

THESIS

THE ROLE OF WILDFIRE AND TOPOGRAPHY IN SHAPING ASPEN REGENERATION
AFTER THE HAYMAN FIRE, CO, USA

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ABSTRACT

THE ROLE OF WILDFIRE AND TOPOGRAPHY IN SHAPING ASPEN REGENERATION AFTER THE HAYMAN FIRE, CO, USA

Unusually rapid and widespread mortality in Quaking aspen (*Populus tremuloides*) has been documented throughout the 21st century primarily as a result of warm, dry weather conditions. Although aspen are not drought-adapted, aspen are well adapted to wildfire. Increases in wildfire severity and extent as a result of climate change may provide opportunities for aspen regeneration, especially at mid- and high-elevation sites. Aspen's sensitivity to drought suggests that regeneration following fire might be constrained to cooler and wetter topographic locations on the landscape which reduce drought stress on vegetation. While aspen mortality is demonstrated to occur at low elevation sites, aspen establishment and persistence is known to occur at high elevation sites due to cooler, wetter conditions. Low- and high-elevation aspen persistence is well-understood; however, patterns of aspen regeneration and persistence at mid-elevation sites is still relatively unexplored. We use the 2002 Hayman fire (Colorado, USA) to explore whether high-severity wildfire has provided opportunities for aspen regeneration at mid-elevations in which aspen was not observed before the fire. If regeneration has occurred, we ask if regeneration is contingent on topographic conditions. Cool, wet microclimates created by fine-scale topography at mid-elevations may allow for increased aspen regeneration, however this is unexplored in the Hayman landscape. Our findings demonstrate that the Hayman fire provided opportunities for aspen regeneration at mid-elevation sites in which aspen were not observed before the fire and that the density of regeneration is contingent on topography. Specifically, aspen regeneration is most dense at mid-elevations on steep slopes. Ecosystem management may focus on threats to aspen health and vigor (i.e. ungulate herbivory) on steep slopes at mid-elevations rather than at low-elevation sites.

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Chapter 1

Introduction

Unusually rapid, widespread mortality in Quaking aspen (*Populus tremuloides*) has been documented across much of its range throughout the 21st century [Worrall et al., 2013, Worrall et al., 2008, Bartos et al., 2001, Worrall et al., 2010, Rogers, 2002]. Warm, dry weather conditions are thought to be the primary cause of these population declines [Worrall et al., 2013]. Increased temperatures coupled with drought conditions, which amplify water stress for vegetation [Breshears et al., 2005], have become frequent in the western US since ca. 2000. Aspen decline associated with these weather conditions implies that aspen is not adapted to these global change type drought events, which may continue to increase in intensity and severity throughout this decade [Breshears et al., 2005]. Projected increases in landscape-scale aspen mortality [Worrall et al., 2013] could be ecologically and economically detrimental. Aspen stands are biodiversity hotspots for native plants, insects, birds, and mammals [Kashian et al., 2007] and large drivers of recreation and tourism industries throughout western North America [Kaye et al., 2005].

Aspen mortality rates are expected to increase as suitable habitat is reduced in a warming, drying world. Species distribution models project that about a quarter of the current aspen cover will no longer be viable for the species by 2060 [Worrall et al., 2013]. Reductions in distribution extent are most intense at low elevations and at sites that amplify warm, dry climatic conditions, such as southwest-facing aspects [Worrall et al., 2013]. Warm, dry weather conditions increase drought stress in mature aspen stands and their root systems initiating dieback, which also reduces the ability of these aspen to regenerate in high densities. While low elevations are demonstrated to be unfit for current and future aspen regeneration for these reasons [Rother and Veblen, 2016], regeneration at high-elevation sites has been documented as a result of cool, wet climatic conditions [Landhausser et al., 2010, Elliott and Baker, 2004]. Increased aspen regeneration at high elevations is expected to continue throughout the coming centuries [Elliott and Baker, 2004] as low elevations experience greater intensity of drought conditions. Although the suitability of high and

low elevations for current and future aspen regeneration is well understood, aspen regeneration at mid-elevation sites is still relatively unexplored.

Aspen regeneration at mid-elevation sites is complex. Many sites at mid-elevations also experience drought conditions which have been implicated in aspen mortality [Worrall et al., 2008]. However, fine-scale variability in topography at mid-elevation sites could provide critical modifications to on-site weather and climate for aspen. This variability creates cool, wet microclimates [Dobrowski, 2011] which are decoupled from regional climate. For example, northeast-facing, steep slopes can remain cool and wet at mid-elevations [Dobrowski, 2011], perhaps supporting aspen regeneration even as regional climate becomes warmer and drier. Cool, wet microclimates may increase suitable aspen distribution across mid-elevations despite regional warming and drying trends.

Aspen regeneration may be stimulated across suitable aspen distribution by wildfire in the coming century. Aspen are uniquely adapted to wildfire, with root systems that alter hormone production to promote suckering in response to disturbance [Brown and DeByle, 1987]. Clonal suckering allows aspen populations to quickly establish in post-fire landscapes [Brown and DeByle, 1987] when compared with other species which depend on seed dispersal. Aspen also establish after wildfire as a result of seedling germination more often than previously thought [Romme et al., 2005, Landhausser et al., 2010, Elliott and Baker, 2004, Turner et al., 2003a]. For successful germination, aspen seeds require reduced competition and exposed mineral soil, both of which are characteristic of post-fire landscapes [Turner et al., 2003a]. Aspen seeds are small and can travel up to 15 km from live forest [Jayen et al., 2006], giving them an advantage in extensive burn areas over conifer species with heavier, larger seeds. Given aspen's fire adaptations [Turner et al., 2003a, Brown and DeByle, 1987] and small seed size, high-severity wildfire could initiate a shift from conifer to aspen cover in some situations. Aspen's sensitivity to drought suggests that regeneration following fire might be constrained to cooler and wetter topographic locations on the landscape.

Warm, dry climatic conditions also drive wildfire frequency and intensity [Westerling et al., 2011]. Increased frequency of high-intensity, severe wildfire has been documented throughout western North America, particularly since the start of the 21st century [Westerling et al., 2011, Liu et al., 2010]. Eighteen wildfires greater than 20,000 hectares have burned in Colorado since 2000 [MTBS, 2017]. As a result, Colorado provides numerous opportunities to study aspen response to wildfire in topographically complex landscapes.

To consider the increasing trend in frequency of high-severity, extensive wildfire throughout western North America, we chose to conduct our study in high-severity portions of Colorado's largest wildfire to date, the Hayman fire. Forest regeneration after high-severity fire in response to topography has been explored at low elevations (<2700 m) in the Hayman landscape, and extremely limited post-fire aspen regeneration has been reported [Rother and Veblen, 2016, Chambers et al., 2016]. Ponderosa pine and Douglas-fir seedlings were reported in lower densities in high-severity burn areas when compared to portions of the forest that were burned with less severity [Chambers et al., 2016]. Primary constraints on conifer regeneration were distance to seed source, unfavorable climate, and elevation [Chambers et al., 2016, Rother and Veblen, 2016]. Elevation was positively correlated with regeneration density for all conifer species [Chambers et al., 2016]. However, only 10 plots in the Chambers et al. study were above 2490 m in elevation [Chambers et al., 2016]. The study conducted by Rother and Veblen in 2016 was also limited to lower elevation sites (below 2590 m) [Rother and Veblen, 2016]. Therefore, post-fire tree regeneration after high-severity fire at mid-elevations in the Hayman landscape is still relatively unexplored.

Mid-elevation sites may help expand suitable aspen distribution as low-elevation sites are lost from aspen's range. It is important to understand patterns in aspen regeneration and persistence across topographically complex landscapes for aspen management and conservation in a rapidly changing world. Furthermore, understanding trends in forest regeneration after wildfire will provide insight into forest dynamics under a changing climate. The goal of this study is to examine aspen regeneration in response to high-severity wildfire at mid-elevation sites. We quantified post-

fire aspen regeneration in the field and used Bayesian regression models to further investigate the effects of fine-scale topography on regeneration.

My analysis focuses on the following hypotheses:

1. The Hayman fire provided opportunities for aspen regeneration at mid-elevation sites (2600-3000m) in which aspen was not observed before the fire.
2. If the Hayman fire has provided opportunities for aspen regeneration, regeneration is contingent on topographic influences on weather and climate. Specifically, aspen regeneration is most dense at cooler, wetter site conditions (i.e. steep, northeast-facing slopes).

