ECOSYSTEMS

Abiotic Factors Modify Ponderosa Pine Regeneration Outcomes After High-Severity Fire

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ABSTRACT

Large high-severity burn patches are increasingly common in southwestern US dry conifer forests. Seed-obligate conifers often fail to quickly regenerate large patches because their seeds rarely travel the distances required to reach core patch area. Abiotic factors may further alter the distance seeds can travel to regenerate a patch, which would change expected post-fire regeneration patterns. We used the presence and density of ponderosa pine regeneration as a proxy for seed dispersal to quantify the effect of abiotic factors on seed dispersal into high-severity patches. We established 45 transects in burn patches across the Gila National Forest, NM, USA, to measure regeneration density in areas that varied by aspect, slope, and prevailing wind direction relative to intact forest. We modeled the effect of abiotic factors on regeneration presence and density, comparing density estimates against a distance-only model to assess differences in model performance and expected regeneration density. We found the highest regeneration densities on north-facing aspects that were near, downwind, and downslope of intact forest, which decreased in density and likelihood as conditions for seed dispersal became less favorable. Accounting for abiotic factors improved model performance and increased regeneration density estimates compared to the distance-only model. Our findings indicate that regeneration presence and density vary as a function of the interaction between abiotic factors and distance to the primary seed source, which is determined by patch characteristics. Therefore, abiotic factors will have a smaller effect on regeneration outcomes in large, simple patches, which have more area further from the patch edge.

Key words: aspect; conifer regeneration; high-severity fire; ponderosa pine; seed dispersal; slope; wind.

HIGHLIGHTS

- Wind, slope, aspect, and overstory tree density alter patch regeneration patterns.
- Locations downslope and downwind of intact forest have higher regeneration density.
- Aspect influenced survival, increasing regeneration density on north slopes.

INTRODUCTION

The area of forest burned at high severity has exponentially increased across southwestern US dry conifer forests in recent decades (Singleton and others 2019). Conifer regeneration has declined within high-severity patches over the same period, leading to non-forested ecosystems in areas where seedlings fail to establish (Coop and others 2020). There are two contributing factors to widespread conifer regeneration failure—dispersal limitations and climatic conditions that exceed the physiological thresholds of dispersing species (Stewart and others 2021). Dispersal limitations occur when portions of large high-severity patches are too far from surviving conifer trees to receive seed, a limitation that can be overcome with artificial regeneration if climatic conditions can support seedlings (Chambers and others 2016; Haffey and others 2018; Ouzts and others 2015). However, dispersal distance is not fixed and high-severity burn patch attributes, such as topography and shape, could change the distance conifer seeds can travel (Chambers and others 2016; Collins and others 2017). Determining how abiotic factors influence seed dispersal and regeneration patterns is central to predicting where seed dispersal is likely to be a limiting factor after high-severity fire (Coop and others 2020; Hanbury-Brown and others 2022).

Many conifers rely on wind to disperse large and heavy seeds, which fall rapidly to the ground and lead to low seed rain in areas far from intact forest (Clark and others 1999; Coop and others 2020). Ponderosa pine (*Pinus ponderosa*), a species in the 78th percentile of seed weight for conifers globally, disperses nearly all its seed within two tree heights (generally up to 80 m) of the parent tree, which should limit dispersal into high-severity areas (McDonald 1980; Moles and Westoby 2006). However, ponderosa pine regeneration can be found over 100 m from the nearest seed source in high-severity patches, indicating that factors other than seed size and aerodynamics may influence dispersal distance (Chambers and others 2016; Haffey and others 2018; Haire and McGarigal 2010). Abiotic factors, such as wind and topography, can alter pine seed dispersal into open habitat by changing the horizontal and vertical distance seeds travel from the canopy to the ground (Damschen and others 2014; Trakhtenbrot and others 2014). As conifer forests in the southwest often occupy mountainous areas with diverse topography and variable wind patterns, these abiotic factors may also alter ponderosa pine seed dispersal patterns across high-severity patches (Ruel and others 1998; Zeng and others 2004).

The majority of the area burned at high-severity in the southwestern US since the 1990s has been comprised of large patches (> 100 ha), which, as their size increases, have an increasing area that is beyond the dispersal distance of seed-obligate conifers (Singleton and others 2021a; Stevens and others 2021). Large high-severity patches can have areas with low regeneration potential, often termed "core area," which can be quantified using distance thresholds from the patch edge (Collins and others 2017; Coop and others 2020). The proportion of core area varies between large patches of different shapes, as "simple" patches with circular shapes contain more core area than similarly-sized "complex" patches that are more ovular, sinuate, or intermittently spotted with islands of intact forest (Collins and others 2017; Singleton and others 2021b). Despite recognition that larger and simpler high-severity patches are increasing total core area in recent southwestern fires (Singleton and others 2021b), the impact of changing patch characteristics on seed dispersal and regeneration in areas that can receive seed has not received similar attention. Coupled with an incomplete understanding of abiotic effects on seed dispersal, these knowledge gaps limit predictions of ponderosa pine natural regeneration patterns in southwestern high-severity patches, which are needed to help assess post-fire ecological impacts, vegetation modeling, and the need for artificial regeneration (Hanbury-Brown and others 2022; Jung and others 2023; Shive and others 2018).

