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Tree Regeneration Spatial Patterns in Ponderosa Pine Forests Following Stand-Replacing Fire: Influence of Topography and Neighbors

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Abstract: Shifting fire regimes alter forest structure assembly in ponderosa pine forests and may produce structural heterogeneity following stand-replacing fire due, in part, to fine-scale variability in growing environments. We mapped tree regeneration in eighteen plots 11 to 15 years after stand-replacing fire in Colorado and South Dakota, USA. We used point pattern analyses to examine the spatial pattern of tree locations and heights as well as the influence of tree interactions and topography on tree patterns. In these sparse, early-seral forests, we found that all species were spatially aggregated, partly attributable to the influence of (1) aspect and slope on conifers; (2) topographic position on quaking aspen; and (3) interspecific attraction between ponderosa pine and other species. Specifically, tree interactions were related to finer-scale patterns whereas topographic effects influenced coarse-scale patterns. Spatial structures of heights revealed conspecific size hierarchies with taller trees in denser neighborhoods. Topography and heterospecific tree interactions had nominal effect on tree height spatial structure. Our results demonstrate how stand-replacing fires create heterogeneous forest structures and suggest that scale-dependent, and often facilitatory, rather than competitive, processes act on regenerating trees. These early-seral processes will establish potential pathways of stand development, affecting future forest dynamics and management options.

Keywords: pair-correlation function; mark-correlation function; high-severity fire; species interaction; topographic niche; vegetation assembly; early-seral forests; secondary succession

1. Introduction

Disturbances, management, and ecological processes imprint their signatures on the spatial pattern of forest structure throughout forest development. Interpreting these spatial patterns while using other sources of information such as species' silvics provides insights into forest stand dynamics [1]. One ecosystem where studies of spatial patterns have led to an improved understanding of stand dynamics is in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.)-dominated forests of western North America. In many of these forests, relatively frequent, low- to mixed-severity fires historically shaped structure and composition, creating and maintaining generally open, uneven-aged stands consisting of a mosaic of individual trees, tree groups, and openings [2]. These mosaics have been characterized as aggregated at sub-hectare scales and with heterogeneous spatial patterns of tree sizes

(e.g., within a group, interior trees were often smaller than peripheral trees) [2,3]. Fires responded to and reinforced these spatial patterns [2] and these fire-dependent patterns regulated elements of forest dynamics including demography [4], mortality [4], tree growth [3] and regeneration [5].

As the density and spatial arrangement of tree locations and sizes affect forest dynamics [6–8], understanding patterns of initiating stands is critical for anticipating the consequences of altered fire regimes [9,10]. Many ponderosa pine forests are experiencing greater occurrence and extent of high-severity, stand-replacing fires due, in large part, to a century of fire exclusion, past land uses, and changing climate [11–13]. Because of distance-limited seed dispersion, large stand-replacing patches often beget sparse post-fire tree regeneration, generating concern that forest developmental pathways may be altered by shifts towards greater high-severity fire [14,15]. Such changes will have long-lasting repercussions for forest structure and composition [14,15].

Recent syntheses of stand development suggest that severe, stand-replacing fires induce spatially complex forest structures [10,16]. Patterns of sparse stand regeneration are hypothesized to be especially heterogeneous, influenced by large and fine-grained variability in growing environments [7,8]. Competition is thought to largely influence patterns [8], resulting in the spatial segregation of trees into monospecific groups [17] and diminished growth between competing neighbors [18]. Other studies, however, suggest that positive interactions may be more important as neighbors ameliorate moisture stress in the absence of canopy cover [8,19]. Positive interactions would form heterospecific groups in contrast to competitive interactions [17]. As much as tree interactions inform spatial patterns, abiotic influences on resource availability are also likely to be important, reflecting niche preferences and promoting fine-scale aggregation [20,21]. For example, the higher evaporative demand on southwestern aspects or lower soil moisture retention on steep slopes inhibit regeneration less so than on northeastern or shallower slopes [15]. Moreover, sparsely regenerating stands may also develop a heterogeneous spatial arrangement of tree sizes due to biotic interactions and differential growth rates across abiotic gradations [7,8]. How patterns of regenerating trees manifest is therefore contingent on the prevailing growing environment and requires examination of the roles of biotic and abiotic factors such as tree interactions and topography [8].

Further, tree regeneration patterns are modulated by traits of species composing the regeneration [22]. For example, in ponderosa pine-dominated forests, wind is an important disperser of ponderosa pine and Douglas-fir *(Pseudotsuga menziesii* (Mirb.) Franco) seeds; the heavier seed size of ponderosa pine may not disperse as far as lighter Douglas-fir seeds [14,15,23]. In contrast, lodgepole pine *(Pinus contorta* Dougl. ex Loud.) cones are often serotinous [24] which could result in concentrated seed dispersal around dead parent trees. However, lodgepole pine seeds are also light and easily wind-dispersed [23]. Quaking aspen *(Populus tremuloides* Michx.) sprouts clusters of ramets around preexisting genets and does not primarily rely on wind dispersion to regenerate [25]. Once regeneration occurs, species' tolerance to heat, light, and moisture availability, which vary by abiotic and biotic environmental conditions, can influence establishment and growth [22]. These differential traits make it pertinent to examine tree regeneration patterns using a species-specific approach.

