DISSERTATION

CAUSES, CONSEQUENCES, AND MANAGEMENT OF TREE SPATIAL PATTERNS IN FIRE-FREQUENT FORESTS

Submitted by
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ABSTRACT

CAUSES, CONSEQUENCES, AND MANAGEMENT OF TREE SPATIAL PATTERNS IN FIRE-FREQUENT FORESTS

Increasingly, restoration treatments are being implemented to dually meet wildland fire hazard reduction alongside ecological objectives. Restoration treatments however deviate from conventional fuels treatments by emphasizing the re-creation of forest structure present prior to EuroAmerican settlement, notably the retention of single and grouped trees interspersed between canopy openings. As these historical forests persisted over cycles of fire returns, it is assumed that restoring these historical complex tree spatial patterns will, in turn, restore historical ecological processes. This includes more benign fire behavior that results in only partial tree mortality, allowing persistent and partial retention of forest cover over cycles of fire return. The qualitative description of historical forest structure, lacks, however, a clear process-based explanation detailing the interactions of heterogeneous forest structures and fire. While fires were historically frequent, it is unclear what role fire played in the genesis and maintenance of tree spatial patterns. If models of tree spatial dynamics can be improved and the interactions between tree spatial patterns and fire can be elucidated, forest managers will have an improved understanding of the implications of restoration-based fuels hazard reduction treatments both during fire-free periods and during fire events.

The aims of this dissertation were to: 1) explore the causes of tree spatial patterns in dry fire-frequent forests; 2) investigate the consequences of tree spatial patterns on potential fire behavior and effects; 3) determine how alternate silvicultural strategies targeted at manipulation of tree spatial patterns can influence fire behavior and effects. In Chapter 2, I explored spatial patterns of tree regeneration over 44 years in absence of fire. In cooler periods, regeneration preferred clustering in openings, including openings following overstory mortality and away from overstory trees. Mortality risk of regeneration was heightened nearer overstory trees. In warmer periods, these trends reversed, likely because of a 'nurse effect' from the overstory. In anticipation of climate change, these results suggest silviculturists may benefit by capturing regeneration mortality in within openings while keeping regeneration near the overstory. In Chapter 3, I found that regenerating trees also form heterogeneous patterns following stand-replacing fires. In these sparse, early seral forests, all species were spatially aggregated, partly attributable to the influence of topography and beneficial interspecific attractions between ponderosa pine and other species. Results from this study suggest that scale-dependent, and often facilitatory, rather than competitive, processes act on regenerating trees. In Chapter 4, I studied the interaction between fire and tree spatial patterns, both historically and in modern forests. Tree mortality in the historical period was clustered and density-dependent because tree mortality was greater among small trees, which tended to be assembled in tightly spaced clusters. Tree mortality in the contemporary period was widespread, except for dispersed large trees, because most trees were a part of large, interconnected tree groups. Postfire tree patterns in the historical period, unlike the contemporary period, were within the historical range of variability found for the western United States. This divergence suggests that decades of forest dynamics without significant disturbances have altered the historical means of pyric pattern maintenance. In

Chapter 5, I examined how fuels treatment designs with different manipulations of tree spatial patterns may influence treatment effectiveness. I simulated fires on hypothetical cuttings which manipulated the arrangement of crown fuels horizontally and vertically, either increasing the distance between tree crowns or not, and either removing small trees or not. All cutting methods reduced fire behavior and severity, but the results confirm possible tradeoffs between ecological restoration and hazard reduction; treatments that separated tree crowns reduced severity the most because these treatments reduced crown fire spread. But these can easily be overcome where restoration treatments incorporate small tree removal, because this action limits crown fire initiation. Managers could also incorporate managed fires to reduce surface fuel loads and use more aggressive cuttings to further gains in hazard reduction, regardless of cutting method used.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1 – INTRODUCTION

1.1 Problem Statement and Framing

Dry forests in the western US are increasingly impacted from severe fires due to anthropogenic climate change and fuels accretion from over a century of fire suppression (Westerling 2006; Fule et al. 2014). Prior to EuroAmerican settlement, fires in these forests were frequent, occurring once every few to 35 years on average; fire severities were low to moderate, killing only a portion of the forest canopy (Covington and Moore 1994). However, land management practices including fire suppression, grazing, timber production, and development of human infrastructure since the late 19th Century have led to altered fire regimes. Contemporary forests now have greater tree densities relative to the pre-settlement era, including a greater proportion of shade-tolerant, fire-sensitive species (Battaglia et al. 2018). This is compounded by impacts of warmer, drier conditions associated with climate change including longer fire seasons (Westerling 2006) and higher frequencies of droughty fuel conditions when ignitions can occur (Richardson et al. 2022). Consequently, when fires now occur, landscapes are increasingly impacted by large 'mega fires' with large patches of high severity fire effects (Fornwalt et al. 2016). Such historically uncharacteristic mega fires are resulting in undesirable ecological and social effects (Schoennagel et al. 2017). This includes large patches of tree mortality, in which forests may not recover in a timely manner, potential for mass erosion, reduced air quality, and threats to life and property (Rhoades et al. 2011; Schoennagel et al. 2017; Stevens-Rumann and Morgan 2019). Fuels hazard reduction treatments (fuels treatments), silvicultural entries focused on reducing surface and canopy fuels (Agee and Skinner 2005), are one critical management practice to mitigate these undesirable outcomes (Fulé et al. 2012; Kalies and Yocom Kent 2016).