Chapter 2

Methods

2.1 Study Area

The Hayman fire started due to anthropogenic causes in central Colorado in June, 2002. It burned approximately 52,000 hectares of land belonging to the Pike-San Isabel National Forest, private owners, the city of Denver, and the state of Colorado [MTBS, 2017]. Approximately 22,000 hectares were categorized as high-severity burn (100% tree mortality) [MTBS, 2017]. The fire spanned elevations from 2286 to 3657 m [MTBS, 2017]. Ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) dominated the forest canopy before the fire and Blue spruce (*Picea pungens*), lodgepole pine (*Pinus contorta*), and aspen were infrequently reported as part of the pre-fire canopy [U.S. Forest Service, 1984]. The nearest weather station (Cheesman) is located within the burn perimeter at an elevation of 2100 m [Western Regional Climate Center, 2008]. This station reports an average yearly minimum temperature of -12°C and an average yearly maximum temperature of 28.6°C. Average annual total precipitation is 40.28 cm and average annual total snowfall is 1.42 meters [Western Regional Climate Center, 2008].

The Hayman fire burned an area in which the historic fire regime is characterized as a mixed-severity regime of frequent low-severity, and infrequent high-severity fires [Romme et al., 2003]. A previous study by Romme et al. [2003] revealed that the earliest known widespread fires in this region occurred between 1500 and the late 1800s, with a mean fire interval of 50 years. One fire since the late 1800s is known to have killed overstory trees. It burned in 1963 and was relatively small, burning only about 40 hectares [Romme et al., 2003]. Fire exclusion has affected the Hayman area for centuries, starting with reduced fuel loads after intense grazing and logging activity throughout the 19th century and continuing with active fire suppression policies throughout the 20th century [Romme et al., 2003].

2.2 Field Methods

We selected 156 sampling locations using stratified random sampling methods in R [Assal et al., 2014, R Core Team, 2016]. Plots were randomly balanced by three strata: pre-fire forest cover type, elevation, and heat load index. We obtained pre-fire and post-fire spatial vegetation data from the Pike San-Isabel National Forest [U.S. Forest Service, 1984]. Distance to post-fire live forest for each plot was calculated using this post-fire spatial vegetation data (see supplemental data in appendix). We derived the abiotic variables (elevation and heat load index) from a digital elevation model (DEM) [Gesch et al., 2002]. Heat load index was calculated using the ArcGIS Geomorphometry and Gradient Metrics Toolbox [Evans, 2014]. This index accounts for both slope steepness and aspect, allowing for a more concise stratification process. All plots were limited to high-severity burn patches above 2600 m [MTBS, 2017]. We also limited plots to areas in which pre-fire aspen presence was not reported [U.S. Forest Service, 1984]. The location of plots relative to pre-fire forest cover type and elevation are shown in figures 2.1 and 2.2 respectively.

We visited all 156 plots during the summer of 2017. We navigated to each sampling location using a hand-held GPS unit and established a 20 x 20 m plot with the randomly selected point at the southwest corner. If we arrived at a plot with evidence that aspen was present before the fire (dead standing or fallen aspen killed in the fire), we omitted the plot from the study. At each plot's southwest corner, we recorded elevation, aspect, and slope steepness using a compass and hand-held GPS unit. The number of individual aspen stems in each plot were counted and recorded. Stems that were not visibly joined above the soil were counted as individuals. If counts exceeded 100 stems per plot, we visually estimated the number of stems in the remainder of the plot. To relate ocular estimates to actual stem counts and ensure their accuracy, we developed a calibration model. We recorded a visual estimate as well as an actual count of all stems in 45 plots that had more than 100 aspen stems to parameterize this model. The details of the calibration model are described in the subsequent section. In addition to measuring aspen stem density, we also counted the number of conifer seedlings in each plot and recorded the species. All of the conifer seedlings counts were exact.

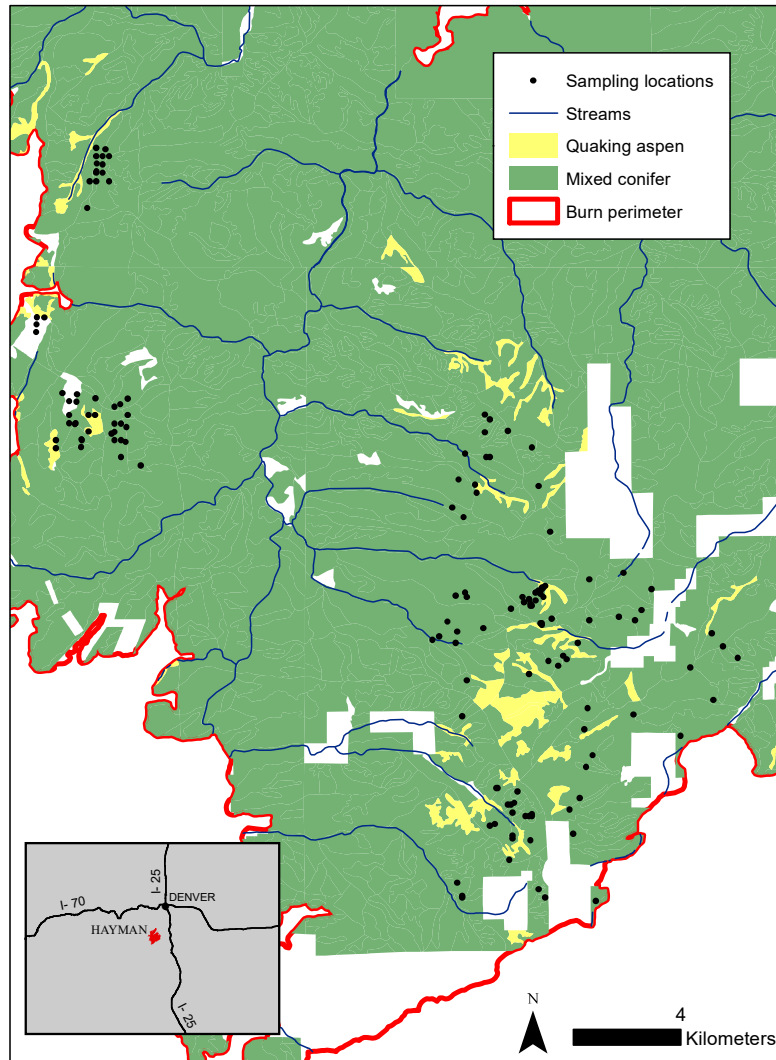


Figure 2.1: Distribution of sampling locations in relation to the pre-Hayman fire forest cover type in Colorado, USA. Mixed conifer cover consists of ponderosa pine, Douglas-fir, and lodgepole pine.

Finally, in each plot we cored the three largest dead standing trees killed in the Hayman fire at a height of 40 cm. Cored trees were selected to establish a rough estimate of the time since last fire. We recorded the diameter at breast height and species (if possible) of every tree cored. The increment cores were prepared using standard dendrochronological methods [Stokes, 1996]

