's K functions [48], in the R package spatstat [44,45]. This approach was used to test for departure from a spatially random pattern across distance scales to understand at what distance post-fire regeneration exhibits a random, clustered, or regular pattern. The spatial relationship between residual trees and post-fire regeneration was evaluated using a bivariate K-function [50,55]. The bivariate K-function calculates the expected mean number of post-fire regenerating trees within a given radius (r; i.e., distance) of an arbitrary residual tree. This approach evaluates attraction between trees and regeneration within r. The null hypothesis of spatial independence between the two groups is refuted where values of K(r) fall above or below the bivariate inhomogeneous Poisson null model simulation envelope. The inhomogeneous Poisson null model envelope is calculated using random toroidal shifts of one pattern relative to the other during each of the 999 Monte Carlo iterations. A K(r) above the simulation interval is indicative of a positive spatial association (attraction; i.e., there is more regeneration than would be expected within r). Where K(r) falls below the confidence interval, there is a negative spatial association (repulsion; i.e., less regeneration than would be expected within r). This approach explores at what distances trees and regeneration show attraction and repulsion.

Potential drivers of post-fire conifer regeneration density were modeled using a Neyman–Scott point-process model, which is routinely used to describe clumped spatial patterns [50,56]. Least squares techniques were used to optimize the model parameters. Simulation envelopes were generated using the Neyman–Scott distribution, after the parameters had been fit to the data, to test for a departure from the Neyman–Scott process. Simulations of CSR were generated through 999 iterations of a Monte Carlo simulation. If the K(t) plot for the observed data falls within the simulated envelope for the Neyman–Scott process, it suggests that the pattern has the properties of the specified model. Nearest residual tree distance (m) and height (m), burn severity [57,58], topographic wetness index (TWI) [59], topographic position index (TPI) [60,61], elevation (m), and nearest aspen cluster density and distance (m) were explored as drivers of post-fire conifer density. All variables were initially placed in the model. Variables of least significance were removed from the model one at a time until all remaining variables were significant at an α of 0.05. We calculated topographic measurements (TWI, and TPI) using 30 m resolution digital elevation models (Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM); [62]). We used base tools in ArcGIS 10.3 (ESRI, Redlands, CA, USA) with the Geomorphology and Gradient Metrics toolbox for these calculations.

3. Results

3.1. Residual Forest Structure

The residual forest was dominated by conifers that survived the wildfire. Overstory trees (i.e., >1.4 m tall) accounted for 99% of the residual forest on average (Table 2), and advanced regeneration accounted for the remainder. Ponderosa pine was the dominant species (71% of trees on average) in the residual forest and Douglas-fir was the second most common species (27%). A mean DMI of 0.6 ± 0.02 indicated that ponderosa pine was very dominant and therefore more likely to be surrounded by the same species (Table 2). Residual tree density ranged from 167 to 197 TPH across all plots, while average percent canopy cover was 31.5 ± 1.8% (Table 2) due to overstory trees occurring in groups with overlapping crowns. The average nearest neighbor distance between overstory trees in the residual forest was 2.9 ± 0.1 m and the average distance to the nearest tree for any point within the plots was 6.1 ± 0.3 m. CEI suggested that trees were clustered, and Ripley's K suggested that this clustering occurred at radii less than 30 m (Table 2; Figure 2). Average indices of horizontal (DZI_{DBH}) and vertical (DZI_{TH}) structure showed moderate vertical differentiation and clear horizontal differentiation (Table 2).

Table 2. Residual forest structure within the Hayman Fire plots (H1, H2, and H3) 11–12 years following burning. This summarization includes all conifers and aspen (POTR) which represents 0.61% of the residual trees. Measures of trees per hectare (TPH), % ponderosa pine (PIPO), % Douglas-fir (PSME), % aspen (POTR), basal area (BA), quadratic mean diameter (QMD), Clark and Evans index (CEI), Durchmischung index (DMI), horizontal differentiation (DZI_{DBH}), and vertical differentiation (DZI_{TH}) are included in this summary.