Ecological restoration treatments build upon the principles of fuels reduction, by incorporating historical characteristics of pre-settlement dry forests (Churchill et al. 2013b; Stephens et al. 2021). Like conventional fuels treatments, restoration treatments reduce surface and canopy fuel loads and favor fire-resistant species such as *Pinus ponderosa* (Dougl. ex Laws.). Restoration treatments however also aim to create or maintain heterogeneous forest structures analogous to these forests' pre-settlement conditions. Historically, these forests were relatively open, containing a mixture of canopy gaps and meadows (Lydersen et al. 2013; Matonis and Binkley 2018). Except for a few larger and older isolated trees, most trees were arranged in small groups numbering from 2 to 20 trees (Clyatt et al. 2016). By recreating these heterogeneous arrangements of forest structure which were once present, forest managers aim to incorporate many ecological objectives (Reynolds et al. 2013a; Stephens et al. 2021); fire hazard reduction is generally seen as also an achievable objective based on the reasoning that these dry forests endured through intervals of fire return (Larson and Churchill 2012; Hessburg et al. 2015; Stephens et al. 2021).

The scientific basis for this heuristic—long-term persistence of historical dry forests is evidence that heterogeneous tree spatial patterns are a critical strategy to restore resilience to fire—however, is under studied. It is believed that heterogeneous forest structures fostered lower fire severities, and these lower fire severities promoted heterogeneous forest structures through partial tree mortality, forming a feedback loop (Larson and Churchill 2012; Addington et al. 2018). However, an understanding of how spatial arrangements of forest structure interact with fire behavior is still immature given the fire environment is complex, consisting of spatiotemporally dynamic fire-fuel-atmosphere interactions (Larson and Churchill 2012; Parsons et al. 2017). Secondly, empirical studies on the genesis and maintenance of complex forest structures (e.g., Fulé and Covington 1998; Yu et al. 2009) are limited (Donato et al. 2012; Larson and Churchill 2012). A complete conceptual model of how complex forest structures in dry forests develop and persist through fire is needed to inform the development of silvicultural prescriptions which seek to restore complex forest structures while meeting fire hazard reduction goals.

The goals of this dissertation are to: 1) explore the causes of tree spatial patterns in dry fire-frequent forests; 2) investigate the consequences of tree spatial patterns on potential fire behavior and effects; 3) determine how alternate silvicultural strategies targeted at manipulation of tree spatial patterns can influence fire behavior and effects. To address these goals, this dissertation uses spatial pattern recognition and process modelling. Spatial patterns indicate the consequences of how underlying processes, such as fire, shape forest structure (Stoyan and Penttinen 2000). Process-based physical fire modelling, which can explicitly represent the fire environment at fine scales, is useful for investigating how fire behavior responds to within-stand variations in forest structure (e.g., Parsons et al. 2017). The combination of pattern recognition and process modelling is especially applicable for developing conceptual models of fire-mediated spatial forest dynamics (Lutz et al. 2018).

1.2 Background

The consensus view that fires mediated the formation and maintenance of tree patterns in dry forests has developed since the mid-20th Century. In the early 20th Century, it was originally suggested that frequent (return intervals <35 yr.) recurrences of low and mixed-severity fires successively eroded the forest canopy (Lieberg 1902; Pearson 1950). Later research revealed however that frequent fires consumed some trees as well as surface fuels, lowering the risk of fire-caused mortality after successive fires (Pearson 1950; Weaver 1951). As a consequence, frequent fires regulated forest structure, reducing the potential of stand-replacing fires and retaining a mixture of age cohorts (Cooper 1961; Harrington and Sackett 1990). Reconstructions of historical forest structures have led researchers to hypothesize that these fires yielded heterogeneous, uneven-aged forest structures through periodic tree mortality, stimulated fire-adapted understory plants, and created temporally and spatially variable conditions for tree regeneration (Show and Kotok 1924; Larson and Churchill 2012; Knapp et al. 2013). If this hypothesis is supported, fires were a key component in regulating the complex mosaics of scattered individual trees, groups of trees, and canopy openings occupied by understory plants or regenerating trees (Larson and Churchill 2012) (Figure 1).