Given that patch characteristics and abiotic factors have the potential to modify seed dispersal and resultant regeneration patterns, we asked: How do abiotic factors influence the distance ponderosa pine seeds disperse and establish from intact forest and how does this affect the density of regeneration in a high-severity patch? We hypothesized that (1) favorable patch locations downslope and downwind of intact forest would contain more regeneration at greater distances compared to unfavorable locations upslope and upwind of intact forest and (2) models incorporating the effect of abiotic factors would have different regeneration density estimates that were more accurate than estimates calculated using distance to the nearest seed source.
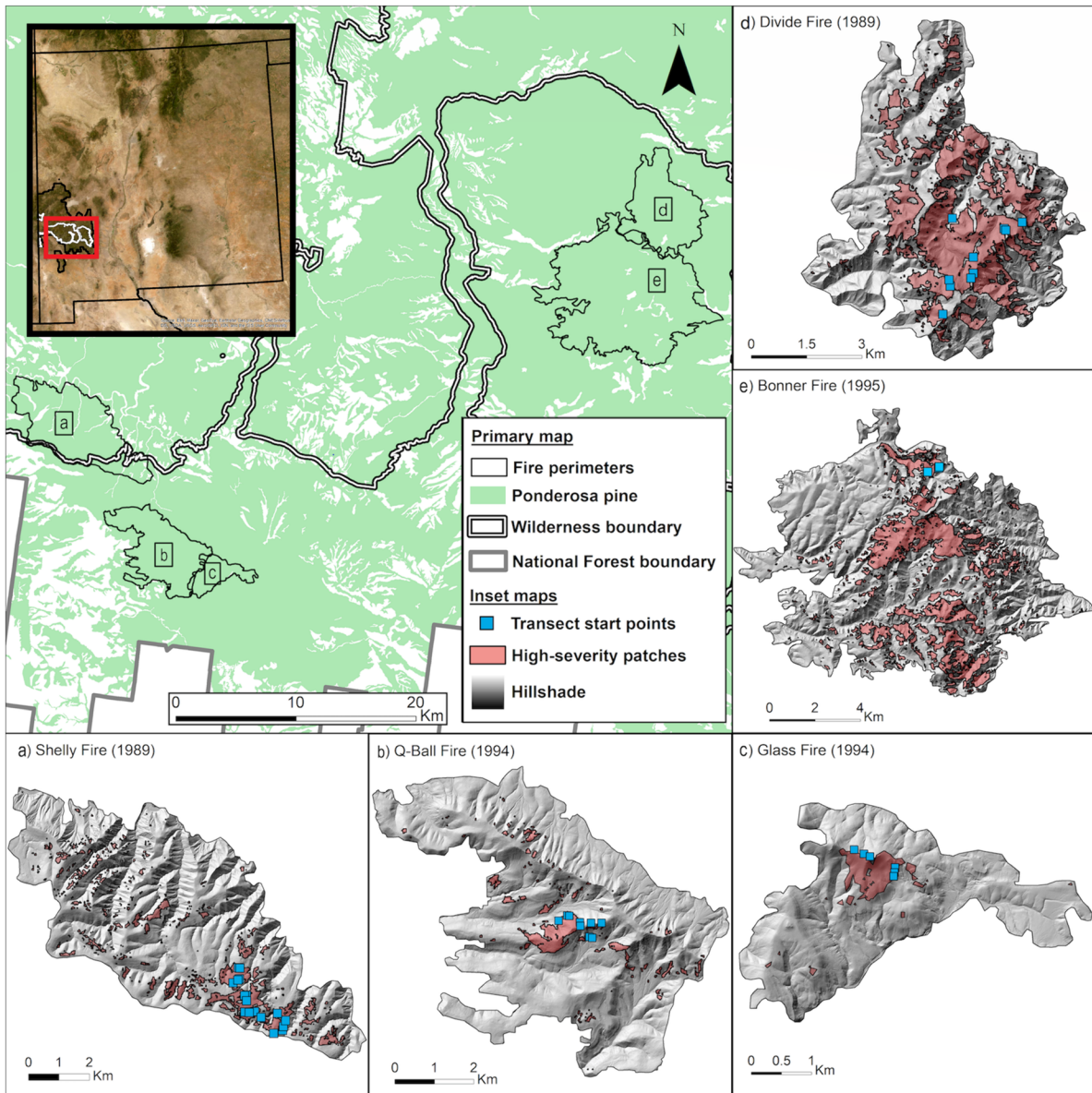
Figure 1. A map of plot and transect locations ($n = 45$) across the five sampled fire footprints located with the southern and eastern portions of the Gila National Forest, NM, USA. We determined fire boundaries and severity using the Monitoring Trends in Burn Severity dataset. We determined the distribution of forests containing ponderosa pine using the Gila National Forest terrestrial ecological unit inventory. We calculated hillshade using the Hillshade tool in ArcMap 10.8 with a 10 m digital elevation model.

METHODS

Study Sites

We sampled high-severity patches from fires that occurred in the ponderosa pine forest type across the Gila National Forest, New Mexico (Figure 1). The Gila represents a portion of the southeastern range of ponderosa pine in the U.S. (Burns and Honkala 1990), which historically burned every 4–8 years at low-severity to create stands with low-

to-moderate tree density (Boucher and Moody 1998; Rixon 1905; Swetnam and Dieterich 1985). Starting in the early 1900s, widespread fire suppression increased fire return intervals by more than 120 years in some areas and increased the rate of ponderosa pine survival and recruitment into the overstory (Covington and Moore 1994; Swetnam and Dieterich 1985). The resulting high tree density, combined with increases in fuel aridity and wildfire occurrence over the past 50 years, has led to large portions of some fires burning at high

severity (Abatzoglou and Williams 2016; Fulé and others 1997; Singleton and others 2019).

Vegetation assemblages in the Gila range from desert grasslands at lower elevations to ponderosa pine forests at mid elevations and subalpine conifer forests at upper elevations (Keane and others 2000). The climate of the Gila is semi-arid, with a mean annual temperature of 12 °C and mean annual precipitation of 385 mm between 1990 and 2020 (https://www.ncdc.noaa.gov/cdo-web/datatools/normals, Gila Hot Springs station, NM; 1706.9 m). The region experiences a bimodal precipitation regime, with precipitation occurring as snow in the winter and rain during the summer monsoonal period (Sheppard and others 2002). Soils in the region are a mixture of Ustalfs and Ustolls suborders (NRCS 2022).