Plot	H1	H2	H3	Average	Standard Error
Residual Trees (%)	99	99	100	99	0.4
Residual Regeneration (%)	1	1	0	1	0.4
TPH	167	197	173	179	9
Canopy Cover (%)	29	35	30	32	2
% PIPO	74	73	65	71	3
% PMSE	22	25	34	27	4
% POTR	3	1	0.4	1	1
BA (m^2 ha^{-1})	8	11	8	9	1
QMD (cm)	25	27	23	25	1
Nearest Neighbor (m)	3	3	3	3	0.1
Distance from Nearest Tree (m)	6.2	5.6	6.6	6.1	0.3
CEI	−0.3	−0.2	−0.3	−0.3	0.01
DMI	0.6	0.6	0.6	0.6	0.01
DZI_{DBH}	0.5	0.53	0.5	0.5	0.01
DZI_{TH}	0.3	0.3	0.3	0.3	0.01

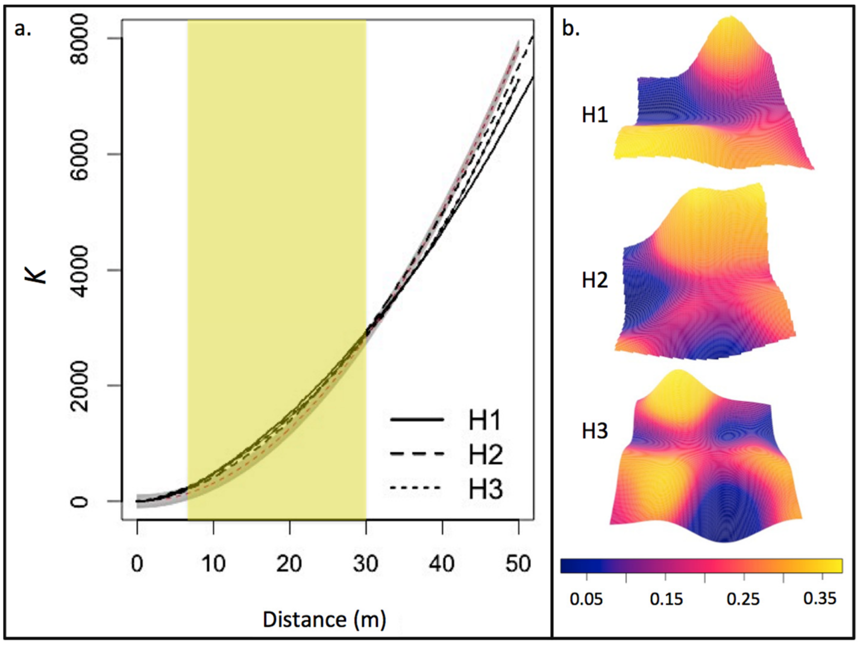

Figure 2. (**a**) Ripley's K for residual trees in the Hayman Fire plots (H1, H2, and H3). A clustered point pattern is indicated by an observed K(r) (black lines) that is above the complete spatial randomness (CSR) simulated envelope (gray shaded region), whereas a regular point pattern is indicated by an observed K(r) that falls below the envelope. Trees exhibited clustering at distances up to ~30 m (yellow shaded region); (**b**) Perspective plots of residual tree density (trees m^{-2}) in the Hayman Fire, with density represented by the height and color of the plot.

3.2. Post-Fire Regeneration

Unlike the sparse advanced regeneration observed in the residual forest, post-fire regeneration was dense, averaging 685 TPH. Ponderosa pine accounted for 73% of post-fire regeneration on average, while Douglas-fir and aspen accounted for 18% and 8%, respectively (Table 3). Focusing on post-fire regenerating conifers, TPH averaged 630, and height averaged 0.33 m. Just 32% of post-fire regenerating conifers were found under residual forest canopy cover, on average. Ripley's K indicated that post-fire conifer regeneration exhibited a clustered pattern across all distances in H1 and H2, and at distances up to 30 m in H3, beyond which patterns were regular (Figure 3). Evaluating bivariate changes in conifer regeneration densities relative to those of residual trees indicated that regeneration and trees were attracted at very short distances (<0.5 m) and repulsed at distances >1 m (Figure 4).