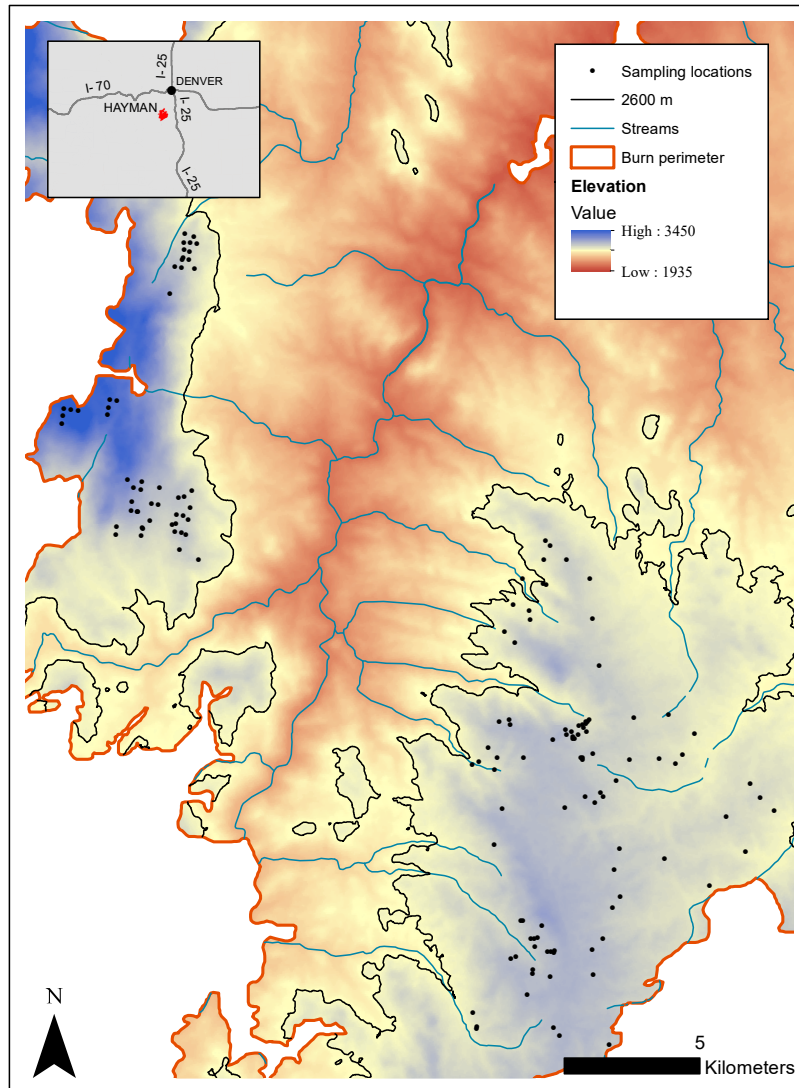


Figure 2.2: Distribution of sampling locations in relation to elevation in the Hayman fire landscape, Colorado, USA.

and annual rings were counted using a stereomicroscope. The year of the Hayman fire (2002) was assumed to be the year of the outermost ring.

2.3 Data Analysis

We developed hierarchical Bayesian models to investigate the ecological processes shaping tree regeneration after the Hayman fire. A hierarchical structure allowed us to model uncertainty in observations separately from uncertainty in the processes governing regeneration. Bayesian analyses provide a straightforward interpretation of parameter estimates and confidence envelopes. Given the complexity of ecological systems, Bayesian models are a valuable tool for disentangling complex relationships among variables.

We calibrated observed (actual) aspen stem counts to ocularly estimated stem counts using

$$[\gamma, \sigma, \lambda \mid \mathbf{y}] \propto \prod_{i=1}^{45} \text{Poisson}(y_i \mid \lambda_i) \text{ gamma}(\lambda_i \mid \frac{(\gamma_0 + \gamma_1 x_i)^2}{\sigma^2}, \frac{\gamma_0 + \gamma_1 x_i}{\sigma^2}) \quad (2.1)$$

$$\times \text{normal}(\gamma_0 \mid 0, 0.0001) \quad (2.2)$$

$$\times \text{normal}(\gamma_1 \mid 0, 0.0001) \quad (2.3)$$

$$\times \text{uniform}(\sigma \mid 0, 200) \quad (2.4)$$

where $\mathbf{y}_i$ is a 45-element vector drawn from a Poisson distribution and represents the number of aspen stems estimated ocularly in calibration plot i with mean λ_i . A Poisson distribution was selected because the data are counts of aspen stems. λ_i is drawn from a gamma distribution with shape $\frac{(\gamma_0 + \gamma_1 x_i)^2}{\sigma^2}$ and rate $\frac{\gamma_0 + \gamma_1 x_i}{\sigma^2}$. γ are the regression parameters and x_i are the actual stem counts at calibration plot i . A gamma distribution was selected for the mixture model because the results of the model are continuous and non-negative. Uninformative normal priors were specified γ_0 and γ_1 . An uninformative uniform prior was specified for σ . The output from this calibration model was used to inform the model comparing estimated aspen stem counts and topographic variables (Eq. 5).

We analyzed effects of topographic variables on aspen stem counts using:

$$[\boldsymbol{\beta}, \sigma, \boldsymbol{\gamma}, \boldsymbol{\lambda} \mid \mathbf{y}_a, \mathbf{y}_e] \propto \prod_{i=1}^{112} \prod_{j=1}^{112} \text{Poisson}(y_{a,i} \mid \lambda_i) \text{gamma}(\lambda_i \mid \frac{(\mathbf{x}_i \boldsymbol{\beta})^2}{\sigma^2}, \frac{\mathbf{x}_i \boldsymbol{\beta}}{\sigma^2}) \quad (2.5)$$

$$\times \text{Poisson}(y_{e,j} \mid \gamma_0 + \gamma_1 \lambda_j) \text{gamma}(\lambda_j \mid \frac{(\mathbf{x}_j \boldsymbol{\beta})^2}{\sigma^2}, \frac{\mathbf{x}_j \boldsymbol{\beta}}{\sigma^2}) \quad (2.6)$$

$$\times \text{normal}(\boldsymbol{\beta} \mid 0, 0.0001) \quad (2.7)$$

$$\times \text{gamma}(\sigma \mid 75, 1) \quad (2.8)$$

$$\times \text{normal}(\gamma_0 \mid 4.25, 14435380) \quad (2.9)$$

$$\times \text{normal}(\gamma_1 \mid 0.0052, 40696) \quad (2.10)$$

where $\mathbf{y}_a$ is a 109-element vector of actual aspen stem counts (counts we performed exactly) in the i th plot. A Poisson distribution is appropriate as the data are counts. λ_i is drawn from a gamma distribution with shape $\frac{(\mathbf{x}_i \boldsymbol{\beta})^2}{\sigma^2}$ and rate $\frac{\mathbf{x}_i \boldsymbol{\beta}}{\sigma^2}$. A gamma distribution was mixed with the Poisson to allow more of a flexible variance in the likelihood than would be possible using a Poisson alone. This formulation is identical to a negative binomial with a mean and a dispersion parameter. We prefer it because it shows that each plot is allowed to have its own mean (λ_i). $\mathbf{x}$ represents the independent variables: elevation (x_1) at plot i , "northeastness" (x_2) of plot i , and slope steepness (x_3) of plot i .

Heat load index was excluded from our Bayesian regression analysis in favor of our field measurements of aspect and steepness because we concluded that these field measurements are more accurate than an index. Aspect was transformed to "northeastness" by subtracting 45 from the aspect recorded at each plot and taking the absolute value. $\boldsymbol{\beta}$ is a three-element vector of regression coefficients. The regression coefficients are interpreted as follows: the intercept (β_0) is the offset in aspen stem counts that occurs at the average elevation, northeastness, and steepness of each plot. β_1 is the multiplicative change in aspen stem density per change in elevation. β_2 is the multiplicative change in aspen stem density per change in northeastness. β_3 is the multiplicative change in aspen stem density per change in slope steepness.

The quantity $\mathbf{y}_e$ is a 48-element vector representing estimated aspen stem counts (counts that were estimated ocularly when stem numbers exceeded 100) in the j th plot. We modeled the

data as arising from a Poisson distribution with mean $\gamma_0 + \gamma_1 \lambda_j$. λ_j is drawn from a gamma distribution with shape $\frac{(\mathbf{x}_i \boldsymbol{\beta})^2}{\sigma^2}$ and rate $\frac{\mathbf{x}_i \boldsymbol{\beta}}{\sigma^2}$. Uninformative normal priors were specified for the regression parameters, $\boldsymbol{\beta}$. The prior for σ was specified with mean 75 and variance 1. Informative priors for γ_0 and γ_1 were derived from the calibration model (Eq. 1) and ensure accuracy of our estimated stem counts, $\mathbf{y}_e$. The independent variables (elevation, northeastness, and steepness) were standardized by subtracting their means and dividing by their standard deviations [Gelman and Hill, 2009] to allow comparison of the magnitude of the effects of the regression coefficients on aspen stem density and to aid in the interpretation of the intercept.

We modeled response of conifer density to variation in topographic variables using

$$[\boldsymbol{\beta}, \mathbf{z}, \sigma, \boldsymbol{\lambda} \mid \mathbf{y}_c] \propto \prod_{i=1}^{112} \text{Poisson}(y_{c,i} \mid \lambda_i(1 - z_i)) \text{gamma}(\lambda_i \mid \frac{(\mathbf{x}_i \boldsymbol{\beta})^2}{\sigma^2}, \frac{\mathbf{x}_i \boldsymbol{\beta}}{\sigma^2}) \quad (2.11)$$

$$\times \text{Bernoulli}(z_i \mid \phi) \quad (2.12)$$

$$\times \text{normal}(\boldsymbol{\beta} \mid 0, 0.0001) \quad (2.13)$$

$$\times \text{gamma}(\sigma \mid 75, 1) \quad (2.14)$$

$$\times \text{beta}(\phi \mid 1, 1) \quad (2.15)$$

where $\mathbf{y}_c$ is a 112-element vector of observations, assumed to be a Poisson distributed random variable with mean $\lambda_i(1 - z_i)$. We ran this model separately for ponderosa pine and Douglas-fir seedling counts. Therefore, $\mathbf{y}_c$ represents either ponderosa pine counts or Douglas-fir counts. We refer to the species as conifer in the following model explanation because the model was the same for both Douglas-fir and ponderosa pine. Other conifer species were observed in plots too infrequently to support analyses.