Our overarching aim was to identify the spatial patterns of tree regeneration in ponderosa pine-dominated forests following stand-replacing fire, and ascertain how tree patterns are responding to topographic variation and tree interactions. We conducted our study in ponderosa pine forests given their wide geographic range in western North America and the interest of managers in buffering post-fire resiliency of dry forests globally [11]. Specifically, we (1) assessed the spatial patterns of tree locations and heights; (2) examined whether species interactions, in a beneficial or negative manner, were shaping these patterns; and (3) explored the influence of topographic gradations on these patterns. Our results further an ecological understanding of forest recovery and may inform forest management decision making within these and similar dry forests.

2. Materials and Methods

We studied ponderosa pine forests following three wildfires in the western USA: the 2000 Bobcat Gulch Fire (Colorado Front Range), the 2002 Hayman Fire (Colorado Front Range), and the 2000 Jasper Fire (Black Hills of South Dakota; Figure 1). Within the fire footprints, elevation ranged from ~1700 to 2500 m, mean annual precipitation from 48 to 58 cm, and temperature from 5.2 to 7.8 °C [26]. Aside from ponderosa pine, three other species were abundant. Quaking aspen occurred within all three burned areas, often in moister sites [27]. Douglas-fir was common on northerly aspects within the Bobcat Gulch and Hayman Fires [27]. The third, lodgepole pine, occurred on northerly aspects in the Bobcat Gulch Fire [27].

These forests historically experienced fires with a range of severities from low to moderate to high with the latter being infrequent and tied to climatic anomalies [28–30]. The mixture and frequency of severities were significantly spatially variable over landscapes, influenced by complex topography, and over decades, influenced by broad-scale climatic oscillations [28]. Though there is some debate as to the relative historical portion and patch sizes of fire severities across these landscapes [31], it is generally accepted that high-severity fires were not historically as common in extent or occurrence as today [12].

2.1. Data Collection

We established six randomly-located 4-ha (200 m × 200 m) plots in stand-replacing patches (i.e., 100% tree mortality) of each fire, for a total of 18 plots (Figure 1). We excluded areas that were inaccessible (i.e., not on public land or >4 km from a road) or that experienced post-fire logging or planting. We placed three plots per fire adjacent to, and three plots at least 200 m from, living residual forest, permitting statistical accounting of distance–regeneration density relationships. Sampling occurred 11 to 15 years post fire to allow time for tree establishment [32].

In each plot, we recorded locations, species, and heights of all post-fire regenerating trees ≥15 cm tall (Figure 1). Where conspecifics of similar height were densely clustered, we recorded the cluster's centroid, radius, number of individuals, and their average height. Clusters were small with a median count of five trees and radius of 0.5 m. We then assigned random coordinates to clustered trees within their cluster's radius. We considered only those species with a sufficient sample size (≥20 individuals in some plot), leaving ponderosa pine and quaking aspen across all fires, Douglas-fir in the Hayman and Bobcat Gulch fires, and lodgepole pine in the Bobcat Gulch Fire. After filtering, regeneration counts ranged from three trees to 1704 trees per 4-ha plot, averaging 43 trees ha^{-1} across the sampled population (Table 1).

We calculated three topographic measurements within each plot using 10-m resolution digital elevation models [33]: aspect, percent slope, and topographic position index (TPI) [34]. We cosine-transformed azimuthal aspect to a range from zero (southwest) to two (northeast). We measured TPI as the difference in elevation between a location and its surrounding neighborhood, defined as a 10-m radius in this study. We used base tools in ArcGIS 10.3 (ESRI, Redlands, CA, USA) with the Geomorphology and Gradient Metrics toolbox [35] for these calculations.

In ArcGIS 10.3, we also measured the distance from residual forest canopy using supervised classification (see Chambers et al. [14] for method details) on 1-m resolution aerial imagery [33]. We joined topographic measurements and distance from residual forest canopy to each 4-ha plot (Table 1).
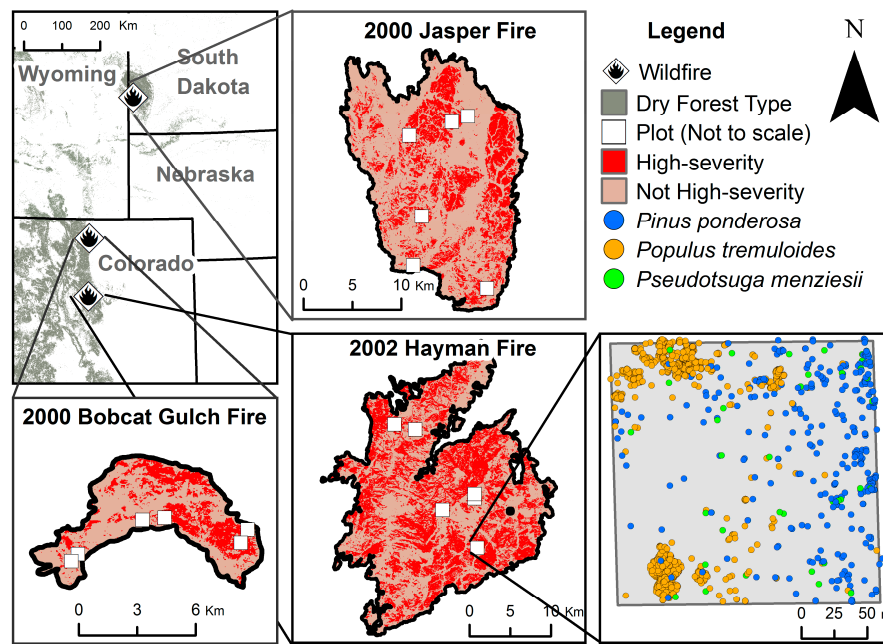
Figure 1. Locations of sampled fires and 4-ha plots within high-severity areas, as well as an example plot of mapped tree regeneration, by species, for illustration.