Table 3. Post-fire regeneration in the Hayman Fire plots (H1, H2, and H3) 11–12 years following burning. Measures of stems per hectare (SPH), stem height, and percent of SPH comprised of ponderosa pine (PIPO), Douglas-fir (PSME), and aspen (POTR) are summarized.

Plot	H1	H2	H3	Average	Standard Error
SPH (Conifers)	728 (613)	1071 (1036)	256 (241)	685 (630)	236 (230)
Stem Height (Conifers)	0.31 (0.28)	0.30 (0.29)	0.41 (0.41)	0.34 (0.33)	0.04 (0.04)
% PIPO	67	80	70	73	4
% PMSE	16	16	23	18	2
% POTR	16	3	6	8	4

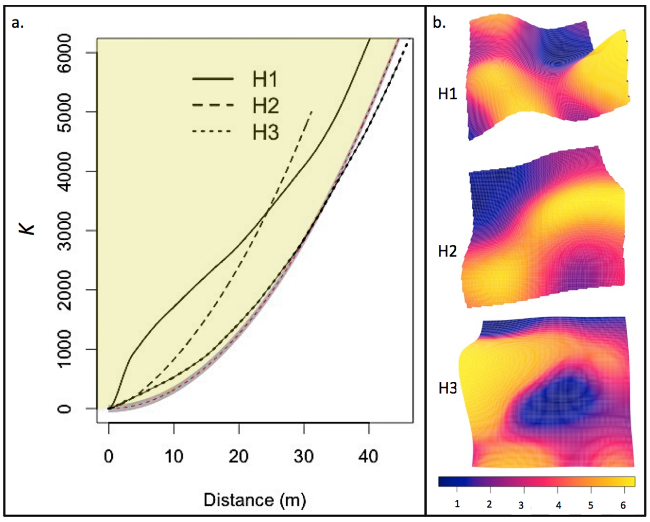

Figure 3. (**a**) Ripley's *K* for post-fire conifer regeneration in the Hayman Fire plots (H1, H2, and H3). A clustered point pattern is indicated by an observed *K*(r) (black lines) that is above the CSR simulated envelope (gray shaded region) and regular spacing is indicated by an observed *K*(r) that is below the envelope. The clustered region is shown in yellow. Clustering in post-fire conifer regeneration occurred across all distances in H1 and H2 and at distances <30 m in H3. Beyond 30 m regeneration occurred in a regular pattern; (**b**) Perspective plots of post-fire conifer regeneration density (stems m^{-2}) in the Hayman Fire, with density represented by the height and color of the plot.

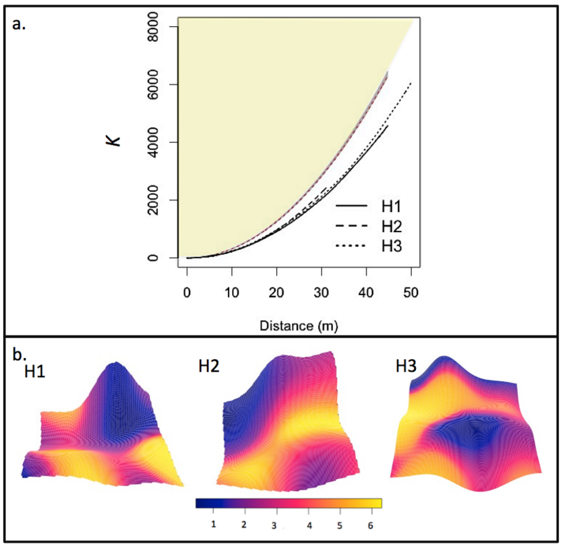

Figure 4. (**a**) Bivariate *K*-functions of associations between residual trees and post-fire conifer regeneration in the Hayman Fire plots (H1, H2, and H3). Attraction (yellow shaded region) is indicated by an observed *K*(r) that is above the CSR simulated confidence envelope (grey shaded region), while repulsion is indicated by an observed *K*(r) that falls below the envelope. Trees and post-fire conifer regeneration showed repulsion at distances greater than 1 m; (**b**) Perspective plots of residual tree and post-fire conifer regeneration density (trees m^{-2}). The height of the plot represents residual tree density and the color indicates regeneration density. Regeneration densities were higher in areas with lower tree densities.