We allowed for extra variation in the observations by hierarchically modeling λ_i as gamma distributed random variable with with shape $\frac{(\mathbf{x}_i \boldsymbol{\beta})^2}{\sigma^2}$ and rate $\frac{\mathbf{x}_i \boldsymbol{\beta}}{\sigma^2}$. $\mathbf{x}_i$ represents the independent variables. x_1 is the elevation of plot i , x_2 is the northeastness of plot i , and x_3 is the slope steepness of plot i . $\boldsymbol{\beta}$ is a three-element vector of regression coefficients that are interpreted as follows: the intercept (β_0) is the offset in conifer seedlings that occurs at the average elevation, northeastness,

and steepness of each plot. β_1 is the multiplicative change in conifer seedling density per change in elevation. β_2 is the multiplicative change in conifer seedling density per change in northeastness. β_3 is the multiplicative change in conifer seedling density per change in slope steepness. z is drawn from a Bernoulli distribution with mean ϕ . ϕ is the probability that the sampling location is not in conifer habitat. This parameter helps us account for the excessive number of zero-values in our conifer seedling counts that arise because some of our plots were in areas where conifer seeds do not germinate and establish successfully.

Uninformative normal priors were specified for the regression parameters, β . An uninformative beta prior was specified for ϕ . The prior for σ was specified with mean 75 and variance 1. The independent variables (elevation, northeastness, and steepness) were standardized as described previously to allow for comparison of the magnitude of the effects of the regression coefficients on conifer seedling density.

2.4 Model Computation and Evaluation

Posterior distributions for unobserved quantities were approximated using the Markov Chain Monte Carlo algorithm implemented in JAGS [Plummer, 2017] and R [R Core Team, 2016]. We ran 3 chains for 10,000 iterations after a burn in of 10,000 iterations. Convergence was assessed visually through trace plots and computationally through the Gelman-Rubin diagnostic [Gelman and Rubin, 1992]. Posterior predictive checks indicated that the calibration (Eq. 1), actual and estimated aspen stem count (Eq. 5), and the ponderosa pine and Douglas-fir seedling count (Eq. 11) showed no evidence of lack of fit. We chose to avoid model selection [Hobbs et al., 2012] as it is known that all topographic variables included in our model affect aspen stem regeneration [Sibold et al., 2006, Kulakowski and Veblen, 2006] and conifer seedling establishment [Chambers et al., 2016, Urza and Sibold, 2017, Rother and Veblen, 2016].

Chapter 3

Results

The 156 plots visited during the summer of 2017 represented a range of elevations from 2600 to 3200 m, a full range of slope aspects, and slope steepnesses between 0-25° (Figure 3.1). Pre-fire aspen were rarely encountered in our plots; 17 of the 156 (10.89%) plots were omitted from our study due to observed pre-fire aspen presence. Our observations of pre-fire forest cover type were consistent with the spatial data we received from the Forest Service.

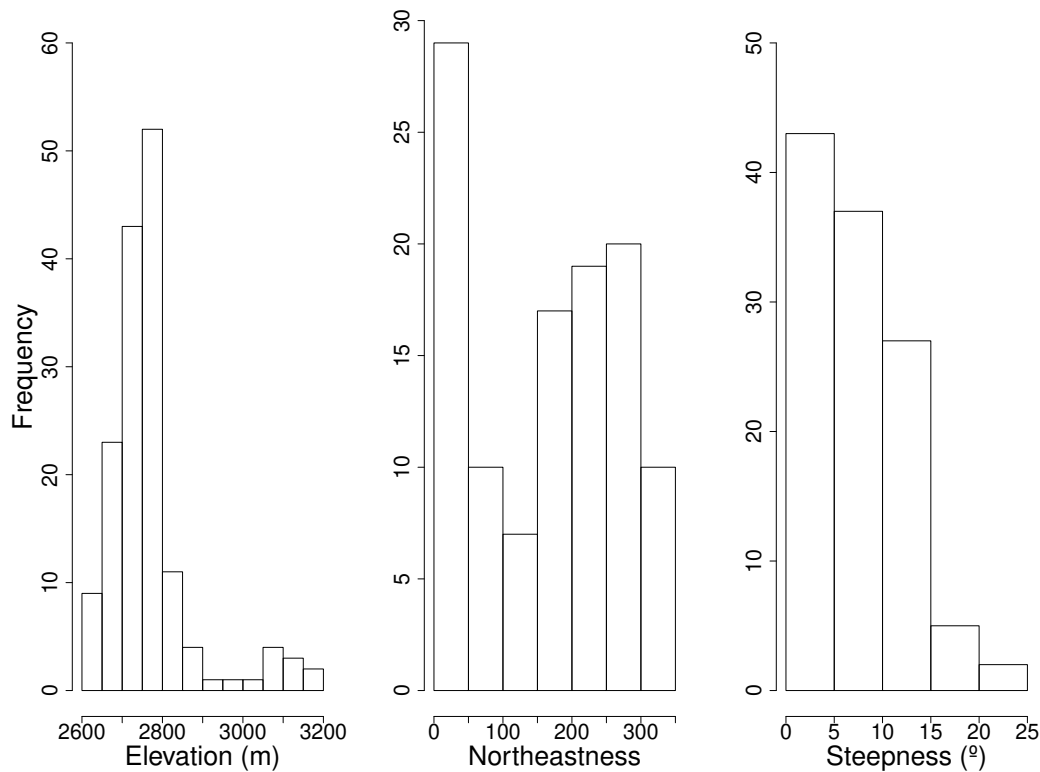


Figure 3.1: Plot distribution over elevation (m), slope "northeastness," and slope steepness (degrees) in the post-Hayman fire landscape. Note: the y-axis differs among plots.

3.1 Aspen Stem Density

Out of the remaining 139 plots after pre-fire aspen screening, 134 (97%) contained at least one post-fire aspen stem. The maximum number of stems per plot was 350 and the minimum was 0. The mean number of stems per plot was 137 (95% BCI= 112.84, 161.71), which equates to 3,425 stems per hectare. Model results (Table 3.1) demonstrate that post-fire aspen stem density was strongly related to slope steepness ($\beta_3= 0.06$, BCI= -0.06, 0.17). Specifically, there was a 86 percent probability that aspen stem density increased with slope steepness. Elevation ($\beta_1=0$.00, BCI= -0.11, 0.12) and slope aspect ($\beta_2=0.00$, BCI= -0.13, 0.11) did not affect aspen stem density; the posteriors were centered on zero (Figure 3.2). 112 out of 139 (80.5%) plots contained at least 40% aspen (Figure 3.3). Aspen patches are threatened by conifer encroachment when aspen cover is less than 40% of the patch [Kaye et al., 2005].