Table 1. Regeneration properties and topographic conditions where regeneration was present; TPI is topographic position index and distance is distance from residual live canopy.

Statistic	Density (Trees ha^{-1}) *	Height (m)	Distance (m) *	Aspect (Unitless)	Slope (%)	TPI
	Ponderosa pine (*Pinus ponderosa*)					
Mean	8.6	0.8	76.2	0.8	9.3	0.1
Std. dev.	14.5	0.5	134.3	0.8	8.7	0.4
Range	1.0–260.0	0.1–3.0	0.0–758.8	0.0–2.0	1.1–51.6	−2.1–3.2
	Lodgepole pine (*Pinus contorta*)					
Mean	0.7	1.2	150.6	1.6	39.2	0.2
Std. dev.	0.5	0.6	119.4	0.5	8.3	0.7
Range	0.0–5.8	0.3–3.0	17.7–457.9	0.1–2.0	16.6–54.4	−1.5–1.8
	Quaking aspen (*Populus tremuloides*)					
Mean	43.5	1.4	338.5	1.2	9.6	−0.4
Std. dev.	66.1	1.0	194.5	0.8	7.4	0.8
Range	0.0–414.3	0.1–4.0	10.6–759.0	0.0–2.0	1.0–49.9	−3.3–2.8
	Douglas-fir (*Pseudotsuga menziesii*)					
Mean	1.5	0.5	107.9	1.6	17.1	0.0
Std. dev.	2.1	0.3	85.1	0.6	12.9	0.6
Range	0.0–30.3	0.1–1.6	3.2–453.5	0.0–2.0	1.5–53.4	−2.1–2.7
	All					
Mean	43.0	1.2	358.9	1.1	9.9	−0.2
Std. dev.	61.2	0.9	205.1	0.8	8.5	0.8

* Tree density is inversely weighted by the sampled intensity of distances from residual forest canopy (i.e., values are the average tree density from 0 to 759 m from residual forest canopy) to control for distance-regeneration density relationships.

2.2. Patterns of Regenerating Tree Locations

To assess spatial patterns of each species, we tested whether trees were distributed randomly (i.e., complete spatial randomness or CSR), uniformly, or aggregated using the distance-dependent univariate pair correlation function, g(*r*) [36]. This function describes the density of mapped points at

distance, r, from any arbitrary point, relative to expectation under CSR [36]. Therefore, when observed statistics of g(r) are greater than expected, tree patterns are aggregated; similarly, lower values than expected suggest uniformity.

We randomly distributed points under a null model 999 times to test for departure from CSR. The null model, an inhomogeneous Poisson process, distributed points under non-constant intensity (points per unit area). Intensity was parameterized by an Epanechnikov smoothing kernel at a bandwidth of 15 m and resolution of 1 m [36]. We chose an inhomogeneous over a homogeneous Poisson process to account for intensity gradients in the observed data [36]. Treating each plot as a replicate, we pooled observed statistics together and null statistics together using ratio estimation [36]. We then tested goodness-of-fit of pooled observations about the pooled null expectation [36,37] over a range of distances, 0 to 15 m (α = 0.05 for all hypothesis tests). The upper limit was selected a priori following recommendation that tests should mirror the scale at which trees' spatial correlation structures generally manifest; this is often near 15 m [36].

We then explored interspecific interactions with the bivariate pair correlation function, $g_{1,2}(r)$. This statistic is like $g(r)$, except it considers only the number of species 2 points located at distance, r, from species 1 points [36]. The statistics' interpretation depends on choice of the null model [38]; our null model was independence. The toroidal shift method is often used to simulate independence [38]; an alternative method is preferred when point patterns display significant inhomogeneity [36]. We simulated independence by randomly displacing species 2 locations within a 15-m radius while holding species 1 locations fixed. This preserves broad spatial structures of species locations, while removing small-scale correlations [36]. Using this analysis, we could determine whether species were located independent of one another, attracted to one another (i.e., statistics above the null expectation), or repulsed from one another (i.e., statistics below the null expectation). The former implies beneficial interactions while the latter, negative interactions [17]. The procedure for handling replication and goodness-of-fit testing for departure from the null model was otherwise identical to the above univariate analysis.

Last, we explored the influence of topography on tree locations, while accounting for the effect of distance from residual forest canopy. We fit an inhomogeneous Cox process model, a weighted generalized linear model with a log-link and Poisson error distribution [37], to estimate the intensity of each species at each location. Models were a function of distance from the residual forest canopy, each of the topographic covariates and, as a random effect, the identity of each plot's fire. To identify statistical significance of topography, we compared this full model to a reduced model with no topographic covariates using the likelihood-ratio test. We assessed these models with a two-step process. For each covariate, we multiplied its range of observations by its estimated coefficient. This is the log-scale relative magnitude of each covariate. Transforming to linear scale yields the factor change in intensity from the lowest to highest observed value of each covariate [37]. Next, we examined model performance; we tested goodness-of-fit of the observed g(r) from our univariate analysis against 999 realizations of the fitted models. Here, we did not pool across plots; significant deviation from the fitted point process in any one plot constituted an incomplete description of the observed pattern. We performed point process modelling in R (v3.2.3, R Core Team 2016, Vienna, Austria) with Spatstat (v1.46-1; [37]).