The Neyman–Scott point-process model adequately described clumped patterns of post-fire conifer regeneration density (stems m^{-2}; Figure 5), while nearest residual tree distance, burn severity, TWI, elevation, and nearest aspen cluster distance were significant drivers of this density (Table 4;

Figure 6). Nearest residual tree distance was negatively correlated with post-fire conifer regeneration, suggesting that post-fire conifer regeneration was more abundant closer to pre-fire residual trees. Unlike the bivariate K-function, the distance to the nearest tree layer considers the location of all trees within a plot to determine a distance value for each location at a 1 m resolution. Burn severity was positively correlated with post-fire regeneration density, indicating that moderate- and high-severity areas were more likely to have higher regeneration densities than low-severity and unburned areas. In plot H1, TWI was negatively correlated with regeneration density and positively correlated with regeneration density in H3. These results suggest that higher moisture levels were associated with greater conifer regeneration except where topographic variation was low. In H1, elevation was negatively correlated with regeneration density and in H3, elevation was positively correlated with regeneration density. The distance to the nearest post-fire aspen cluster was negatively correlated with conifer regeneration in H1 and positively correlated in H3. In the highest elevation plot with more topographic variation (H1), aspen clusters and conifer regeneration showed repulsion, while in the lowest elevation plot with minimal topographic variation (H3), conifer regeneration density was greater closer to aspen clusters.

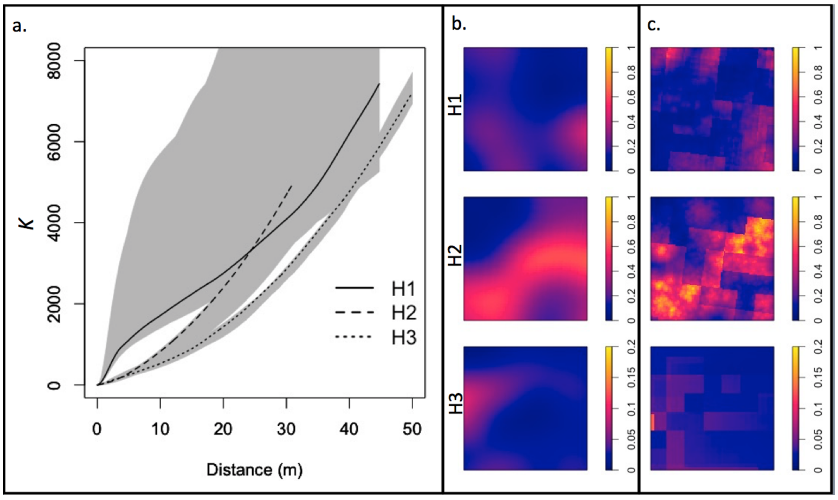

Figure 5. (**a**) Post-fire regeneration density in relation to the Neyman–Scott point process model for plots (H1, H2, and H3) in the Hayman Fire. Observed data (black lines) were within the bounds of the simulated envelope for the Neyman–Scott model (shaded region), confirming that the data were spatially clumped at all distances. Comparing (**b**) observed and (**c**) predicted densities shows that the model is capturing general trends in regeneration density.

Table 4. Estimates of regeneration density (stems m^{-2}) regression coefficients, standard errors (S.E.) and *p*-values for the Hayman Fire plot level point pattern models. The distance to the nearest residual tree, burn severity, topographic wetness index (TWI), elevation, and the distance to the nearest aspen (POTR) cluster were important drivers of post-fire regeneration density.