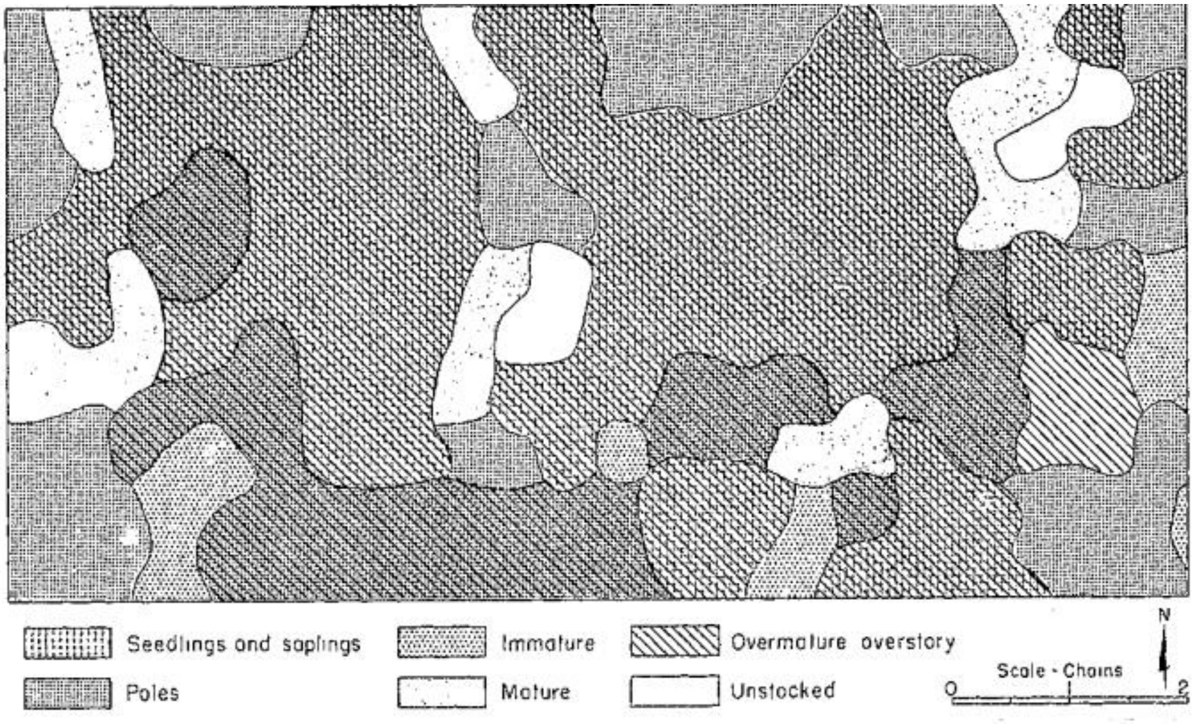

Figure 1.1 Historical map of forest structure diversity

Spatial distribution of within-stand structural stocking stages at the Black Mountain Experimental Forest, CA. Reprinted from Hallin (1959).

There are, however, opposing means by which fires may have impacted tree spatial patterns. Recent syntheses suggest patterns of fire-caused mortality is density-dependent (Larson and Churchill 2012; Hood et al. 2018; Lutz et al. 2018). High stocking within tree groups could permit tree-to-tree fire spread (Stephens et al. 2021); in addition, woody debris and needlecast accumulate underneath tree groups (Banwell et al. 2013; Banwell and Varner 2014). This may lead towards greater intensity and greater severity within groups than in sparser areas (Larson and Churchill 2012). Alternatively, fire-caused mortality may have been greater outside of tree groups. Susceptibility to damage by fire is greater among young and smaller trees (Sieg et al. 2006). Some researchers have observed that these smaller, susceptible trees prefer to establish in meadows rather than within tree groups (Boyden et al. 2005; Sánchez et al. 2009; Fry et al. 2014). Additionally, openings were often "unsafe" sites (Larson and Churchill 2012; Reynolds et al. 2013b) because openings contained greater cover of understory vegetation available for fire consumption (Matonis and Binkley 2018). This included grass-dominated fuelbeds in meadows (Cooper 1961; White 1985; Stephens and Fry 2005; Sánchez Meador et al. 2010), as well as drier and windier conditions, both of which may exacerbate fire behavior near these younger and smaller trees (Bigelow and North 2012).

Those interactions of tree spatial patterns and fire behavior and effects may now be significantly altered in contemporary forests. Fire suppression, in addition to livestock grazing and logging, led to infilling of forest structure at scales from tree neighborhoods (Figure 1.2; Sánchez et al. 2009; Lydersen et al. 2013) to landscapes (Hessburg et al. 2015; Matonis and Binkley 2018). Canopy fuel is now more continuous due to higher tree densities, leading to great potential of crown fire initiation and spread (Hessburg et al. 2005; Reynolds et al. 2013b; Brown et al. 2015). Without canopy gaps to interrupt the spread of crown fires, the resulting continuity in the forest canopy may lead to widespread canopy mortality. Consequently, the residual forest structure after fire may lack the heterogeneous arrangements of tree groups and openings.