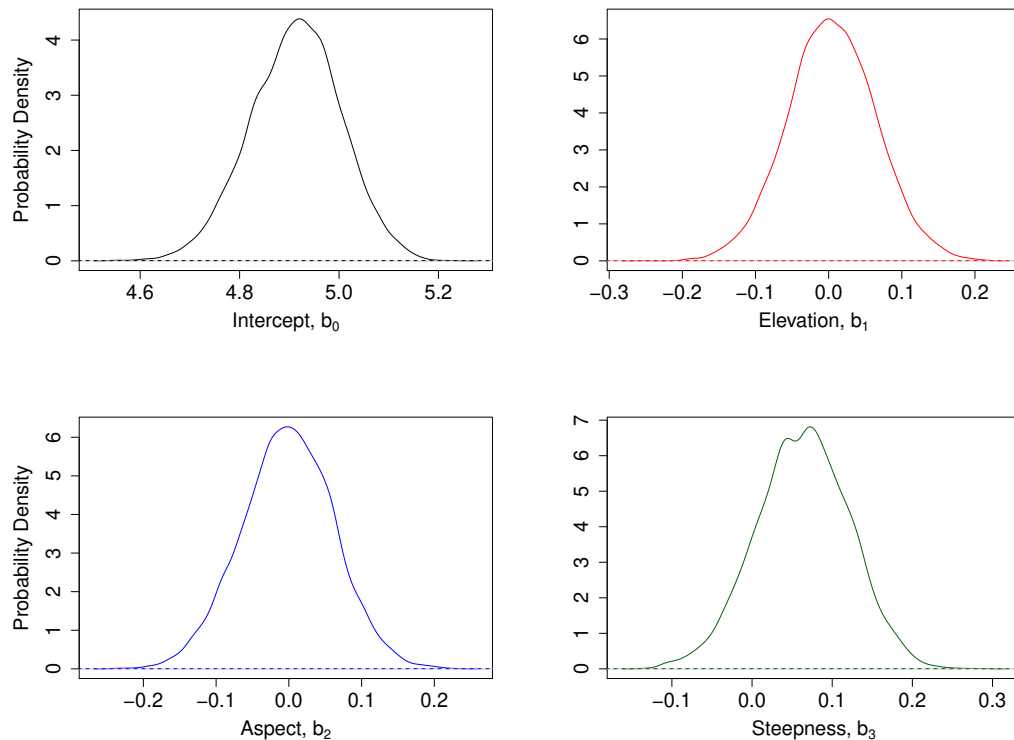


Figure 3.2: Aspen model results. Posterior (solid line) and prior (dashed line) distributions of coefficients using standardized covariates.

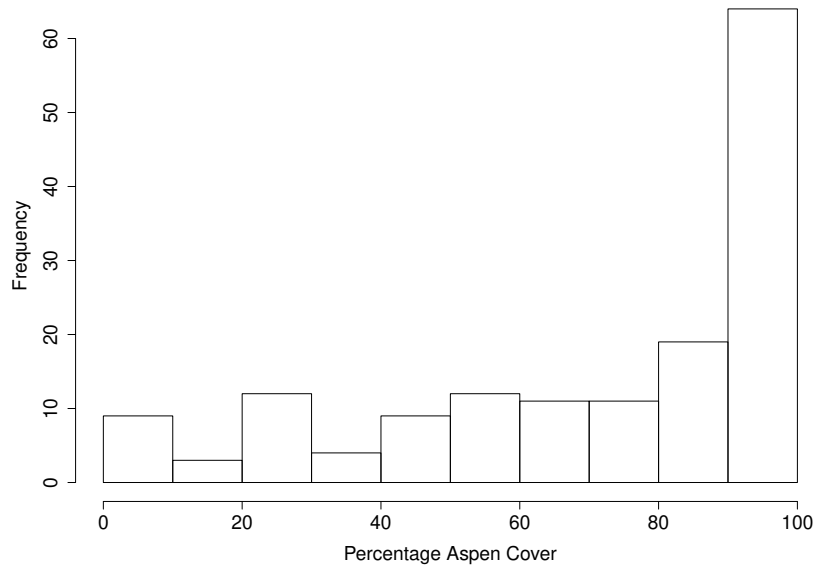


Figure 3.3: Frequency distribution of percentage aspen cover in each plot.

3.2 Conifer Seedling Density

One hundred twelve of the 139 plots (80%) contained at least one post-fire conifer seedling. The mean number of seedlings per plot was 48.68 (95% BCI= 39.27, 57.33), or 1,217 seedlings per hectare. The maximum number of seedlings per plot was 247 and the minimum was 0. Forty nine of 139 (35%) plots contained at least one ponderosa pine seedling and 24 plots (17%) contained at least one Douglas-fir seedling. The mean number of ponderosa pine seedlings per plot was 44.57 (95% BCI= 36.22, 54.13) and the mean number of Douglas-fir seedlings per plot was 36.76 (95% BCI= 28.63, 46.23). No obvious relationship between the distance to live forest and conifer seedling density was apparent although sites with very high numbers of seedlings tended to be relatively closer to seed sources (Figure 3.4). Conifer seedling density was not related to topographic variables (Tables 3.2 and 3.3); the posterior distributions were centered on zero (Figures 3.5 & 3.6).

Table 3.1: Estimates of aspen model parameters including the upper and lower bounds of a 95% credible interval (CI).

Coefficient	Mean	SD	2.5% CI	97.5% CI
Intercept, β_0	4.92	0.09	4.74	5.09
Elevation, β_1	0.00	0.06	-0.12	0.12
Aspect, β_2	0.00	0.06	-0.12	0.12
Steepness, β_3	0.06	0.06	-0.06	0.17
Sigma, σ	205.13	11.78	182.91	229.14
Calibration Model Intercept, γ_0	29.12	4.54	20.20	37.96
Calibration Model Slope, γ_1	0.07	0.00	0.06	0.08

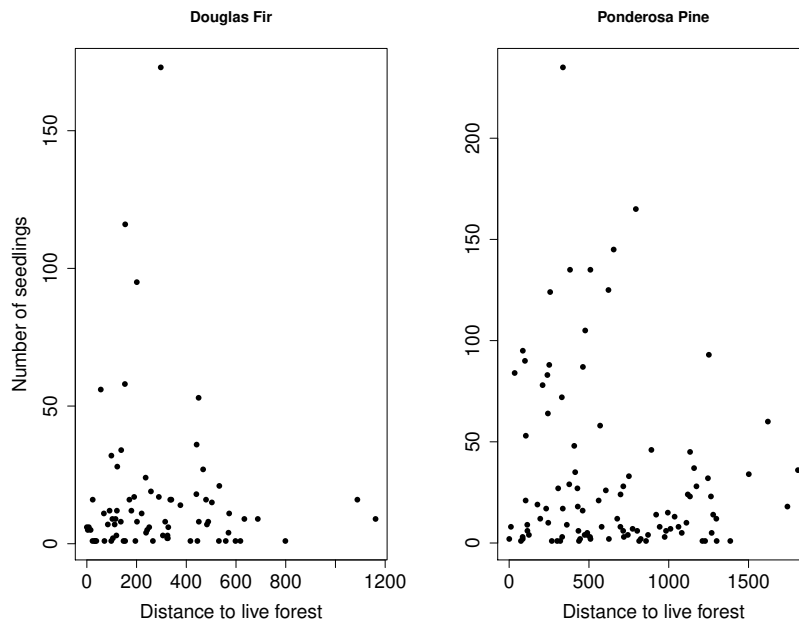


Figure 3.4: Number of post-fire seedlings as a function of distance from sampling location to live forest for both Douglas-fir and ponderosa pine. Each point represents one sampling location.

3.3 Increment Cores

Three hundred eighteen increment cores were taken during sampling to estimate time since last fire in the plots. Although the 318 cores were distributed across all study sites, only 126 of these cores (about 40%) were processed because many were rotten. Establishment dates ranged from 1585 to 1978 (Figure 3.7). Specifically, 87% of the cored trees in the study area established after

Table 3.2: Estimates of ponderosa pine model parameters including the upper and lower bounds of a 95% credible interval (CI).

Coefficient	Mean	SD	2.5% CI	97.5% CI
Intercept, β_0	3.79	0.10	3.59	3.99
Elevation, β_1	0.05	0.06	-0.06	0.16
Aspect, β_2	-0.03	0.05	-0.13	0.08
Steepness, β_3	-0.05	0.06	-0.17	0.06
Sigma, σ	59.09	6.37	47.75	72.49
Phi, ϕ	0.00	0.00	0.00	0.03

Table 3.3: Estimates of Douglas-fir model parameters including the upper and lower bounds of a 95% credible interval (CI).

Coefficient	Mean	SD	2.5% CI	97.5% CI
Intercept, β_0	3.59	0.12	3.35	3.83
Elevation, β_1	-0.01	0.06	-0.14	0.12
Aspect, β_2	0.04	0.06	-0.08	0.17
Steepness, β_3	-0.05	0.07	-0.18	0.09
Sigma, σ	55.54	7.19	42.40	70.38
Phi, ϕ	0.01	0.01	0.00	0.05

1800 and many cores indicated rapid initial growth in the late 1800s. No relationship between the oldest establishment date and the density of aspen stems was apparent.