Plot		Intercept	Nearest Residual Tree Distance (m)	Burn Severity			TWI	Elevation	Nearest POTR Cluster (m)
				Low	Moderate	High			
H1	Estimate	262.627	−0.036	0.357	1.029	0.842	−0.007	−0.112	−0.007
	S.E.	7.530	0.002	0.057	0.063	0.078	−0.014	0.003	−0.014
	p-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
H2	Estimate	−1.113	−0.042	0.657	1.091	0.939			
	S.E.	0.028	0.002	0.028	0.026	0.042			
	p-value	<0.001	<0.001	<0.001	<0.001	<0.001			
H3	Estimate	−49.284		0.266	0.616	0.301	0.002	0.018	0.002
	S.E.	9.175		0.092	0.087	0.098	0.001	0.004	0.001
	p-value	<0.001		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

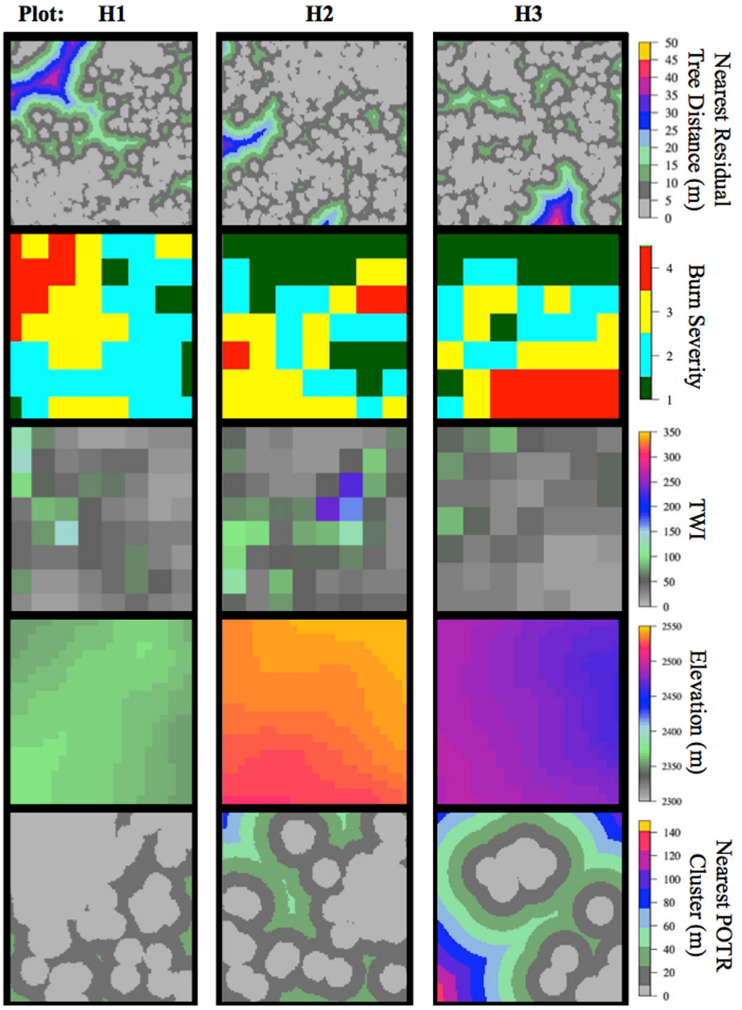

Figure 6. Significant drivers of post-fire regeneration density for the Hayman Fire plots (H1, H2, and H3) include nearest residual tree distance (m), burn severity, topographic wetness index (TWI), elevation, and the nearest aspen (POTR) cluster. Thematic burn severity classes include unburned (green), low- (cyan), moderate- (yellow), and high- (red) severity.

4. Discussion

We examined spatial patterns of post-fire conifer regeneration following the reintroduction of mixed-severity fire in a Colorado ponderosa pine-dominated forest. We hypothesized that (1) trees in the residual forest would be clustered, creating openings and opportunities for regeneration; (2) residual trees and post-fire conifer regeneration would exhibit repulsion; and (3) post-fire regenerating conifer density would not be limited by distance from residual trees. Our results support our hypotheses; moreover, they highlight how other biotic and abiotic factors, such as topography and the location of sprouting species, further complicate spatial patterns in post-fire conifer regeneration.