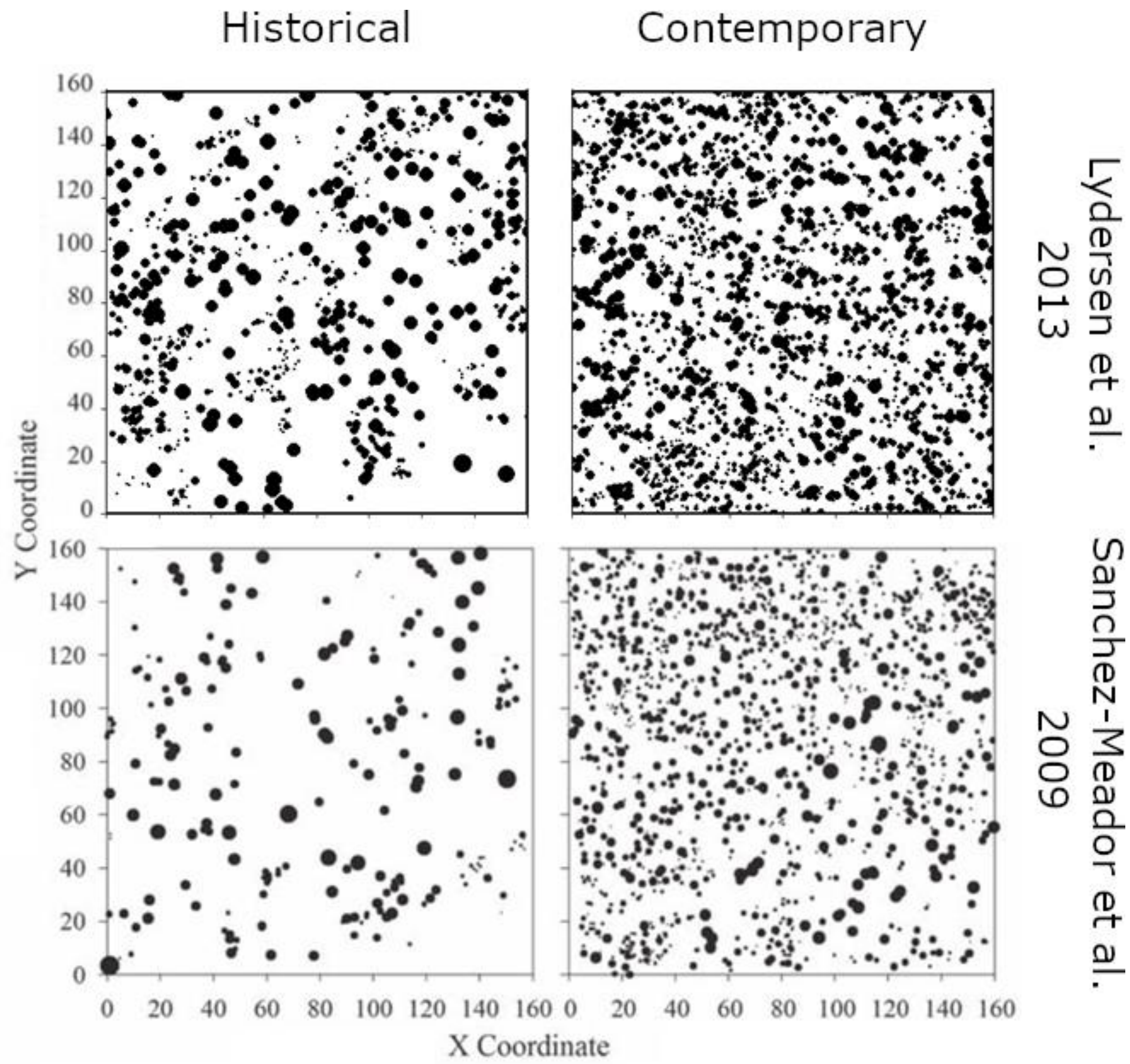

Figure 1.2. Change in forest structure over the past century

Stem-maps of trees from two studies in a Californian mixed-conifer forest (Lydersen et al. 2013) and an Arizonan ponderosa pine forest (Sanchez-Meador et al. 2009) reveal the heterogeneous distribution of trees in the early 20th Century (left), while trees have formed contiguous canopies by the early 21st Century (right). Points, scaled by their diameter at breast height, represent individual tree locations.