Data Collection

High-severity patches result from the removal of most canopy trees, understory plants, and soil organic material during fire, leaving uniform conditions devoid of plants that contrasts with surrounding forests burned at lower severities (Keeley 2009; Reilly and others 2017). A single fire can have one or more high-severity patches and the size and location of those patches result from a combination of forest condition, topography, and weather conditions during the burn period. We sampled ponderosa pine regeneration that established in high-severity patches as a proxy for seed dispersal, given that ponderosa pine seedling establishment can only occur from seed germination. While the relationship between seed dispersal and seedling establishment varies by the degree of seed limitation (Aicher and others 2011), we expected a positive relationship between seed rain and regeneration density because low seed availability and short seed dispersal often limit seedling recruitment in the study system (Coop and others 2020; Nathan and Muller-Landau 2000; Stevens-Rumann and Morgan 2019).

We collected data across high-severity patches created by five fires that burned between 1989 and 1995 as identified by the Monitoring Trends in Burn Severity dataset (MTBS; Figure 1, Eidenshink and others 2007). We selected these fires for data collection using the following criteria: (1) the fire occurred in forest containing ponderosa pine; (2) the fire created at least one high-severity burn patch with area over 160 m from the nearest location not burned at high-severity; and (3) the fire footprint did not re-burn prior to data collection. The other limitation to widespread establish-

ment is abiotic conditions that support germination, survival, and growth. Generally, in the southwestern US, establishment varies by aspect because of the relationship between incoming solar radiation and microclimate (Marsh and others 2022). We accounted for this potential effect by stratifying our sampling by aspect.

We sampled 45 transects across 18 high-severity patches within the five fires. The number of transects per fire ranged from 3 to 18 based on the characteristics and distribution of live tree patch positions by aspect combinations within each fire. We stratified the 45 transect locations by combinations of slope position, slope angle, and aspect to ensure landscape topography was well-represented (Table 1). The stratification included combinations of the live tree patch being either upslope or downslope of the high-severity burn patch and aspects that covered the four cardinal directions. We defined slope position by the change in elevation from the start of the transect near intact forest to the end of the transect in the burn patch. We labeled transects that went uphill from the intact forest as ''upslope'' with positive slope angle values and transects that went downhill from the intact forest as ''downslope'' with negative slope angle values. We calculated slope position and slope angle across each transect using a 10 m digital elevation model (DEM) from the Earth Data Analysis Center in ArcMap 10.8 (EDAC 2021; ESRI 2020). We calculated aspect using the DEM in ArcMap and binned them into the four cardinal directions for analysis.

Transects ran 160 m perpendicular from the edge of intact forest into the high-severity burn patch to collect regeneration data. We selected this transect length because the majority of ponderosa pine regeneration occurs within 160 m from intact forest (Haffey and others 2018; Haire and McGarigal 2010; McDonald 1980). Within each transect, we measured the distance of all ponderosa pine regeneration that occurred within 5 m of the transect centerline from the start of the transect. In transects with dense regeneration (> 2000 individuals ha^{-1}), we only measured regeneration within 1 m of the transect centerline. We paired each transect with nested circle plots in the adjacent intact forest, which we centered 25 m from the transect start point and used to measure stand structure. We measured stand structure using a 1/5th ha circle plot to sample trees > 50.0 cm diameter at breast height (dbh), a nested 1/10th ha plot to sample trees between 15.1 and 50.0 cm dbh, and a nested 1/20th ha plot to sample trees between 5.0 and 15.0 cm dbh. In each plot, we recorded the dbh

Table 1. Number of Transects Sampled and Mean Regeneration Density (individuals ha^{-1} ± standard error) Stratified by Slope Position and Aspect

	Upslope		Downslope		Total	
	Transects	Regen. density	Transects	Regen. density	Transects	Regen. density
North	4	198 (± 117)	4	2006 (± 1545)	8	1102 (± 794)
East	6	117 (± 35)	4	164 (± 119)	10	136 (± 49)
South	7	123 (± 59)	7	58 (± 40)	14	91 (± 35)
West	2	63 (± 44)	11	146 (± 69)	13	133 (± 58)
Total	19	131 (± 33)	26	411 (± 253)	45	286 (± 144)

and species of sampled trees. Field data collection occurred between 2019 and 2021.

Model Parameterization

To determine the effect of abiotic factors on the presence and density of regeneration, we developed 11 candidate logistic and zero-truncated general linear models to form a hurdle model. We selected potential predictor variables based on findings from a review of the literature and implemented a candidate model approach to test sets of predictor variables that we hypothesized could explain seed dispersal and resulting regeneration outcomes. We evaluated and compared the performance among candidate models using a model selection framework and selected the most parsimonious logistic and general linear models to form the top-performing hurdle model (hereafter the full model, Supplemental Tables S1 and S2). We used a hurdle model to account for the high proportion of area within transects with zero regeneration, which general linear models could not adequately explain on their own.