2.3. Patterns of Regenerating Tree Heights

We assessed the patterns of each species' tree heights with the univariate mark correlation function, $k_{mm}(r)$ [36]. This function measures the relationship, formalized using a suitable test function, between marks of pairs of points, m_1 and m_2, separated by r. We used the test function f(m_i, m_j) = $m_i\,m_j$ using tree heights of any arbitrary pair of points, i and j, as marks [36]. The test function statistics were normalized by the square of all tree heights; therefore, $k_{mm}(r)$ < 1 when neighboring trees at r are shorter than, and $k_{mm}(r)$ > 1 when neighboring trees are taller than the mean height of all trees. The former implies negative interactions while the latter, beneficial interactions [18,39].

We then explored the influence of heterospecific proximity on each species' tree heights using the bivariate *r*-mark correlation function, $k_{1m2}(r)$. In this analysis, the test function yields the identity of species 2's height at *r* from species 1 normalized by the mean of species 2's heights [36]; $k_{1m2}(r) < 1$ when species 2 trees at *r* from species 1 trees are shorter than the mean height of all species 2 trees, and $k_{1m2}(r) > 1$ when trees are taller than the mean.

Goodness-of-fit tests and plot replication procedures were identical to those used for the above pair correlation functions. For both $k_{mm}(r)$ and $k_{1m2}(r)$, we simulated null models of independence using 999 random permutations of a species' heights. We performed both the univariate and bivariate analyses for pair correlation and mark correlation functions in Programita [36] using Ripley's edge correction scheme [36].

Finally, we examined the influence of topography on tree heights. We regressed, with mixed-effects general linear models, species' (log) heights on distance from residual canopy and the topographic factors with the identity of each plot's fire as a random effect. Mirroring the Cox process modelling approach above, we compared the full model against a reduced (i.e., intercept-only) model with a likelihood-ratio test, and calculated the relative magnitude of each factor. We used marginal-R^2 (variance explained by fixed-effects only) [40] as an indicator of model fit. We met general linear modelling assumptions.

3. Results

3.1. Patterns of Regenerating Tree Locations

All species had aggregated spatial patterns, with aggregation greatest at smaller scales (Figure 2). In particular, deviance from CSR among lodgepole pine (*p* = 0.025) and Douglas-fir (*p* = 0.003) trees occurred at very small scales, from 0 to 2 m and 0 to 4 m, respectively. Aggregation of ponderosa pine (*p* = 0.001) and quaking aspen (*p* = 0.001) extended farther, out to 9 m. These findings reflect the clustering apparent on initial visual inspection of mapped plots (e.g., Figure 1).
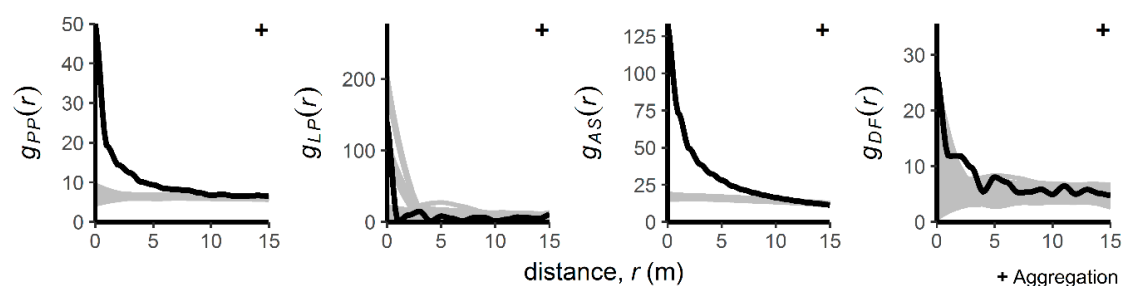

Figure 2. Patterns of replicated, univariate pair correlation functions of post-fire tree regeneration (black lines) among 999 simulations of spatial randomness (grey lines). Symbols indicate goodness-of-fit interpretations of potential departure of observations from randomness. PP is ponderosa pine (*Pinus ponderosa*), LP is lodgepole pine (*P. contorta*), AS is quaking aspen (*Populus tremuloides*), and DF is Douglas-fir (*Pseudotsuga menziesii*).

In addition, interspecific spatial interactions were found to shape tree patterns for half of all species pairs. In every pairwise species association involving ponderosa pine, we detected a pattern of attraction (*p* = 0.001 to 0.019). The pattern of attraction was most clear at scales up to 4 m (Figure 3). Pairs of species not involving ponderosa pine, however, were spatially independent of each other (*p* = 0.059 to 0.800). In no species pair was repulsion evident.
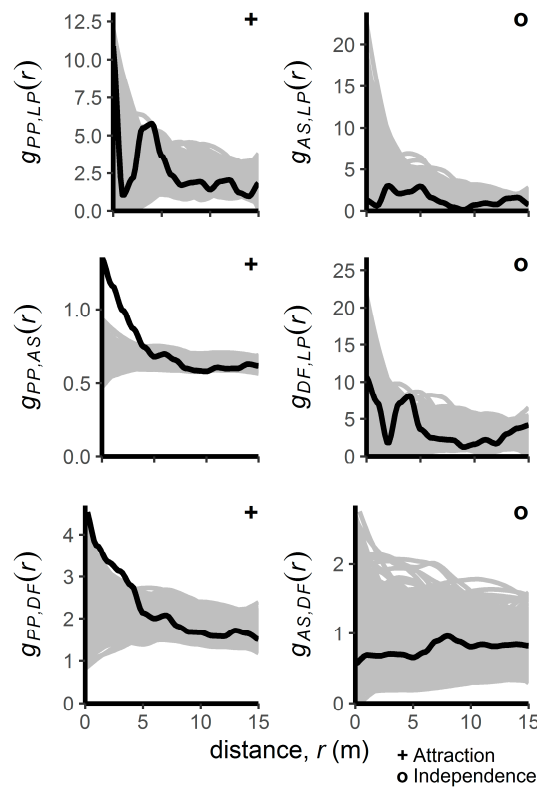
Figure 3. Patterns of replicated, bivariate pair correlation functions of post-fire tree regeneration (black lines) among 999 simulations of independent marking (grey lines). Symbols indicate goodness-of-fit interpretations of potential departure of observations from independence. See Figure 2 for species key.