Spatially heterogeneous restoration treatments are suggested to restore the historically characteristic relationships between forest structure and process (Larson et al. 2012; Tuten et al. 2015; Addington et al. 2018), but structurally-homogenizing treatments continue to be implemented (Underhill et al. 2014), based on aspatial fire hazard reduction principles (Agee and Skinner 2005). Even within treatments designed to increase structural heterogeneity, silvicultural specifications often implement spacing-based targets within tree groups (Tuten et al. 2015). Further understanding of structure-fire interactions in historic forests and in contemporary forests can aid in evaluating effectiveness of alternative, differing silvicultural approaches (Knapp et al. 2017; Lutz et al. 2018).

CHAPTER 2 – CLIMATE IMPACTS THE TREE INTERACTIONS SHAPING PATTERNS OF TREE REGENERATION

2.1 Introduction

Tree spatial patterns are increasingly recognized as an important attribute of forest ecosystems. The spatial patterns of trees shape abiotic and biotic interactions, impacting processes such as competition (Kuehne et al., 2015; Suzuki et al., 2008), facilitation (Ziegler et al., 2017), recruitment (Fajardo et al., 2006; Kuehne et al., 2015; Moeur, 1993), mortality (Das et al., 2011; Kuehne et al., 2015; Suzuki et al., 2008), and functions such as hydrologic regulation (Schneider et al., 2019), habitat provisioning (Knapp et al., 2013; Zagidullina and Tikhodeyeva, 2006), productivity (Schall et al., 2018), soil dynamics (Abella et al., 2013), nutrient cycling (Yankelevich et al., 2006), light availability (Cannon et al., 2019). Tree spatial patterns also affect the severity and distribution of disturbance effects from fire, pests, or pathogens (Bače et al., 2015; Churchill et al., 2013; Malone et al., 2018; Wild et al., 2014; Yu et al., 2009; Ziegler et al., 2020). These processes and effects post disturbance in turn shape future spatial distributions of structure, feeding back to form a complex adaptive system (Puettmann, 2011).

Recognizing forests as complex adaptive systems, policy makers, stakeholders, and the public are increasingly advocating for managed complexity throughout forest ecosystems across the globe, spurred by objectives such as ‘naturalness’, forest restoration, and biodiversity (Brumelis et al., 2011; Fahey et al., 2018; Hessburg et al., 2016; McElhinny et al., 2005; Puettmann, 2011; Schall et al., 2018). Complex forest structures may provide greater resilience to the uncertainty associated with global change (Fahey et al., 2018; Larson and Churchill, 2012; Puettmann, 2011; Puettmann et al., 2015). However, informational limits hinder the implementation of complexity-oriented forest management (Puettmann et al., 2015). In particular, the factors influencing establishment of heterogeneous forest structure has been a key limitation (Bugmann, 2001; Herben and Hara, 2003).

One region where more information is needed to foster complex forest structures is within dry coniferous forests of the western United States. In these systems, there is considerable interest in developing uneven-aged silvicultural systems that promote or restore historically-characteristic, fine-scale heterogeneity (Churchill et al., 2013; Fajardo et al., 2006; Knapp et al., 2017; Kuehne et al., 2015; Larson and Churchill, 2012). As uneven-aged, complexity-oriented silviculture needs to foster tree recruitment, it is necessary to understand regeneration preferences (Fajardo et al., 2006).

Regeneration of ponderosa pine (Pinus ponderosa Dougl. ex Laws.), like many other tree species (Herben and Hara, 2003), exhibits initial spatial patterns of aggregation (Larson and Churchill, 2012). Aggregation emerges primarily from selective filtering for the most ideal locations for germination, establishment, and survival (Pielou, 1960; Ziegler et al., 2017), and secondarily due to seed caching (Vander Wall, 2003). In grassy openings where competition for moisture with understory vegetation is intense, tree regeneration favors establishing under overstory canopies (Abella et al., 2013; Ehle and Baker, 2003). Overstory trees are suggested to also function as nurse trees, by ameliorating droughty conditions and redirecting precipitation (Fajardo et al., 2006; Haase, 2001). Owing to their size, larger overstory trees are more ameliorative relative to intermediately sized trees (Fajardo et al., 2006). Conversely, regeneration can be more prolific in openings where grass is not competitive, suggesting competition from the overstory canopy can deter successful establishment (Malone et al., 2018; Moeur, 1993; Sánchez et al., 2009). Gaps created from recent overstory tree mortality also provide spatial niches for regeneration. Recently formed gaps supply mineral soil, lower understory competition, and better nutrient conditions (Abella et al., 2013; Wild et al., 2014), especially for shade-intolerant species such as ponderosa pine (York et al., 2007). On the other hand, Das et al., (2011) identified that gap creation occurs in locations where stocking is most dense and competition highest; this may inhibit regeneration. After establishment, mortality further shapes tree spatial patterns. In general, clusters of tree regeneration trend towards uniformity via self-thinning (Boyden et al., 2005; Larson and Churchill, 2012; Pielou, 1960). But mortality via competition with the overstory may be more prevalent where conditions lead to establishment near the overstory rather than regeneration clusters (Larson and Churchill, 2012; Lutz et al., 2014). Consequently, the likelihood of regeneration establishment and mortality near large trees or within newly formed tree gaps is likely dependent on competitive pressure from the overstory.