4.1. Residual Forest Structure

The re-introduction of mixed-severity fire after a century of fire exclusion resulted in a clustered spatial pattern of residual trees, with densities that were still higher than those reported for historical forests elsewhere in the region [8]. However, residual tree densities were lower than those reported for undisturbed forests in the region [31,37,63], as well as for recently restored forests [31,63]. Basal area and canopy cover values following mixed-severity fire were also within the range of those reported for restored forests [31,63]. The lack of advanced regeneration suggests that these trees, if they were present before the fire, were killed. Furthermore, the clustered nature of the residual forest suggests that trees survived in groups. These results indicate that fire-caused mortality is at least partly responsible for creating the historical spatial pattern reported in a number of studies [7,8,64]. Many of these studies have speculated that the spatial clustering was a result of fire, but this is one of the only studies that have documented this pattern immediately post-fire.

4.2. Post-Fire Regeneration

Following recent large fires, one of the limiting factors of natural conifer regeneration is a seed source [65], particularly for ponderosa pine which has a relatively large seed. For species without serotinous cones, tree establishment is largely a function of seed dispersal [66] and competition from other species [23,67]. While the conditions created by high-severity fire can lead to dispersal and recruitment limitations [23,25,29], the residual forest structure following mixed-severity fire contained fire-resistant, seed-bearing conifer trees [68], whose location within the landscape, thick bark, and high crown base heights facilitated their survival and post-fire forest recovery. The residual forest following mixed-severity fire was sufficient to support natural regeneration within 12 years following the fire, in a region where seed masting events are episodic [26,69,70] and occur on average every 3–12 years for dominant conifers (ponderosa pine and Douglas-fir), with limited seed availability in intervening years [71].

The clustered spatial pattern of the residual forest allowed for ample openings, which together had a pronounced effect on conifer regeneration density. Our results suggest that, like the residual forest, post-fire regeneration also had a tendency to aggregate at distances up to 30 m. Similar to patterns observed following high-severity fire, distance from the nearest residual tree was a significant driver of post-fire conifer regeneration density [25,27,29]. However in this case, distance does not represent a limitation of seed dispersal, but the influence of both light and available space. That is, the clustered spatial pattern of post-fire regeneration appears to be a direct inverse of the post-fire residual spatial structure. This interpretation is supported by the significant repulsion between residual trees and post-fire regeneration at distances greater than 1 m. It is also important to note that patterns in regeneration density were very similar to patterns observed in the distribution of nearest residual tree distance across plots. This pattern suggests that seed source was not limiting regeneration patterns, and that high regeneration rates largely followed patterns in available space (Figure 7) with slightly higher regeneration occurring in areas due to variations in elevation that influenced moisture conditions and aspen clusters [27]. This result is important because it suggests that the clustered spatial pattern observed in historical ponderosa pine studies is attained, in part, in the regeneration process [7,8,64].

Moderate increases in the availability of resources such as light and water can be enough to influence regeneration establishment and survival [72,73], and drive spatial patterns in forest structure [74]. Similar attraction patterns have been found in Dahurian larch (*Larix gmelinii* Rupr), where its conical canopy is thought to create a light-facilitating environment for regeneration [74]. Results here indicate that at distances farthest from trees, there was less regeneration than would be expected if there were no benefit to being in close proximity of trees. If light were the dominant driver of regeneration success, then regeneration would occur at higher frequencies, at greater distances from overstory trees [74]. Lower light levels created by overlapping canopies and the distribution of small gaps within a plot would also have influenced the relationship between distance from the nearest tree and regeneration density.