We quantified regeneration presence and density by grouping transect regeneration into 10 × 10 m bins by distance from intact forest, counting the number of individuals in each bin, and converting those numbers to binary values or densities of individuals ha^{-1}. We modeled regeneration presence or density as the response variable and combinations of attributes that may affect seed dispersal patterns as predictor variables, including prevailing wind, a variable that combined slope position and slope angle values (hereafter ''slope''), regeneration bin distance to intact forest, ponderosa pine tree height, and the density of ponderosa pine trees larger than 25 cm dbh in the nearby intact forest (hereafter ''ponderosa overstory density'', measured in trees ha^{-1}). We defined bin distance as the distance from the bin centroid to the edge of intact forest. We defined the prevailing wind value as the direction of transects from intact forest relative to the prevailing wind direction. To calculate the prevailing wind value, we used the following equation:

$$\text{Prevailing wind value} = \cos(\text{Transect direction} - \text{Prevailing wind direction})$$

(1)

We determined prevailing wind direction using data from the closer of two RAWS weather stations in the vicinity of the five sampled fire footprints (https://raws.dri.edu/index.html, Zachariassen and others 2003). We defined transects with negative prevailing wind values as ''upwind'' of intact forest and transects with positive prevailing wind values as ''downwind'' of intact forest. We converted upwind values to zero because of improved model performance, which we determined by comparing AICc values using the MuMIn package (Barton and Barton 2015). Areas downwind of intact forest had values that ranged from 0 to 1, with 1 indicating that transects were directly downwind from intact forest.

We assessed the presence or absence of regeneration across all bins using logistic models with a binomial distribution and log link function. We assessed the density of regeneration across 288 bins containing regeneration using general linear models with a Gaussian distribution and identity link function. We parameterized all models using the glm() function from the stats package in R (R Core Team 2020). All predictor variables except for bin distance were specific to each transect, as transects represented the sampling unit. To assess model performance, we compared AICc to determine which model provided the most parsimonious fit with the dataset, retaining the logistic and general linear models with the lowest AICc value (Burnham and Anderson 2002; Supplementary Tables S1and S2).

We checked the normality of model residuals using a Shapiro–Wilk test and homoscedasticity using a non-constant error variance test from the Car package in R (Fox and Weisberg 2019). We checked multicollinearity with a variance inflation factor test, using a threshold of 10 to determine if predictor variables exhibited collinearity (Zuur and others 2009). We tested for spatial autocorrelation among model residuals with a Moran's I test using the testSpatialAutocorrelation() function in the DHARMa package, evaluating spatial autocorrelation both between transects and between bins within a transect (Hartig 2021). We did not find spatial autocorrelation among the residuals for either test. Because of the age of the fires, the seed source for regeneration was the intact forest rather than trees that established following wildfire. Thus, our use of bins as the observation unit did not violate assumptions of independence, as density values from one bin did not fluctuate in relation to the regeneration density of other bins in the transect. We assessed all other assumptions graphically.

We log-transformed bin distance in logistic models to help meet the assumption of linearity. We log-transformed regeneration density, used polynomial transformations on prevailing wind value and ponderosa pine overstory density, and included the aspect of transects as a categorical variable in general linear models to meet normality assumptions. We assessed the accuracy of logistic models and the fit of general linear models to determine the influence of outliers in model estimates using the train() function in the Caret package (Hastie and others 2009; Kuhn 2008). We tested the accuracy of logistic models by splitting the data into training and testing sets, developing a model with the training set and the leave-one-out cross-validation method, and testing predicted outcomes of the model with the testing set with the ConfusionMatrix() function in the caret package. We tested model fit for general linear models by applying a leave-one-out cross-validation method to calculate root-mean-squared error (RMSE).

Model Spatial Extrapolation

We used a model extrapolation procedure to estimate regeneration presence and density across all high-severity patches in the five fire footprints. The best model for estimating regeneration presence and density included distance to seed source, slope, aspect, prevailing wind value, and ponderosa overstory density. However, we could not incorporate ponderosa overstory density into model estimates because we did not have spatially con-

tinuous data for stand structure. Instead, we estimated regeneration presence and density using the best performing and most parsimonious logistic and general linear models that did not use tree height or ponderosa overstory density. The selected logistic and general linear models included distance to seed source, slope, aspect, and prevailing wind value as predictor variables, which we combined to form a hurdle model comprised of abiotic factors (hereafter ''abiotic factors model'').

We quantified distance to seed source by measuring the distance from potential seed sources to locations that burned at high severity within the five fires. We identified potential seed sources using the Gila National Forest terrestrial ecological unit inventory dataset and converted shapefiles of intact forests containing ponderosa pine to 30 m resolution raster data (hereafter ''ponderosa pine pixels''). We identified locations that burned at high severity using the MTBS dataset and converted those locations to 10 m resolution raster data (hereafter ''burned pixels'') to match the abiotic factors model output resolution. We quantified slope using the following equation:

$$\text{Slope} = \tan^{-1} \left(\frac{\text{Burned pixel centroid elevation} - \text{ponderosa pine pixel centroid elevation}}{\text{Distance to seed source}} \right)$$

$$(2)$$

We used 10 m DEM data to determine elevation and calculate the aspect of burned pixels. We calculated prevailing wind direction using wind data from the two nearby RAWS weather stations. Using the abiotic factors model, we estimated likelihood of regeneration presence for each burned pixel that occurred within 160 m of ponderosa pine pixels.

To estimate the likelihood of regeneration presence, we calculated slope, distance to seed source, and prevailing wind values between a burned pixel and every ponderosa pine pixel that occurred within 160 m of the burned pixel, using these values to calculate expected density values. For burned pixels that had multiple ponderosa pine pixels within 160 m, we selected the ponderosa pine pixel that resulted in the greatest likelihood of regeneration presence to represent the primary seed source. We used the greatest likelihood of regeneration presence under the assumption that the patch of live trees closest to a burned pixel would have the most influence on the regeneration outcome of that burned pixel. We did not estimate the likelihood of regeneration presence when calculated slopes were greater than 30 degrees from ponderosa pine pixels to the burned pixel, as our

data set did not contain transects with slopes greater than 30 degrees.