As variability in precipitation and temperature impact the suitability for tree regeneration (Petrie et al., 2016), the relationships among regenerating trees and between regenerating trees and overstory trees may additionally depend on climatic conditions. Per the stress gradient hypothesis, the strength of biotic facilitative interactions increases as the abiotic support for regeneration decrease (Maestre et al., 2009). Recent comparisons of tree spatial patterns across sites with different climates provide some evidence. For example, Rodman et al., (2017) observed that ponderosa pine trees, across all sizes, display greater spatial aggregation under harsher climates, and Fajardo et al., (2006) found that ponderosa pine regeneration tend to occur in proximity to overstory trees within more xeric sites. If the overstory proximity is a predominant driver of tree regeneration suitability, it is surmisable that the areas of suitable microclimate for establishment and survival of tree regeneration shift with climatic conditions.

In this study, I assessed the spatial dynamics of ponderosa pine establishment and mortality over a period of 44 years in the Front Range of Colorado, USA. To infer which biotic interactions influenced the spatial patterning of tree regeneration, I divided the spatial analysis into multiple procedures performed at each measurement period. I first measured the spatial patterning of tree regeneration during each period. Next, I measured the spatial correlations of tree regeneration with smaller and larger living overstory trees, and recently dead trees. I also measured the spatial correlation of tree regeneration with suppressed trees, as these trees may indicate locations of intense competition from the overstory. I then assessed patterns of regeneration mortality with spatial analyses to measure whether self-thinning was occurring within regeneration, and whether mortality was heightened near small and large trees. Finally, I explored whether these regeneration spatial patterns, indicative of biotic interactions, can be suggested to have been modulated by climatic conditions. Specifically, I evaluated whether the variation in the strength of spatial patterns over time was correlated with changes in climate over the 44 years.

2.2 Materials and Methods

2.2.1 Study Site

This study uses six measurements (1974, 1983, 1991, 2001, 2010, and 2018) of a 9.3 ha square plot on the Manitou Experimental Forest within the Pike National Forest of the Colorado Front Range. The site is 40 km northwest of Colorado Springs, CO at an elevation of c. 2500 m and is situated on a southeast-facing aspect with slopes under 5%. Over the past thirty years, precipitation averaged 57.1 cm with most precipitation occurring as rain in May through August; average daily temperatures ranged from a low of -3.9 °C in January to 17.3 °C in July (PRISM Climate Group, 2011).

Ponderosa pine comprises 99.2% of all tree species. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), and blue spruce (*Picea pungens* Engelm.) were infrequently present. The following site history and biophysical description, previously reported by Boyden et al. (2005), follows. The understory includes perennial grasses (Arizona fescue [*Festuca arizonica* Vasey*],* mountain muhly [*Muhlenbergia montana* (Nutt.) Hitchc.]), various forbs, and a minor shrub (common juniper [*Juniperus communis* L.]) component. Soils are classified as the Boyett-Frenchcreek complex typified as well-drained, originating from granite and arkosic sandstone, and having a shallow (2.5 cm) O stratum and gravelly, sandy loam texture. Extensive commercial logging within the region occurring c. 1880 removed an estimated 15% of overstory stocking at the time. No further logging operations nor fires have occurred since, however a mountain pine beetle (*Dendroctonus ponderosae*) outbreak occurred in the early 1980s leading to the death of ~8% of the overstory trees. By 1974, the distribution of overstory tree ages in this site was bimodal, centered about 70 and 170 years of age at breast height.

2.2.2 Site Inventory

During the original measurement period of 1974, all trees at least 1.37 m tall were mapped using a Cartesian coordinate system, tagged, measured for diameter at breast height (DBH), and aged to pith at 1.37 m height. In the subsequent periods from 1983 to 2018, all tagged trees were remeasured for DBH and, from 1991—2018, ingrowing trees at least 1.37 m tall were mapped, tagged, and measured for DBH. Ingrowth was not measured in 1983, requiring us to estimate which of the ingrowth measured in 1991 could have been counted in 1983. I assumed that ingrowth with at least 2.0 cm DBH would have been measured in 1983; this cutoff corresponded with the 75th percentile of DBH for ingrowing trees measured over 2001—2018. Further, I estimated that trees measured in 1974 below 2.0 cm DBH comprised ingrowth occurring between ~1969 to 1974, allowing us to analyze patterns of ingrowth of this measurement period.