The Cox process models indicated that topography also influenced spatial patterns of all species. Topography and distance from residual canopy, together, explained variance in tree locations more than the latter alone (p-values < 0.001). Relative magnitudes of covariates show that slope, primarily, and aspect, secondarily, were most influential among conifers (Table 2). Ponderosa pine abundance was greatest on southwestern aspects and shallow slopes, whereas the other conifers were more abundant on northwestern aspects and steeper slopes. Quaking aspen locations were most strongly driven by topographic position with more individuals in swales (i.e., low TPI). Last, we found distance from residual forest canopy to be negatively related to densities of all conifers. Assessing the fit of these models, we found that the observed $g(r)$ was similar to the simulated statistics of the Cox process models at distances of 4–15 m; however, the models underpredicted tree densities at smaller distances, as corroborated by plot-wise goodness-of-fit tests (p-values < 0.005).

Table 2. Effect of covariates on post-fire tree regeneration intensity (stems m^{-2}), by species, from fittings of inhomogeneous Cox process models.

Covariate	B	SE	t	p	Relative Magnitude
Ponderosa pine (*Pinus ponderosa*)					
(Int.)	−3.549	0.083	−42.798	<0.001	
Distance	−0.006	<0.001	−17.769	<0.001	119.744
Aspect	−0.317	0.058	−5.504	<0.001	1.793
Slope	−0.059	0.006	−10.266	<0.001	13.348
TPI	−0.050	0.070	−0.709	0.478	1.587

Table 2. *Cont.*

Covariate	B	SE	*t*	*p*	Relative Magnitude
Lodgepole pine (*Pinus contorta*)					
(Int.)	−12.536	1.478	−8.483	<0.001	
Distance	−0.004	0.002	−1.855	0.064	24.294
Aspect	0.669	0.500	1.339	0.181	3.811
Slope	0.102	0.029	3.474	0.001	630.665
TPI	0.110	0.327	0.336	0.737	2.706
Quaking aspen (*Populus tremuloides*)					
(Int.)	−5.637	0.492	−11.453	<0.001	
Distance	0.001	<0.001	3.656	<0.001	2.220
Aspect	0.193	0.062	3.101	0.002	1.471
Slope	−0.026	0.011	−2.306	0.021	5.172
TPI	−0.883	0.057	−15.495	<0.001	2955.452
Douglas-fir (*Pseudotsuga menziesii*)					
(Int.)	−9.674	1.474	−6.564	<0.001	
Distance	−0.007	0.001	−6.108	<0.001	265.845
Aspect	0.580	0.190	3.048	0.002	3.190
Slope	0.094	0.018	5.107	<0.001	380.372
TPI	−0.116	0.138	−0.845	0.398	2.857

3.2. Patterns of Regenerating Tree Heights

We mostly found positive autocorrelation of tree heights (Figure 4). When ponderosa pine, lodgepole pine, and quaking aspen were within 15 m of a conspecific, they were taller than expected by random chance (*p*-values of 0.001, 0.036, and 0.001, respectively). Heights of ponderosa pine and lodgepole pine exceeded expectation at distances up to 4 m, while quaking aspen heights were greater than expected across the distance range tested (0–15 m). Douglas-fir was the only species for which we did not detect departure from independent marking (*p* = 0.135).
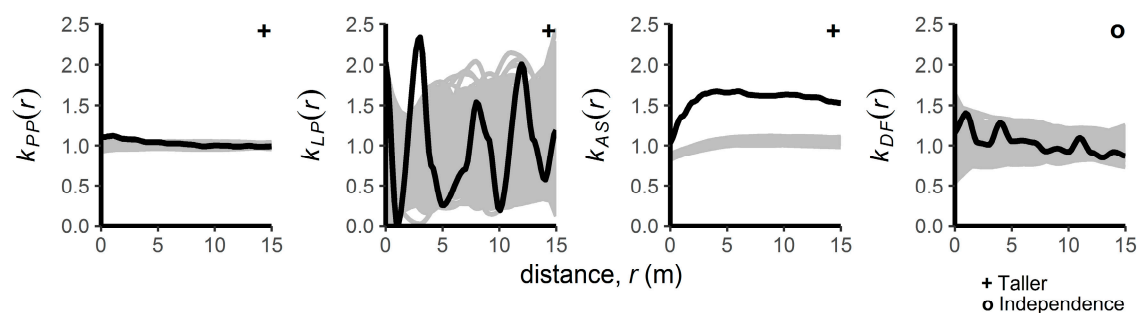

Figure 4. Patterns of replicated, univariate mark correlation functions of post-fire tree regeneration heights (black lines) among 999 simulations of independent marking (grey lines). Symbols indicate goodness-of-fit interpretations of potential departure of observations from independence. See Figure 2 for species key.