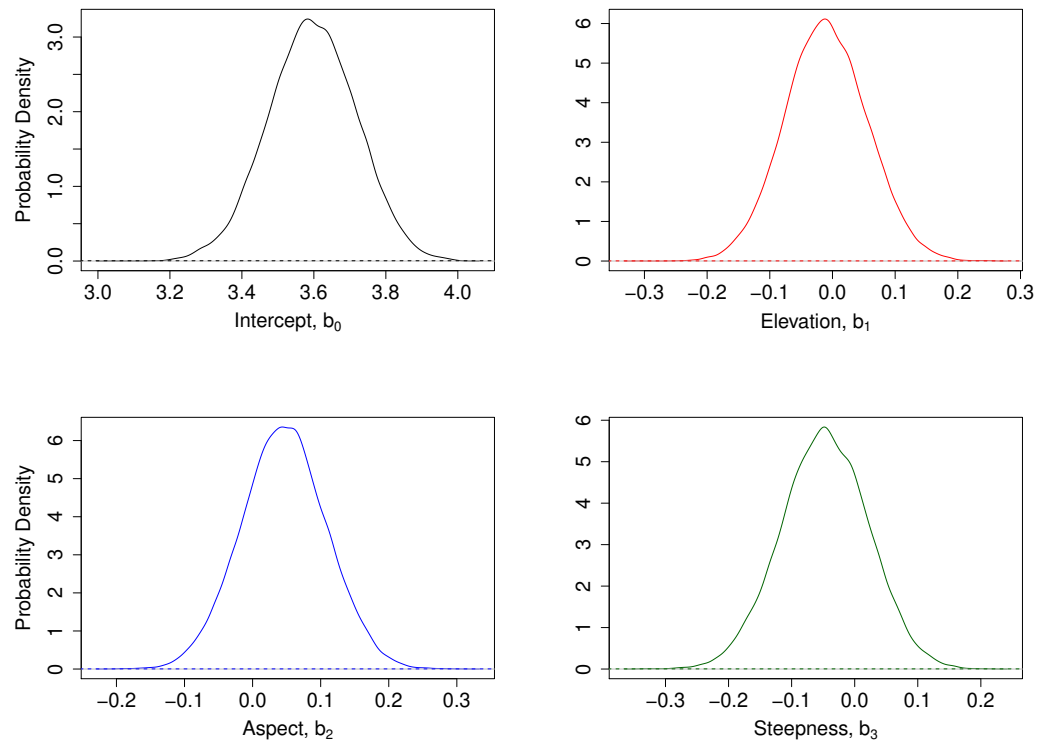


Figure 3.5: Douglas-fir model results. Posterior (solid line) and prior (dashed line) distributions of coefficients using standardized covariates.

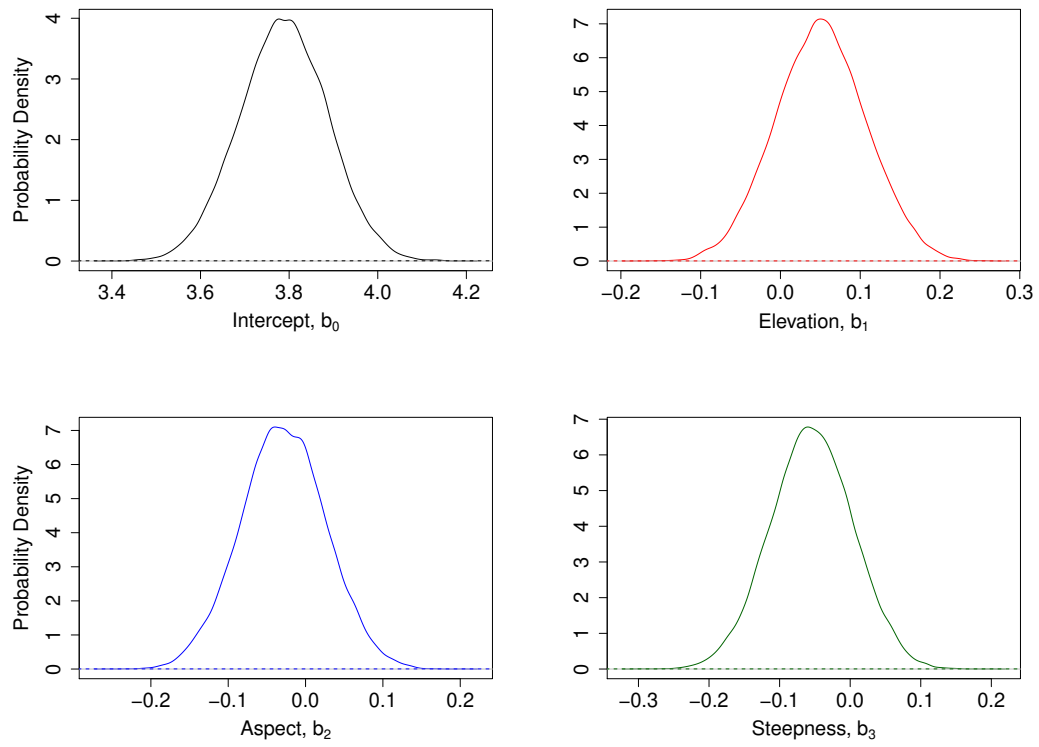


Figure 3.6: Ponderosa pine model results. Posterior (solid line) and prior (dashed line) distributions of coefficients using standardized covariates.

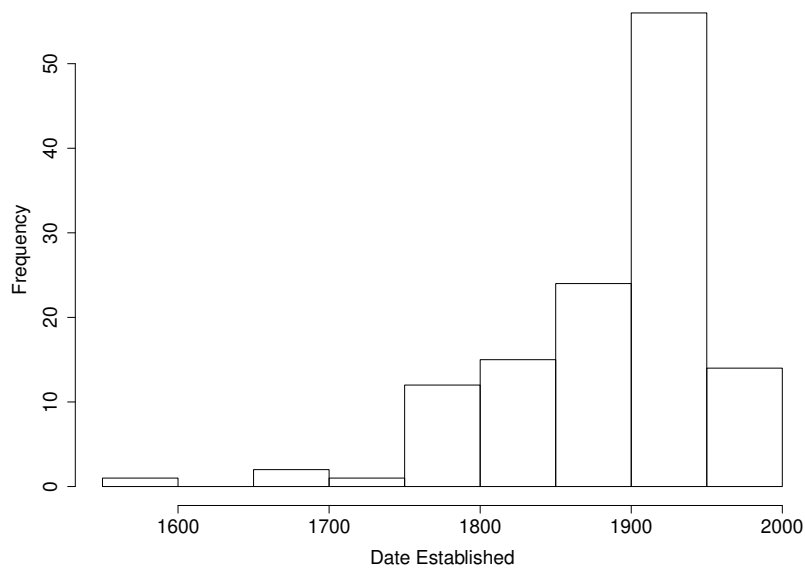


Figure 3.7: Frequency distribution of observed date of establishment for the oldest cored tree in each plot.

Chapter 4

Discussion

Our results demonstrate that wildfire can initiate a shift in cover type through the regeneration niche [Grubb P. J., 1977], specifically by providing an opportunity for aspen to establish in new areas of the landscape that were previously dominated by conifers. This finding supports our first hypothesis. Past studies examining the post- Hayman fire landscape have reported limited post-fire aspen regeneration [Chambers et al., 2016, Rother and Veblen, 2016]. However, these studies were limited to elevations below 2700 m. At mid-elevations (2700 - 3200 m) in the Hayman landscape, we found post-fire aspen regeneration in plots where aspen was not reported by the US Forest Service (1984) before the fire at a density of about 3,425 stems per hectare. Comparisons between low-elevation studies and our mid-elevation study highlight the importance of the influence of topography (elevation) in shaping landscape patterns of establishment.

4.1 Wildfire Creates a Window of Opportunity for Aspen Regeneration

We found prolific post-fire aspen regeneration in areas where aspen was not reported by the Forest Service before the Hayman fire [U.S. Forest Service, 1984]. Nearly all of our plots contained at least one aspen stem and the mean number of aspen stems was 137 stems per plot. These results suggest that aspen may be favored due to observed and projected increases in wildfire as a result of warming and drying climate [Westerling et al., 2011]. Wildfire can promote prolific suckering from dormant, preexisting root systems by altering hormone production in aspen stands [Brown and DeByle, 1987]. Wildfire also creates optimal germination conditions for aspen seeds by exposing mineral soil and reducing competition [Jayen et al., 2006, Romme et al., 2003, Shinneman et al., 2013]. While the latter has been considered a rare occurrence, more recent studies are showing that aspen establishment from seed is more common than previously thought [Elliott and Baker,

2004, Landhausser et al., 2010, Romme et al., 1995]. Aspen seed can travel up to 15 km due to their small size [Jayen et al., 2006] and all of our plots were within 2 km from post-fire live aspen forest (see supplemental data in appendix). We did not directly assess whether the aspen we observed were a result of dormant aspen roots that were present under the conifer-dominated overstory or seeds that germinated and established. The general absence of aspen in the canopy before the fire suggests that much of the recent regeneration is likely from seed.