For analyses, trees were classified as: small overstory, large overstory, suppressed, dead, regeneration, ingrowth. First, trees which had been established (i.e., > 2.0 cm DBH) in 1974 were designated as either small or large trees using a breakpoint of 20 cm DBH. This cutoff separated trees preceding the harvest in the 19th Century (averaging 170 years at DBH) and those establishing shortly thereafter (averaging 70 years at DBH). These small and large trees were additionally classed as suppressed if their percent annualized basal area increment had been within the lowest quartile of all trees, during that measurement period. If a small or large tree died during an observation period, I reclassified that tree as a snag (standing dead tree). Newly observed trees were designated as tree regeneration *just* for the measurement period of initial observation. Afterwards, these trees were classified as ingrowth having grown in over the course of the study.

2.2.3.2 Point Pattern Analyses

To understand the multiple facets of biotic interactions among ingrowth and overstory trees, I split spatial analysis into several specific tests of observed patterning against null point process models (Table 2.1). These tests examine facets of regeneration locations among themselves and with other components of stand structure. I use the term *pattern* specifically to refer to the average spatial correlation between trees relative to the spatial correlation generated from a null model which assumes spatial randomness or spatial independence.

First, I assessed how regeneration locations were patterned in each measurement period (A1). Using a univariate pair correlation function $g(r)$, this function uses an annulus of a given width, 1 m in this study, to count the number of regenerating trees within distance *r* of the average regenerating tree, normalized by the count if points (tree locations) had been distributed under complete spatial randomness (CSR) (Wiegand and Moloney 2013). When values of the empirical function deviate above CSR, tree patterns indicate aggregation; deviations below CSR indicate uniformity. Point pattern analyses use a Monte Carlo approach for hypothesis testing; here, the null model to represent the expected pair correlation function of regeneration, $g_{regen}(r)$, was an inhomogeneous Poisson process which randomly distributed points using a coarse spatial field of expected intensity (points m^{-2}). I parameterized intensity by smoothing over the observed intensity of regeneration locations using an Epanechnikov smoothing kernel at a bandwidth of 15 m and resolution of 1 m^2. I chose an inhomogeneous Poisson process to account for coarse-scale gradients of tree locations in the observed data (Wiegand and Moloney, 2014).

Table 2.1 Hypotheses framework

Analyses used to evaluate spatial interactions, and influence of climate, among regenerating and ingrowth trees; see text for details on analyses.

Analysis	Null hypothesis	Method and spatial null model
A1) Were regeneration randomly located?	Spatial randomness	g(r) with a heterogeneous Poisson process
A2) Were regeneration attracted to prior ingrowth?	Independence between patterns	$g_{1,2}(r)$ with toroidal shift
A3) Were regeneration associated with small or large trees?	Independence between patterns	$g_{1,2}(r)$ with toroidal shift
A4) Were regeneration associated with suppressed or dead trees?	Independence between patterns	$g_{1,2}(r)$ with toroidal shift
A5) Is ingrowth mortality sensitive to intra-class density?	Random mortality of ingrowth	$g_{1,1+2}(r) - g_{2,1+2}(r)$ with bivariate random labelling
A6) Is ingrowth mortality associated with small or large tree proximity?	Random mortality of ingrowth	$c_{1,2}(r)$ with trivariate random labelling
A7) Do patterns display synchronicity?	Lack of cross-correlation	Correlation analysis
A8) Do patterns vary with climate?	Insignificant effect of climate	Distributed lag regression

The second set of spatial analyses refer to hypotheses regarding the locations of regenerating trees relative to other trees. I use a bivariate pair correlation function, $g_{1,2}(r)$ to answer A2—A4.

This function describes whether type 2 points are more or less numerous around type 1 points than expected by chance according to a null point process model (Wiegand and Moloney 2013). Specifically, $g_{1,2}(r)$ results in the average density of type 2 points at distance r from type 1 points and is then normalized by the overall intensity of type 2 points, λ_2. The interpretation of the statistic depends on the null model appropriate given the hypothesis (Goreaud and Pelissier 2003). I used a null model of independence between cohorts and each null model simulation randomly shifted type 2 points around a torus. This preserved the spatial structure of both type 1 and type 2 points but separated their joint structure (Wiegand and Moloney 2013). Further, by shifting type 2 points while keeping type 1 points fixed, this null hypothesis is particularly relevant for tests where the type 1 cohort precedes the type 2 cohort (Wiegand and Moloney 2013). I examined the relationship of regeneration around prior ingrowth, $g_{ingrowth,regen}(r)$, small trees, $g_{small,regen}(r)$, large trees, $g_{large,regen}(r)$, suppressed trees, $g_{suppressed,regen}(r)$, and snags, $g_{snags,regen}(r)$. For $g_{snags,regen}(r)$, I related the positions of regenerating trees to locations where trees had died at least two measurement periods prior, c. 18 yr.; this accounted for a lag between the period of overstory tree death and the time it takes for a tree to potential germinate near a snag and then reach 1.37 m in height in order to be observed during a remeasurement period (c. 20—25 yr.; Boyden et al., 2005). Where empirical statistics exceed the Monte Carlo distribution yielded by simulations of the null model at distance r, the interpretation is that regeneration are attracted to the respective type 1 points at distance r, whereas deviations lower than expectation reflect repulsion, and empirical statistics approximating the null model suggest regeneration locations are independent of the type 1 point in question.