Species associations influenced tree heights in just under one-third of species pairs (Figure 5). Among three pairs, trees of one species near another species were shorter than expected by chance. This included both quaking aspen and Douglas-fir around ponderosa pine, across the full range of distances observed (*p* = 0.001). In addition, ponderosa pine was shorter when near Douglas-fir (*p* = 0.049), particularly at distances <2 m from a Douglas-fir. However, in each of these instances, the effect size was small; proximity to heterospecifics conferred about a ~5% decrease in tree height.

In just one species pair did we find a positive relationship: Douglas-fir trees within 5 m of quaking aspen were significantly taller (*p* = 0.030). Here again, the effect size was relatively small.
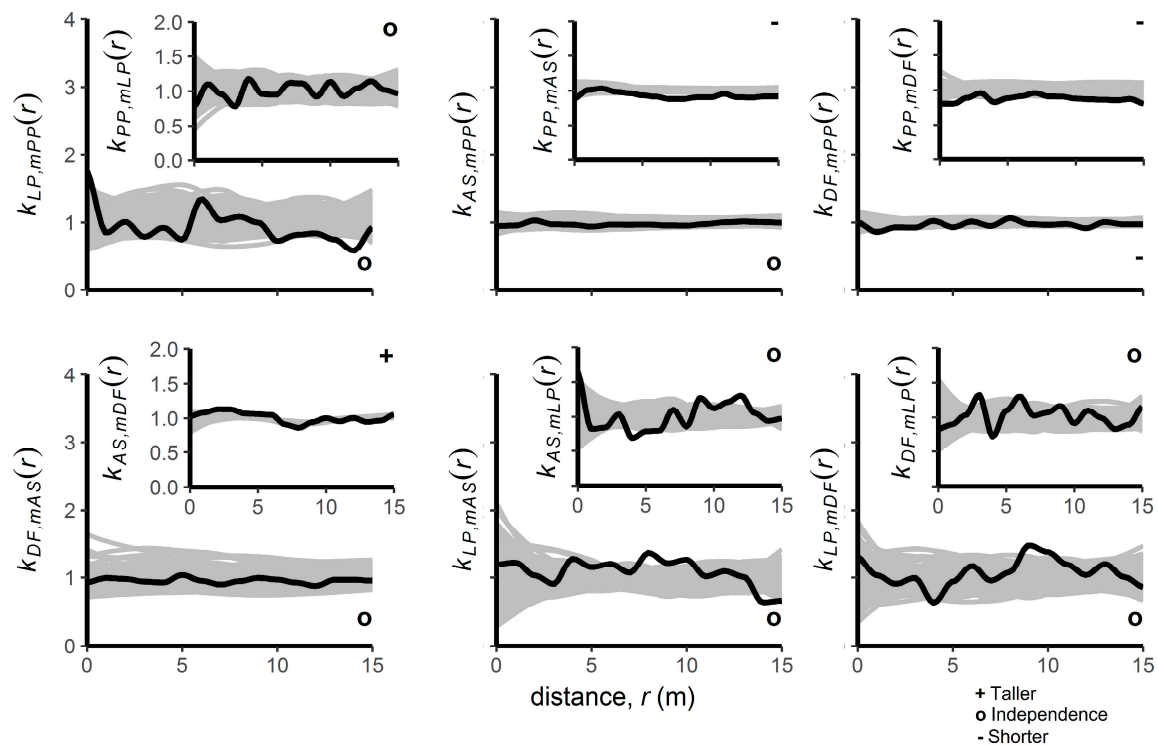

Figure 5. Patterns of replicated, bivariate mark correlation functions of post-fire tree regeneration heights (black lines) among 999 simulations of independent marking (grey lines). Symbols indicate goodness-of-fit interpretations of potential departure of observations from independence. See Figure 2 for species key.

Topographic variability minimally influenced tree heights. We found the full model of tree heights performed better than a reduced model, only for ponderosa pine (*p* = 0.004) and quaking aspen (*p* < 0.001). However, full models were only able to explain 2.1% of the variability in ponderosa pine heights and 15.9% of the variability in quaking aspen heights (Table 3). Full models were no better than reduced models for lodgepole pine (*p* = 0.861) and Douglas-fir (*p* = 0.249).

Table 3. General linear models of tree regeneration (log) heights on topographic covariates and distance (from residual forest canopy), by species.