We estimated regeneration density among pixels with a likelihood of regeneration presence above 40% and assigned pixels with a likelihood below 40% a density value of zero. We used 40% to represent the hurdle in model extrapolations because 40% of our transect bins contained regeneration and ponderosa pine regeneration had similar rates of presence in burn patches near intact forest across the region (Haffey and others 2018; Rother and Veblen 2016). We calculated expected regeneration density using aspect and the calculated slope, distance to seed source, and prevailing wind values from the primary seed source. We excluded pixels from patches smaller than 1 ha from the analysis because the greatest distance within these patches to intact forest was under 50 m, which Chambers and others (2016) found to be a threshold for high rates of seed dispersal and regeneration. This left 257 patches across the five sampled fires. We prepared spatial data in ArcMap 10.8 and performed all spatial analyses using the raster (Hijmans 2021), rgdal (Bivand and others 2021), and rgeos (Bivand and Rundel 2020) packages in R version 4.0.3.

Distance-Only Model and Abiotic Factors Analysis

To determine if abiotic factors improved model performance and changed expected regeneration density compared to past findings, we compared the abiotic factors model against a hurdle model that exclusively used distance to the nearest seed source to estimate regeneration density (hereafter ''distance-only model''). We only included distance to the nearest seed source as a parameter in this model because it has consistently been used to explain post-fire regeneration patterns of seed-obligate conifer species in other studies (Stevens-Rumann and Morgan 2019). To parameterize the distance-only model, we used a logistic model with regeneration presence as the response variable and log-transformed bin distance to intact forest as the predictor variable. We combined the logistic model with general linear model that used log-transformed regeneration density as the response variable and bin distance to intact forest as the predictor variable. To assess changes in model performance after incorporating abiotic factors, we calculated AICc, RMSE, cross validation accuracy, and R^2 for the distance-only model and compared values with the abiotic factors model.

To assess changes in expected regeneration density caused by abiotic factors, we calculated the difference in expected regeneration densities between model extrapolations from the abiotic factors and distance-only models. To calculate expected regeneration density with the distance-only model, we used the model spatial extrapolation procedure outlined in the last section across all pixels in the 257 patches. To calculate the change in expected regeneration densities, we subtracted the extrapolated pixel values calculated with the distance-only model from the values calculated with the abiotic factors model. We used the resulting pixel values to assess the combined effects of abiotic factors on changes in expected regeneration density. To visualize these combinations, we categorized pixel values by slope position, wind position, and aspect and modeled the change in regeneration density as a function of distance to intact forest using simple linear regression. We also tallied the number of pixels that occurred within the four combinations of slope and wind position from the primary seed source to assess the frequency of dispersal conditions that caused the most regeneration to establish in burned pixels. All statistical analyses were performed in R version 4.0.3.

RESULTS

Empirical Data and Full Model Outputs

Patch areas were most likely to contain regeneration at high densities on north-facing aspects that were downwind, downslope, or close to intact forest, reflecting the significant predictor variables in the full model. Transects downwind of intact forest (539 ± 362 individuals ha^{-1}) had regeneration densities that were four times greater than transects upwind of intact forest (124 ± 34 individuals ha^{-1}). The full model reflected the effect of wind on the presence and density of regeneration, as areas downwind of intact forest had a 67% greater chance of containing regeneration and 60–380% higher densities than expected in areas upwind of intact forest (Figures 2 and 3). Areas downslope of intact forest contained regeneration densities that were three times greater than areas in upslope positions, despite the locations of upslope transects (14.0 degrees ± 2.2 standard error) having comparable slope angles to the locations of downslope transects (14.5 degrees ± 1.8, Table 1). As a result, slope had a negative coefficient in the full model, which indicated that more regeneration was expected downslope of intact forest (Figure 3). The coefficient for slope also indicated that areas
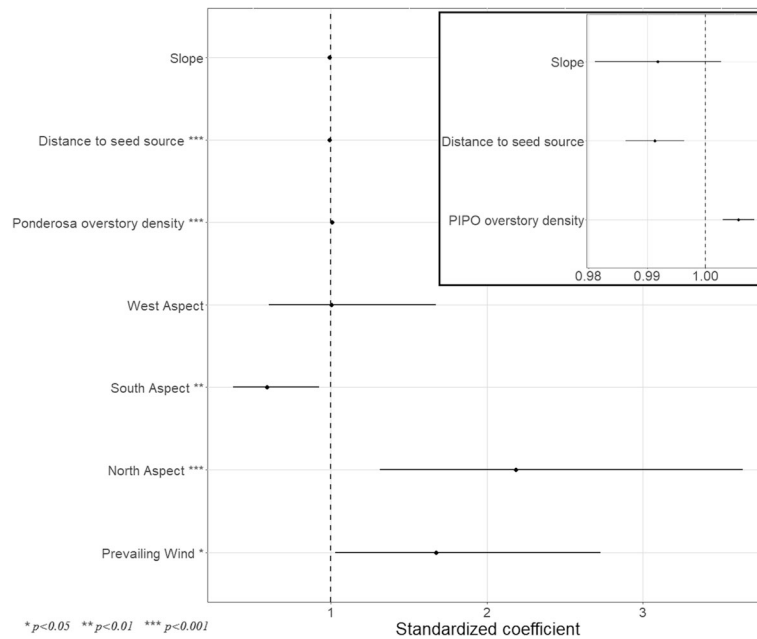
Figure 2. Marginal effects with 95% confidence intervals of variables included in the logistic model used to form the full model. North-facing aspect and prevailing wind had the largest effects on regeneration presence, with some areas having 2–3 times greater odds of containing regeneration compared to areas upwind of intact forest or located on other aspects. Areas that were far from intact forest also had a lower likelihood of containing regeneration, with a 10 m increase decreasing the likelihood of an area containing regeneration by 7%. Coefficients were converted to an odds ratio using an exponential transformation.
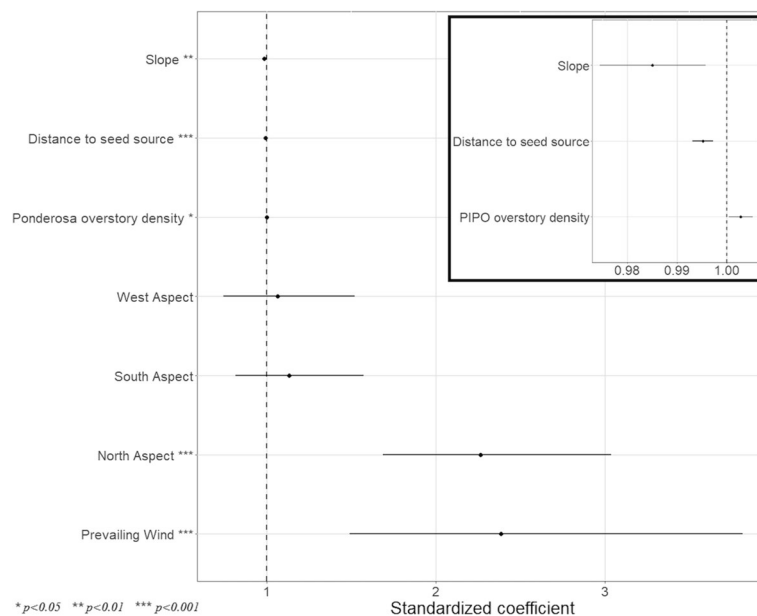