4.2 Aspen Regeneration is Influenced by Topography

Aspen regeneration after the Hayman fire was mediated by topography. With the knowledge that slope steepness amplifies the effects of slope aspect on weather and climate [Dobrowski, 2011], we hypothesized that aspen stem growth would be most dense on cool, wet, steep, northeast-facing slopes [Dobrowski, 2011]. While we did not find an effect of slope aspect on aspen stem density, our models demonstrated that aspen stem density increased with slope steepness (Table 3.1), with an 85.83 percent probability that aspen stem density increases with slope steepness. The effect of slope steepness without an effect of slope aspect suggests that temperature and precipitation are not driving the relationship we observed between aspen regeneration and slope steepness.

A previous study found increased aspen regeneration on thin, rocky soils [Larsen and Ripple, 2003]. These soil types are often associated with steep slopes that are prone to soil erosion. While we did not assess soil quality in our study, the results of Larsen and Ripple's work [2003] in combination with results from other previous work suggest that soil quality could be an important driver of patterns in post-fire aspen regeneration [Frey et al., 2003, Smith et al., 2011].

The absence of an effect of slope aspect on aspen stem density is surprising because aspen are not drought adapted and aspect can mitigate or exacerbate heat stress [Dobrowski, 2011]. Perhaps our study's limitation to mid-elevation sites negates the effect of slope aspect. While aspen are predominantly seen on northern aspects at lower elevations and at southern aspects at higher elevations in the region [Worrall et al., 2008], at mid-elevations, aspect may not influence aspen stem density given the moderate climatic conditions. Furthermore, younger aspen stands are more toler-

ant of drought conditions [Worrall et al., 2013]; young post-fire aspen on southwest-facing slopes may be more resilient than older aspen on the same slope aspect, perhaps delaying drought-induced mortality.

Our study's focus on mid-elevations may also explain our surprising finding that elevation did not influence aspen regeneration density. We expected to find increased aspen regeneration at higher elevations given that lower elevations experience higher temperatures and more intense drought conditions. A relationship between aspen stem density and elevation within the mid-elevation band is not present (Table 3.1). However, comparisons between previous research in the Hayman landscape at low elevations below 2700 m [Rother and Veblen, 2016, Chambers et al., 2016] and our study suggest a threshold for post-fire aspen regeneration at about 2700 m in the Hayman landscape, above which aspen regeneration is supported post-fire. While aspen will not be a prominent species in the Hayman landscape at low-elevations, at elevations greater than 2700 m aspen regeneration is abundant.

4.3 The Hayman Landscape: Past, Present, and Future

Before the Hayman fire, the last known high-severity, extensive wildfires occurred in this region in the late 1800s [Romme et al., 2003]. After these late 1800s wildfires, conifer species primarily regenerated and grew to dominate the pre-Hayman fire forest canopy [U.S. Forest Service, 1984]. Our tree age data corroborates these findings. The majority (87.2%) of the pre-2002 trees that we cored established after 1800 (Figure 3.7) and the cores show rapid growth at that time. This analysis suggests a disturbance event that eliminated competition on the landscape, allowing for rapid growth. Our results, in combination with past studies suggest that post-fire aspen regeneration is unique to the Hayman fire forest recovery [Romme et al., 2003]. If aspen had regenerated after the late 1800s fires, it is probable that we would have observed them in our plots given their life spans of up to 200 years [Kashian et al., 2007].

The absence of pre-Hayman fire aspen in our plots may be a result of lacking seed sources or pre-existing root systems. If aspen regeneration after the late 1800s fires was possible from

pre-existing root systems or nearby live aspen forest, perhaps mid-elevation sites were too cool to support regeneration. Aspen are extremely sensitive to cold soil temperatures [Landhausser et al., 2010], which can prevent germination or regeneration. Warming climatic conditions at mid-elevations today may support unique aspen regeneration at mid-elevation sites after the Hayman fire.

While the pre-Hayman fire forest canopy was dominated by conifers, our results suggest that the post-Hayman fire forest canopy will be dominated by aspen until conifer species potentially replace aging aspen stands (Figure 3.3). The relationship between aspen and conifer species can often be thought of as cyclical; aspen establish early after a disturbance and within one aspen regeneration, shade-tolerant conifers can replace aspen and dominate the canopy [Kulakowski et al., 2004] until wildfire occurs again [Kaye et al., 2005] and aspen regenerate. These cycles of aspen and conifer replacement are known to occur over 100 - 300 years [Kashian et al., 2007]. It is also possible for aspen stands to be self-replacing [Kulakowski et al., 2004, Kurzel et al., 2007, Smith and Smith, 2005], therefore potentially never converting to a conifer-dominated canopy. Previous work suggests that aspen stands are threatened by conifer encroachment if aspen cover makes up less than 40% of the canopy [Kaye et al., 2005]. 80% of our plots had 40% or more aspen cover (Figure 3.3). While it is difficult to predict future forest recovery patterns at mid-elevations in the Hayman landscape, the density of conifer seedlings that we observed at mid-elevations suggests that conifers may not replace aspen unless subsequent high-severity wildfire occurs.

Past studies conducted in the Hayman fire landscape suggest that conifers are not regenerating in the same densities that they did before the fire [Rother and Veblen, 2016, Chambers et al., 2016]. These studies find limited conifer regeneration at low elevations (<2700 m) [Chambers et al., 2016, Rother and Veblen, 2016], and remark that higher elevations (> 2490 m) within their study areas supported more dense post-fire conifer regeneration than lower elevations [Chambers et al., 2016]. These findings are in direct agreement with our conifer regeneration observations. At mid-elevations, we observed a mean number of 48 conifer seedlings per plot, or 1,217 seedlings per hectare, which is well above the mean of 118 stems per hectare found by Chambers et al.(2016)

in high-severity burn areas and stocking requirements (370 stems per hectare). We found a mean of 44.74 (95% BCI= 36.22, 54.13) ponderosa pine seedlings per plot, and a mean of 36.76 (95% BCI= 28.63, 46.23) Douglas-fir seedlings per plot. Comparisons between our study and others allow us to identify a threshold at about 2700 m, above which high density conifer regeneration is able to occur despite the harsh conditions post-fire.

Our Bayesian analysis indicates that there is no effect of elevation, aspect, or steepness for both ponderosa pine and Douglas-fir seedling density (Tables 3.2 & 3.3). Our limit to mid-elevation sites might have negated effects of these variables in our models. The aforementioned 2700 m elevation threshold may be providing cool and wet enough conditions such that within mid-elevations, elevation, aspect, and slope steepness do not control conifer seedling density. Ziegler et al. [2016] conducted a study which examined regeneration after the Hayman fire and found that ponderosa pine regeneration depended on facilitation by other vegetation in the harsh, post-fire environments. Perhaps aspen stems have provided ample shade and moisture for ponderosa pine and Douglas-fir to establish, facilitating future competitive forest dynamics between aspen and conifer species [Ziegler et al., 2017]. Aspen persistence at mid-elevations may therefore depend on locations in which aspen are growing and conifers are not [Ziegler et al., 2017].

Conifer regeneration post-Hayman fire is also controlled by distance to seed source [Rother and Veblen, 2016, Chambers et al., 2016]. Past studies at low elevations (< 2700 m) in the Hayman landscape have identified a threshold of 50 m from seed sources, above which extremely limited conifer regeneration will occur [Chambers et al., 2016]. Only 18 of our plots were less than 50 m from live ponderosa pine forest post-fire and 5 plots were less than 50 m from live Douglas-fir forest post-fire (see supplemental data in appendix). We found no relationship between distance to seed and number of conifer seedlings per plot (Figure 3.4), therefore, it does not seem that distance to seed is mediating conifer establishment in our plots. Instead, it seems that the cool, wet environments above the 2700 m threshold are facilitating conifer establishment once seed does arrive.