Covariate	$\hat{\beta}$	Std. Err.	t	p	Rel. Mag.
Ponderosa pine (*Pinus ponderosa*); (marginal-R^2 = 0.021)					
Intercept	−0.760	0.151	−5.030	<0.001	
Distance	0.001	<0.001	3.110	0.002	1.595
Aspect	−0.026	0.026	−0.998	0.318	1.054
Slope	−0.006	0.004	−1.565	0.118	1.352
TPI	0.048	0.025	1.930	0.054	1.294
Lodgepole pine (*Pinus contorta*); (marginal-R^2 = 0.271)					
Intercept	−0.178	0.671	−0.264	0.793	
Distance	0.003	0.001	1.995	0.054	3.652
Aspect	−0.153	0.273	−0.562	0.578	1.348
Slope	−0.004	0.013	−0.327	0.745	1.177
TPI	−0.054	0.148	−0.364	0.718	1.192

Table 3. *Cont.*

Covariate	$\hat{\beta}$	Std. Err.	t	p	Rel. Mag.
Quaking aspen (*Populus tremuloides*); (marginal-R^2 = 0.159)					
Intercept	−1.153	0.210	−5.502	<0.001	
Distance	<0.001	<0.001	2.333	0.020	1.445
Aspect	−0.112	0.014	−8.037	<0.001	1.251
Slope	0.046	0.003	17.861	<0.001	9.648
TPI	−0.143	0.011	−13.118	<0.001	2.397
Douglas-fir (*Pseudotsuga menziesii*); (marginal-R^2 = 0.021)					
Intercept	−1.319	0.127	−10.349	<0.001	
Distance	0.001	<0.001	1.656	0.099	1.421
Aspect	0.233	0.067	3.497	0.001	1.592
Slope	−0.005	0.003	−1.635	0.104	1.305
TPI	−0.005	0.063	−0.082	0.935	1.025

4. Discussion

Our results suggest that, after more than a decade following stand-replacement fires in ponderosa pine-dominated forests, tree regeneration was heterogeneously patterned, displaying aggregation and positive density–height relationships among conspecifics. Although a number of complex interacting processes influence tree regeneration patterns, our results indicate that topographic effects and biotic interactions, redolent of beneficial interactions, contributed to the aggregated patterns. However, *just* interspecific associations promoted spatial patterning of tree sizes, but only among a few pairs of species and marginally at that.

Further, our observed patterns stand in contrast to other studies of conifer regeneration, wherein density was one to two orders of magnitude greater during stand initiation [41,42]. Those studies found relatively simpler patterns and no effect of topography nor biotic interactions on those patterns. This may indicate that the mechanisms controlling early stand development may be contingent on regeneration density [8].

Moreover, topography and tree interactions acted on spatial patterns of regeneration at different scales. Specifically, topography, after accounting for seed dispersal limitation, explained tree location patterns at scales greater than ~4 m, whereas tree interactions explained both location and size patterns at scales less than ~4 m. This separation of scales may result from trees modifying their immediate growing environment. For example, Nguyen et al. [43] noted a larger separation scale of 15 m for larger trees within mature forests. If the separation scale relates to tree size, we expect that topography might diminish in influence as our sites' trees grow.

4.1. Intraspecific Spatial Patterns

Our observed intraspecific aggregation among all species supports the idea that aggregation is the predominant pattern in ponderosa pine-dominated forests [2,6]. After stand-replacing fire, both topography and intraspecific interactions played roles in formation of aggregation. At coarser scales, we found topography was explanatory in ways specific to species. On flatter and southwestern hillsides, we found greater abundance of ponderosa pine. Meanwhile, other conifers were more abundant on steeper and northwestern slopes, and quaking aspen were common in swales. At finer scales, we suggest that both species-specific regeneration strategies and intraspecific facilitation generated aggregation. Species-specific regeneration strategies may promote aggregation of both quaking aspen and lodgepole pine because both bear adaptions—resprouting and serotiny respectively, which yield ramets and seedlings, respectively—centered around parent trees [24,25]. In contrast, ponderosa pine and Douglas-fir lack in-situ seed sources following stand-replacing fire [44]. Rather than a species-specific regeneration strategy, we suspect that improved fitness nearer to conspecifics [45] resulted in increased survival of regeneration due to beneficial interactions.

As facilitatory effects can increase with proximity, this selection for aggregation may play upon itself, inducing a positive aggregating feedback [46].

Through our analysis of tree height patterns, we found size hierarchies at small-scales. That is, trees were taller in denser, rather than sparser, neighborhoods. Accumulating evidence from tropical and temperate forests suggest that such size hierarchies develop early during secondary succession [39,47]. These size hierarchies are often attributed to resource inequity [48]; if resource inequity across abiotic gradients regulates local densities, as our results suggest, conspecifics should be not just more numerous but taller in suitable areas [49]. However, Suzuki et al. [39] and Stoll and Pratt [45] demonstrated that, even in otherwise homogeneous environments, tree interactions sufficiently produce unequal growing conditions and lead to size hierarchies. Given that we found little relationship between topography and tree heights *and* that size hierarchies occurred at finer scales than topographic-related tree density, our results support the latter cause of size hierarchies: denser neighborhoods can improve growth as intraspecific facilitation improves resource conditions. Our interpretation warrants evaluation using controlled studies to verify the general and species-specific means of tree pattern regulation. This is especially pertinent because interactions among different abiotic and biotic factors can induce analogous patterning [20].

4.2. Interspecific Spatial Patterns

Facilitation may have also shaped patterns of regeneration among heterospecifics. Unlike other species, ponderosa pine was more abundant on southwestern aspects, exposing individuals to greater moisture stress and posing a survival risk [15]. This is counterintuitive, though it may be that survival was greater where individuals were near nurse trees. Patterns of spatial attraction to all other species may explain the existence of ponderosa pine on southwestern slopes. Spatial attraction via facilitation has also been identified among conifers following low- to moderate-severity fires in ponderosa pine forests [50]. In addition, Fajardo et al. [5] demonstrated that, as water availability decreased, ponderosa pine trees were more apt to establish nearer to Douglas-fir. In contrast, other conifers and quaking aspen were not attracted to other species in our study. Presumably, this is because these species were more abundant in northeasterly aspects and swales which confer less moisture stress. Our study adds to accumulating evidence that regeneration of ponderosa pine may especially depend on facilitation in harsh (e.g., post stand-replacement) environments [5].