Figure 3. Marginal effects with 95% confidence intervals of variables included in the general linear model used to form the full model. North-facing aspect and prevailing wind had the largest effects on regeneration patterns, with areas containing 2–3 times more regeneration than areas upwind of intact forest or located on other aspects. The negative effect of slope indicates that areas downslope of intact forest were expected to contain more regeneration than upslope areas. Coefficients were standardized using an exponential back-transformation.

Table 2. Comparison of Model Estimates and Performance Between the Abiotic Factors and Distance-only Models

Predictors	Abiotic factors model		Distance-only model	
	Estimates	std. error	Estimates	std. error
Logistic model				
(Intercept)	0.7775	0.4033	0.69133*	0.3482
Regeneration Bin Distance [log]	−0.2867 ***	0.0863	−0.2688 **	0.0835
Aspect [N]	0.7745 **	0.2526		
Aspect [S]	−0.7412 ***	0.2217		
Aspect [W]	−0.2769	0.2465		
Combined slope	−0.0078	0.0055		
Prevailing wind	0.4212	0.2414		
Observations		720		720
R^2 Tjur		0.076		0.015
delta AICc		0		34.932
Cross validation accuracy		0.6250		0.6667
General linear model				
(Intercept)	5.9241 ***	0.1478	6.0704 ***	0.1168
Regeneration Bin Distance	−0.0051 ***	0.0011	−0.0048 ***	0.0013
Aspect [N]	0.8197 ***	0.1588		
Aspect [S]	−0.2383	0.1662		
Aspect [W]	−0.2236	0.1868		
Slope	−0.0190 **	0.0058		
Prevailing wind [1st degree]	3.6670 ***	0.9975		
Prevailing wind [2nd degree]	−4.1574 ***	1.0142		
Observations		288		288
R^2/R^2 adjusted		0.320/0.303		0.044/0.044
delta AICc		0		85.435
Cross validation RMSE		1794.884		1856.556

The abiotic factors model represented the most accurate and parsimonious logistic and general linear models that excluded tree height and ponderosa overstory density. [*]represents $p < 0.05$, [**]represents $p < 0.01$, and [***]represents $p < 0.001$.

downslope of intact forest had greater regeneration densities when slope increased, while the opposite was true for areas in upslope positions. Transects downwind of intact forest (539 ± 362 individuals ha^{-1}) had regeneration densities that were four times greater than transects upwind of intact forest (124 ± 34 individuals ha^{-1}).

Distance to seed source had a negative effect on the presence and density of regeneration, as the full model indicated that a 10 m increase in distance to the seed source reduced the odds of regeneration presence by 7% and expected density of regeneration by 5% (Figures 2 and 3). North-facing transects contained the highest regeneration densities (Table 1), which were two times greater than the regeneration densities of transects facing other directions (Figure 3). While south-facing locations had comparable regeneration densities to areas that faced east or west, they had a 41% lower chance of containing regeneration. Unlike the other variables

that altered seed dispersal, the effect of aspect suggested differences in growing conditions that affected seedling establishment and survival. North-facing aspects are cooler and wetter than areas on other aspects because they generally receive less solar radiation, which increases seedling survival in this semi-arid climate (Marsh and others 2022). Conversely, south-facing aspects receive more solar radiation, which increases local temperature, aridity, and the likelihood of seedling mortality (Crockett and Hurteau 2023).