The residual forest structure following the re-introduction of mixed-severity fire, combined with the mix of burn severities and environmental conditions, is perpetuating ponderosa pine-dominated forests. Fire can act as a mechanism of change in plant community composition by altering the composition of species in the residual forest [75], or by producing post-fire conditions that favor the establishment of species that did not dominate the pre-fire forest [75,76]. Moisture requirements, one of the most important characteristics that affects post-fire tree establishment, are likely to change following fire. The moisture preference of trees can have a strong influence on the distribution of species, even at relatively small scales, including after fire, when ambient conditions can be warmer and drier than pre-fire conditions [77]. Unlike high-severity fire, mixed-severity burns had more positive effects on the residual forest structure for conifer species and subsequent conifer regeneration [68]. Similar to patterns observed by Kemp et al. [27], conifer species composition did not vary substantially between the residual trees and post-fire regeneration. Ponderosa pine was the dominant residual tree species and the species composition of regeneration suggests that this pattern will continue.

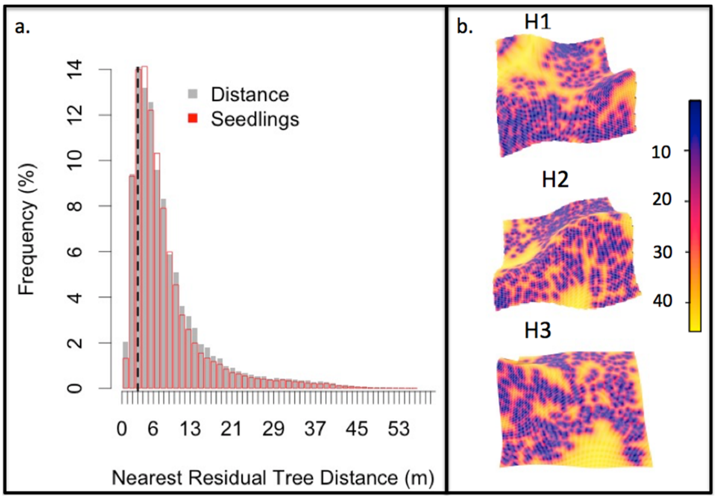

Figure 7. (**a**) The distributions of all post-fire regeneration (red) and nearest residual tree distance (gray) within plots by nearest residual tree distance (m) in the Hayman Fire. The vertical black line marks distances under canopy cover; (**b**) Post-fire perspective plots where the height of the plot represents the density of post-fire regeneration and the color indicates the distance to the nearest residual tree (m) for each 4-ha plot (H1, H2, and H3).

4.3. Study Limitations

Major limitations of this study include the low sample size and the lack of information on the pre-fire forest structure. Although we measured the forest structure following mixed-severity fire, assessing how the forest structure changed as a result of fire was not possible. Additionally, it is important to note that like in many other analysis methods, the driving factors and processes that cause different or even similar spatial patterns (i.e., clustered, random, and regular), including facilitation (positive effect) or competition (negative effect), are open to interpretation [74]. A clustered spatial pattern can be an indication of species having similar ecological requirements [78], facilitation among individuals [79,80], or dispersal limitations at larger scales [81].

5. Conclusions

Forest spatial structure yields important clues to understanding tree interactions with the environment as well as the dynamics of forest communities. The development of spatial patterns resulting from positive and negative associations and environmental factors is an important topic in ecosystem research [74], and has been used here to understand patterns in post-fire regeneration following mixed-severity fire. Predicting plant community responses to changing environmental conditions is a key element of forecasting and mitigating the effects of global change. Disturbance can play an important role in these dynamics, by initiating cycles of secondary succession and generating opportunities for communities of trees to reorganize.

Acknowledgments: This research was funded by the United States Forest Service (USFS) National Fire Plan (NFP-13-16-FWE-43) and the Rocky Mountain Research Station (RMRS). The views expressed in this manuscript are those of the authors alone and do not necessarily reflect the stance of the RMRS or the USFS.

Author Contributions: P.J.F., M.A.B., J.M.I., and C.H.S. conceived and designed the study; M.E.C. and P.J.F. managed the fieldwork; S.L.M. analyzed the data; S.L.M. wrote the paper with input from the other authors.

Conflicts of Interest: The authors declare no conflict of interest.

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