It is important to note we did find some evidence for competition, particularly between Douglas-fir and ponderosa pine. That these species spatially attracted each another implies beneficial interactions regarding initial establishment; however, the marginally stunted growth of these heterospecific neighbors may suggest that post-establishment growing conditions may be shifting towards competition, as we discuss below.

4.3. Limitations and Future Research Directions

Although our study has provided insights into the potential roles of topography and tree interactions in the pattern of regeneration following high severity fires, the interpretation of our results is constrained by several limitations. Previous research has suggested that the rate and pattern of tree regeneration in ponderosa pine forests is influenced by a number of complex interacting phenomena, including the spatial variability in solar radiation, temperature, precipitation, soil edaphic factors, herbivory, regeneration mechanisms, and the caching and perching behavior of wildlife [14,21,51]. Our study design indirectly accounted for the abiotic processes using topographic surrogates. Although a number of studies have shown a strong correlation between topographic variables and abiotic attributes including temperature, moisture and soil edaphic factors, the lack of direct measurement limits our ability to discern the exact mechanisms controlling regeneration pattern. As an alternative approach to directly measuring these abiotic factors, we could have included additional variables that are known to influence the fine scale patterns of temperature and moisture such as the presence of stumps and coarse woody debris [14,21,51]. Given the fine-scale

variability of such factors [52], we would expect that their inclusion would have resulted in increased resolution and understanding of regeneration pattern at scales under 4 m. Further research that aims to better understand the influence of various mechanisms across scales could shed additional light on how environmental conditions affect regeneration patterns and stand initiation following large, severe wildfires.

In addition, ponderosa pine recruitment and establishment is highly dependent on inter-annual climate [32]. Because of this dependency, our study may provide limited understanding for regeneration following future large, severe fires or for the longer-term trajectory on our study sites. Specifically, changes in moisture regimes following the fire event could lead to changes between facilitation and competition among species. For example, previous research has suggested that as moisture stress increases, the degree of aggregation and interspecific attraction may increase [5]; whereas, others have indicated that facilitative relationships may reverse to competitive ones [53], inducing negative density-dependent patterns [17]. Measurements of spatial patterns in multiple burned areas under varying climatic conditions could further help determine how plastic spatial patterns are in response.

4.4. Ecological and Management Implications

Anticipating how current patterns of tree regeneration may influence future forest dynamics is complex and fraught with uncertainty. However, building on prior research, we hypothesize that the current predominance of beneficial tree interactions may beget greater competition in the future [8,54]. Within conspecifics, size hierarchies may lead to within-patch self-thinning of smaller, poorer competitors and relaxation of aggregation towards a more random or even uniform forest structure [4,25,39]. The two-way competition, indicated by patterns of tree height between ponderosa pine and Douglas-fir, could produce eventual mortality of poorer competitors [8], though field studies demonstrate that fairly equal competitors can coexist in proximity despite mutually-inhibiting growth [5,18]. Conversely, the slightly shorter stature of quaking aspen near ponderosa pine hints at one-way competition; in many coniferous forests, competition drives mortality of quaking aspen, producing interspecific spatial repulsion [55]. The long-term persistence of quaking aspen may therefore depend on spatial refuges isolated from conifers. Thus, the facilitatory processes during regeneration may have established conditions for competitive forest dynamics.

Given that future patterns of forest structure and ecosystem function are conditioned on prior events [1], forest managers can adopt strategies post-fire to influence desired pathways of stand development. These strategies can accelerate spatially-complex forest structure desired in many ponderosa pine forests [8]. We found that patterns of regeneration exhibited some features of desired and historical conditions, such as tree grouping [2], spatially-heterogeneous tree size patterns [8], and environmental-specific distributions of tree species [27]. Yet, our observed tree densities 11 to 15 years post fire were lower than average historical tree densities reported for ponderosa pine forests in the Front Range and Black Hills (100–140 trees ha^{-1}) [56,57]. If managers choose to augment natural regeneration, patterns of naturally recovering landscapes can inform efforts to address deficiencies [58] and enhance recovery [59]. Plantings should reinforce local patterns of fine-scale heterogeneity [12], such as those we found, leveraging both topographic gradients and presence of facilitatory woody plants [16].

5. Conclusions

Our findings lend empirical evidence to models of forest development which state that stand initiation, where sparse, is likely to be spatially heterogeneous and resulting patterns may, in part, be due to topographic conditions and tree interactions. In addition, our observed patterns indicate that facilitation dominated over competition during the initial decade of establishment of these ponderosa pine-dominated forests. This seemingly contrasts with models of early stand development which state tree competition, and not facilitation, is largely responsible for forming spatially complex forest

structure [7,8]; however, these models of forest development generalize stand initiation over the first few decades. It may be that competition increases during the latter half of stand initiation. In summary, our results lead us to suggest that, in addition to density-dependency, general models of early forest development may need to account for temporally-dynamic and scale-dependent roles of the abiotic environment and tree interactions.

Finally, heterogeneous forests tend to have more rapid successional dynamics than homogeneous forests [20]. If post-fire actions emulate, rather than overwrite, the complex patterns of reinitiating forests, ecologically-based forest management may encourage faster development of desired, complex forest structure.

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