Model Comparison and Extrapolated Effects of Abiotic Factors

Accounting for abiotic factors (for example, wind, slope, and aspect) improved model performance and altered regeneration density estimates relative to the distance-only model. The distance-only and abiotic factors models had similar coefficients for
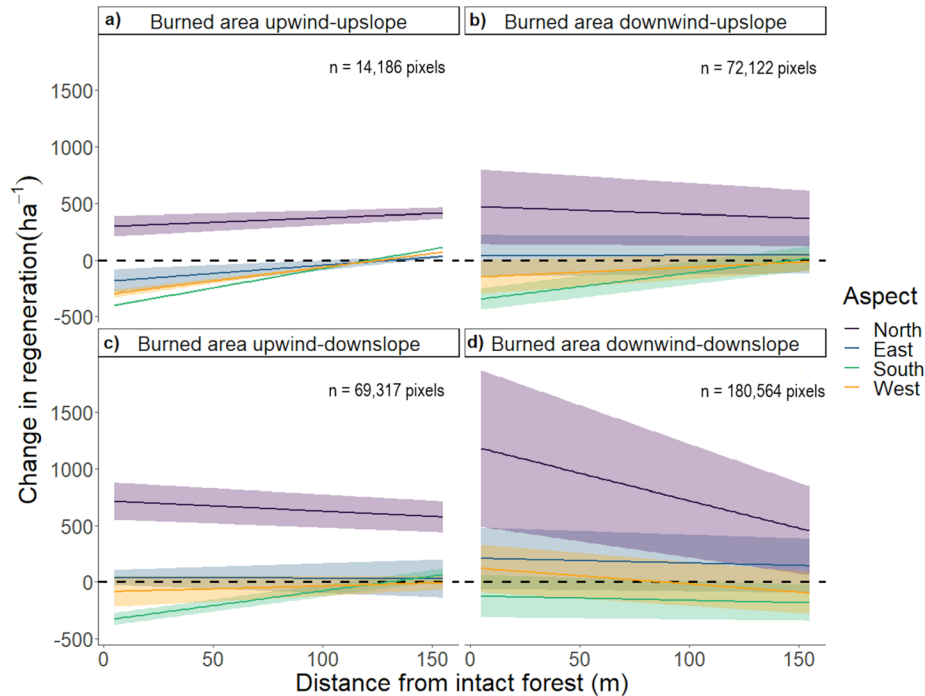
Figure 4. Change in estimated regeneration density (± one standard deviation) after accounting for wind, slope, and aspect. Change in estimated regeneration density was calculated by subtracting pixel values from the abiotic factors model by values from the distance-only model. The differences in model estimates were categorized by slope position (top vs. bottom), wind position (left vs. right), and aspect (colors), from which 16 simple linear regressions were quantified to visualize trendlines. The black dashed line represents no difference between the abiotic factors and distance-only pixel values, with values above the line indicating that estimates from the abiotic factors model contained more regeneration than estimates of the same pixels in the distance-only model.

distance to seed source, but the inclusion of wind and topographic variables led to a higher R^2 and lower AICc values in the abiotic factors model (Table 2). The abiotic factors model estimated greater regeneration density in 54% of burned pixels at an average of 525 more individuals ha^{-1} in these areas. The increase in average regeneration density was greatest on north-facing aspects because of better growing conditions (Figure 4).

When comparing results on north-aspects with distance-only estimates, approximately 97% of pixels had greater regeneration density estimates from the abiotic factors model. North-facing pixels had the largest estimated increases (from a mean of 1177 more individuals ha^{-1} at 5 m to a mean of 454 more individuals ha^{-1} at 155 m) in areas that were downwind and downslope of the primary seed source (Figure 4d). In cases where north-facing pixels were either upslope or upwind of the intact forest, the abiotic factors model estimated regeneration density that was consistently higher than the distance-only model, and regeneration density was fairly consistent across the 160 m distance from the intact forest. For example, north-

facing locations in downwind and upslope positions from intact forest averaged approximately 500 more individuals ha^{-1} across the entire 160 m distance compared to the distance-only estimates (Figure 4b). Pixels on other aspects had similar regeneration density estimates between the abiotic factors and distance-only models except in areas positioned upwind, upslope, and near intact forest, where the distance-only model overestimated regeneration density. The differences in model performance and outputs show that abiotic factors provide additional information for estimating regeneration patterns in areas near intact forest that distance to the nearest seed source does not capture.

DISCUSSION

Increasingly large high-severity burn patches can have large areas within which conifers cannot regenerate because the distance to live trees is beyond the dispersal distance (Coop and others 2020). While distance to live trees is an important predictor of regeneration (Stevens-Rumann and

Morgan 2019), there is regeneration density variability in areas near intact forest that distance to seed source poorly explains (Haffey and others 2018; Haire and McGarigal 2010). We found that slope, prevailing wind direction, aspect, overstory tree density, and the relative position of seed sources accounted for more variability in regeneration patterns than distance to seed source alone. When extrapolating the relationships among abiotic factors across large high-severity patches, we found expected regeneration density differed from estimates using distance alone, indicating that these variables help explain post-fire regeneration patterns that can affect long-term stand dynamics within high-severity patches.

Slope and prevailing wind direction influenced regeneration patterns by altering the distance and direction that seeds dispersed from intact forest to the surrounding landscape. Similar to results from other research, we found that regeneration densities are greater downslope and downwind of live trees. The greater vertical distances between the canopy and downslope locations allow seeds to travel as much as 12 times further from the parent tree (Kim and others 2022). Wind interacts with slope and open habitat to increase the proportion of seed that disperses downwind of seed sources and the distance they travel into high-severity patches (Damschen and others 2014; Trakhtenbrot and others 2014). Because greater seed density typically leads to more seedling establishment (Dovčiak and others 2005; Reid and others 2023), we can assume that the higher regeneration density we measured was driven by increased propagule pressure.

Overstory density, distance to seed source, and aspect combine with wind and slope to alter seed source availability, the expected proportion of seeds that land in patch locations, and the number of individuals that establish following dispersal. Overstory density alters the number of seeds available to disperse into the patch (Keyes and Maguire 2007), resulting in more regeneration among areas near intact forest with more large and mature seed trees (Puhlick and others 2012). Areas far from seed sources receive fewer seeds because large and heavy ponderosa pine seeds rarely disperse far from the parent tree (McDonald 1980; Moles and Westoby 2006), causing these areas to have lower regeneration densities than areas in similar wind and slope positions that are closer to surviving overstory trees (Stevens-Rumann and Morgan 2019). Rather than influencing seed dispersal, aspect changes growing conditions that affect seedling establishment and survival (Bonnet and others 2005, Marsh and others 2022), resulting

in greater regeneration density on north-facing aspects compared to other locations in similar positions for seed dispersal. These findings indicate that observed regeneration patterns can result from the combined effects of abiotic factors, live tree position, and live tree density that affect the initial stages of reforestation for wind-dispersed, seed-obligate conifers.