4.4 Management Implications and Conclusions

Understanding forest recovery trends after wildfire is extremely important for ecosystem management in an era of climate change [Turner et al., 2003b]. Dense aspen regeneration in an otherwise harsh post-fire environment will stimulate and foster the success of a diverse range of species [Kashian et al., 2007]. Furthermore, established aspen stands promote moist stand conditions and serve as a natural fire break; therefore, aspen regeneration lowers the risk of future high-severity, extensive wildfire [Shinneman et al., 2013]. The extent and intensity of the Hayman fire provided a unique window of opportunity for widespread aspen regeneration. Managers may be interested in re-creating the ecological effects of the Hayman fire with prescribed burning; however the severity and size of the Hayman fire is unique to wildfire and not possible to emulate with prescribed burns.

Given the smaller extent of prescribed burns, they may increase browse pressure on regenerating aspen stems. Elk browse can stunt aspen regeneration, potentially negating any positive effects of fire on aspen [Romme et al., 1995, Kaye et al., 2005, Kauffman et al., 2010]. Although we did not explicitly consider browse pressure in this study, we did not observe extensive effects of herbivory on aspen regeneration. It is possible that the large extent of the Hayman fire mediated any browse pressure on regenerating stems. Managers focused on reviving ecosystem health and vigor after high-severity disturbance may instead focus on other treatments to conserve aspen at steep, mid-elevation sites that will support aspen growth into the future instead of low elevation sites in which aspen will be lost [Worrall et al., 2013] as a result of climate change [Breshears et al., 2005].

Our study suggests that aspen will not be lost from western landscapes as a result of climate change. While aspen may be lost at low elevations as a result of climate change, wildfire and topography are creating new opportunities for aspen regeneration at mid-elevation sites. Future studies should monitor changes in the optimal topographic positions for aspen regeneration over time as warming and drying trends continue. This work should also examine relationships between aspen, wildfire, and topography in other post-wildfire landscapes throughout the mountain west.

It is also important to understand how topography mediates trends in types of aspen regeneration; future studies should assess whether regeneration is a result of suckers or seedling establishment.

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Appendix: Distance to Post-Fire Seed Source

Table 1. Distance from each sampling location to post-fire live forest in meters.

Plot number	Quaking aspen (m)	Douglas-fir (m)	Ponderosa pine (m)
0	268.678	111.899	361.381
1	290.379	122.376	697.942
2	659.824	502.907	579.585
3	994.297	617.740	509.574
4	533.974	396.398	715.206
5	663.068	145.083	1385.558
6	387.918	467.695	677.118
7	623.408	532.854	773.600
8	210.114	23.553	560.813
9	489.538	314.578	743.707
10	759.558	572.496	489.001
11	789.143	621.329	444.600
12	872.986	265.640	1061.055
13	408.814	335.497	696.994
14	675.399	238.157	1133.566
15	327.141	136.646	427.733
16	323.131	479.361	605.722
17	111.056	120.837	654.943
18	1059.588	1088.118	1081.496
19	719.340	220.445	1036.734
20	852.332	397.496	982.922
21	980.387	242.866	1173.509

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Table 1 – continued from previous page

Plot number	Quaking aspen (m)	Douglas-fir (m)	Ponderosa pine (m)
22	32.347	183.223	1278.273
23	168.747	188.982	1268.849
24	490.966	305.865	1621.083
25	517.826	339.897	1501.517
26	585.932	115.478	1809.557
27	521.420	1161.347	1251.317
28	25.035	242.712	1297.986
29	305.571	444.724	994.173
30	209.729	324.461	1132.998
31	450.526	236.521	1743.512
32	1477.553	233.209	307.169
33	859.270	315.094	974.435
34	1402.721	84.348	429.918
35	406.430	98.243	1227.765
36	308.905	72.035	506.640
37	494.995	153.083	793.879
38	63.795	78.876	104.530
39	53.038	58.861	62.576
40	90.195	68.502	123.805
41	81.713	98.637	146.990
42	527.339	687.662	1119.244
43	822.152	375.157	1010.785
44	797.959	450.427	103.338
45	680.612	569.732	1158.655

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Table 1 – continued from previous page

Plot number	Quaking aspen (m)	Douglas-fir (m)	Ponderosa pine (m)
46	339.703	171.122	34.579
47	82.774	201.643	242.784
48	171.380	154.030	336.056
49	41.240	38.143	814.444
50	102.143	250.863	177.254
51	99.152	190.304	239.597
52	217.389	283.472	85.693
53	192.343	188.173	256.897
54	536.067	297.380	1245.555
55	103.784	639.662	870.114
56	330.092	558.800	943.115
57	876.014	314.691	381.467
58	139.845	81.260	631.896
59	284.163	193.566	11.156
60	159.730	318.507	85.145
61	134.182	31.432	625.026
62	0	416.580	473.047
63	226.900	327.506	1110.674
64	472.742	200.958	622.227
65	19.411	42.991	921.032
66	88.394	122.030	194.851
67	252.537	147.533	714.422
68	443.083	376.295	251.248
69	1520.686	102.715	332.209

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Table 1 – continued from previous page

Plot number	Quaking aspen (m)	Douglas-fir (m)	Ponderosa pine (m)
70	497.853	441.618	407.883
71	785.419	311.035	476.556
72	298.877	488.329	508.965
73	193.816	70.735	99.127
74	606.339	195.189	73.905
75	1116.553	94.458	802.371
76	1080.062	440.535	1264.400
77	585.749	843.671	1300.156
78	917.501	32.578	462.194
79	1001.189	56.032	569.969
80	324.141	91.396	337.018
81	70.926	289.591	750.406
82	136.588	138.139	209.600
83	129.412	323.173	113.550
84	20.240	118.823	267.134
85	159.616	325.804	84.512
86	556.431	861.103	824.552
87	286.457	633.559	857.641
88	484.689	798.574	1210.960
89	978.466	597.847	718.746
90	183.511	99.480	325.683
91	124.147	173.656	320.315
92	307.987	35.889	442.586
93	213.359	3.819	434.054

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Plot number	Quaking aspen (m)	Douglas-fir (m)	Ponderosa pine (m)
94	291.661	492.242	886.068
95	378.994	179.133	245.033
96	230.578	638.579	688.528
97	399.054	531.110	1199.693
98	611.625	543.107	1323.032
99	697.327	516.754	615.184
100	636.996	449.571	489.530
101	608.703	419.790	460.553
102	231.125	0	330.050
103	456.484	154.264	114.478
104	186.717	22.726	823.084
105	1994.074	104.755	0.643
106	692.710	483.042	376.541
107	223.837	257.798	231.908
108	155.752	8.057	891.222
109	986.139	15.183	413.782
110	241.675	0	300.858
111	570.930	362.936	437.423
112	62.826	291.564	154.477
113	50.808	261.329	128.206
114	34.613	290.529	170.476
115	59.525	108.460	446.621
116	233.380	587.980	897.007
117	566.044	590.416	425.473

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Plot number	Quaking aspen (m)	Douglas-fir (m)	Ponderosa pine (m)
118	1817.444	39.854	98.835
119	516.405	418.114	514.467
120	327.252	59.745	412.805
121	261.741	17.703	434.800
122	146.815	52.233	356.726
123	242.331	143.003	271.159
124	173.347	136.452	22.286
125	230.146	108.769	0
126	433.151	17.974	54.582
127	455.393	336.624	434.040
128	828.898	205.002	1223.208
129	295.951	75.073	146.113
130	307.904	234.129	883.586
131	250.221	247.095	509.786
132	246.865	129.135	597.072
133	568.821	364.648	913.160
134	174.499	203.520	747.123
135	100.965	400.305	930.043
136	293.465	151.565	728.501
137	599.209	218.456	1111.881
138	372.223	224.510	779.853
139	424.495	121.076	884.612
140	537.139	302.091	1066.978
141	622.045	523.703	789.117

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Plot number	Quaking aspen (m)	Douglas-fir (m)	Ponderosa pine (m)
142	474.376	202.638	1094.639
143	805.154	502.985	788.650
144	148.060	6.764	419.085
145	176.593	184.392	669.118
146	176.569	72.752	187.384
147	100.805	0	265.637
148	264.790	127.787	450.679
149	376.166	459.485	676.333
150	127.956	109.654	519.757
151	767.221	0	1357.089
152	247.860	116.588	485.465
153	303.579	106.122	818.860
154	344.805	888.079	326.040
155	193.750	805.624	199.146