Aspect affects growing conditions by influencing the microclimate of patch locations. Changes in aspect cause patch locations to receive different amounts of solar radiation (Marsh and others 2022). The resulting difference in heat loading and moisture availability alters the physiological constraints that govern conifer seedling establishment and survival. While the odds of seedling mortality increase in warmer and drier conditions that characterize south-facing aspects (Crockett and Hurteau 2023), the cooler and wetter environment of north-facing aspects increases the rate of seedling survival in semi-arid environments (Hankin and others 2019). With sufficient seed dispersal, patch areas on north-facing aspects can support high regeneration densities within 30 years after fire, which may mature into forests with cone-bearing trees under expected ponderosa pine stand dynamics (Burns and Honkala 1990; DeWald and Mahalovich 2008). This suggests that north-facing locations in favorable seed dispersal positions have the highest probability of becoming nucleation sites that regenerate areas beyond the range of seed dispersal from intact forest at the patch edge (Yarranton and Morrison 1974).

While regeneration patterns resembled the expected effects of abiotic factors on seed dispersal and establishment, we used regeneration presence and density as a proxy for seed dispersal rather than measuring seed rain in high-severity patches. This meant that other factors may have influenced observed and estimated regeneration outcomes by altering seed density, expected regeneration patterns, and the likelihood of germination and seedling survival. Granivores alter seed density by consuming or caching conifer seeds on the landscape within two weeks of dispersal from the parent tree, meaning many seeds are removed from the location where they land following wind dispersal (Compton 2004; Vander Wall 1994, 2023). Overstory density affected measured regeneration presence and density in the full model, but we could not incorporate it into spatial extrapolations, which led to the model used for extrapolation explaining less of the variability than the full model. Competition, soil accessibility, and ground cover alter seed germination by changing soil

moisture, temperature, and nutrient availability, causing more seeds to germinate in areas with less resource competition and greater access to soil nutrients and water (Bonnet and others 2005; Crockett and Hurteau 2022; LePage and others 2000). Future studies should consider accounting for granivory and soil type in study design, quantifying continuous spatial layers of stand structure, and using seed traps that allow direct measurements of seed rain from intact forest to reduce the potential for confounding error and improve estimates of patch regeneration outcomes.

Accounting for abiotic factors caused estimates of regeneration presence and density to reflect the variability of seed dispersal and seedling establishment near intact forest that distance to seed source does not explain. Southwestern dry conifer forests often reside in mountainous areas and burn patches that typically occur in areas of complex topography and variable wind patterns (Ruel and others 1998; Zeng and others 2004). The resulting diversity of abiotic factors interact to create a range of seed dispersal and establishment conditions that resembles the range of regeneration densities that exist within areas near intact forest (Haffey and others 2018; Haire and McGarigal 2010). Accounting for the effect of abiotic factors improves and oftentimes increases estimated regeneration patterns, which can alter long-term patch stand dynamics.

The change in stand dynamics that results from altered regeneration outcomes can have long-term implications on carbon balance and water cycling within the ecosystem. Greater estimated regeneration densities can result in more individuals reaching maturity, which increases carbon capture and decrease water availability within the stand (DeWald and Mahalovich 2008; Law and others 2003). However, changes in climate are expected to interact with abiotic factors like aspect to reduce the number of ponderosa pine regeneration events, which decreases the potential of reforestation and the resulting carbon storage capacity across high-severity patches in the southwest (Jung and others 2023; Keyser and others 2020). Therefore, accounting for the effects of abiotic factors on regeneration patterns in post-fire vegetation models can improve forecasts of ecological succession, carbon modeling, and resource availability within high-severity burn patches across southwestern dry conifer forests (Hanbury-Brown and others 2022; Jung and others 2023). Additionally, this information can be used to identify locations where natural regeneration is likely to be sufficient for reforestation and allow managers to target areas where artificial regeneration will accelerate reforestation.

Patch characteristics interact with abiotic factors to alter expected regeneration patterns by controlling the distance seeds must disperse from intact forest to reach locations in high-severity patches. Large patches with simple shapes contain more area at greater distances from the patch edge than smaller patches with complex shapes, causing a greater proportion of large patches to exist beyond the expected range of conifer seed dispersal and have poor regeneration (Collins and others 2017; Coop and others 2020; Singleton and others 2021b). Our results suggest that the influence of abiotic factors on regeneration outcomes is most likely to cause increased density within 160 m of intact forest. Yet, as our regeneration density differences between aspects suggest, recent poor conifer regeneration may be more a function of microclimatic conditions in increasingly large high-severity patches (Singleton and others 2019; Coop and others 2020).

Our results demonstrate that the presence and density of conifer regeneration vary as a function of abiotic factors and the relative position of seed sources in high-severity patches. Accounting for the influence of abiotic factors on regeneration outcomes provides a more accurate representation than a distance-only approach for predicting how ponderosa pine forests can propagate from intact forest into severely burned patches. Our results, particularly because we used established seedlings as a proxy for seed dispersal, are indicative of the influence that aspect has on seedling establishment. Accounting for these factors provides both a more accurate representation of post-fire ponderosa pine establishment and a less pessimistic prediction for post-fire reforestation than the more common distance-only approach to predicting tree seedling establishment.

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DATA AVAILABILITY

Data and code used in this research are available at: https://doi.org/https://doi.org/10.5061/dryad.2547 d7wxh.

Declarations

Conflict of interest   The authors declare no conflict of interest.

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