Next, I used a bivariate pair correlation function with a different form of hypothesis test to examine whether mortality among ingrowth was spatially random or density dependent (A5).

Here the form was $g_{1,1+2}(r)$-$g_{2,1+2}(r)$ (Yu et al. 2009). This difference examines if there were more surviving or dead ingrowth around dead ingrowth than there were surviving or dead ingrowth around surviving ingrowth, $g_{dead,dead+survive}(r)$-$g_{survive,dead+survive}(r)$ (concisely referred to as $dd_{ingrowth}(r)$). Random labelling is the preferred null model to test a process that affects a set of points subsequently (Goreaud and Pelissier 2003); therefore, each of the Monte Carlo simulations was a random labelling as surviving or dead while keeping the locations of all ingrowth fixed. For this test, positive and negative deviations suggest positive and negative density-dependence respectively, while non-significant deviations indicate risk of mortality is spatially independent of ingrowth density.

Last, I investigated the impact of overstory trees on ingrowth mortality rates (A6). The tests were based on a trivariate form of the mark correlation function, $c_{1,2}(r)$, which averages a test function on marks (i.e., quantitative measurements) of type 1 points separated by a given distance r from a type 2 point (Biganzoli et al. 2009; Wiegand and Moloney 2013). I used a test function, $t = m_1$ which calculated, from a type 2 point (either small or large trees), the mean identity of a type 1 (ingrowth) point's mark, where mark identities were binary, either 1 for dead ingrowth or 0 for surviving ingrowth. Thus, $c_{1,2}(r)$ here represents the mortality rate of ingrowth at distance r from small, $c_{small,ingrowth}(r)$, and large overstory trees, $c_{large,ingrowth}(r)$. A positive, or negative, deviation indicates significantly higher, or lower, mortality rates of ingrowth, respectively, at distance r from overstory trees. In the null model of trivariate random labelling, all locations were fixed as were classifications of either ingrowth or trees of either small or large size class, but the designation of survival or death within ingrowth locations were randomly assigned.

I applied the Diggle-Cressie-Loosmore-Ford Goodness-of-Fit (GoF) test to determine the deviation of empirical statistics against expectations generated from the Monte Carlo procedure using 399 simulations of each null model. Inference testing using this GoF test is a percentile rank of the sum of squared deviations for the empirical correlation function. While the GoF test typically uses the raw statistics from correlation functions, I used a modification of the GoF test developed by Myllymäkia et al. (2015); I first studentized statistics for each empirical and simulated correlation function, *S'i(r)*:

$$S_i'(r) = \frac{S_i(r) - \overline{S(r)}}{\hat{\sigma}_{S(r)}},$$

Equation 2.1

where $S_i(r)$ is an empirical or simulated correlation function, $\overline{S(r)}$ is the mean under the simulated null model, $\hat{\sigma}_{S(r)}$ is the sample standard deviation of $S(r)$. Then I applied the GoF test to calculate the test statistic u_i' (Eq. 2.2):

$$u_i' = \sum_{r=0}^{15} (S_i'(r) - \overline{S'(r)})^2,$$

Equation 2.2

The test statistic is the sum of squared deviations between $S_i'(r)$ and $\overline{S'(r)}$, the mean of the 399 simulated null models, over a range of distance *r*. In this study, I calculated correlation functions over *r* from 0 to 15 m. I then used a non-parametric means to calculate the significance of the test statistic of the empirical ($i = 0$) test statistic, u_0' (Eq. 2.3),

$$\hat{p}_0 = 1 - \frac{rank[u_0'] - 1}{400},$$

Equation 2.3

where $\hat{p}_0$ is the complement of the percent rank of u_0'. The GoF test collapses dimensionality of *r* into a scalar, simplifying hypothesis testing. And, studentization is a standardized measure of effect size (Wiegand and Moloney 2013; Myllymäki et al. 2015; Velázquez et al. 2016). By removing dimensionality and standardizing, u_0' therefore facilitates a simple and scale-accumulated comparison to assess the strength of a pattern (e.g., deviance).

A second advantage of $S_i(r)$ is that these values can be used to construct confidence intervals. Specifically, the minimum 2.5% rank and the maximum 97.5% rank, across all distances r, can be de- studentized back to a linear scale to construct 95th percentile global envelopes of maximal absolute deviation (Wiegand and Moloney 2013; Myllymäki et al. 2015). I plotted the empirical correlation functions against these global envelopes to determine direction of deviance as this information is lost in Eq. 2. I performed all point pattern analyses in Programita (Wiegand and Moloney 2013) using the edge effect correction scheme described by Wiegand and Moloney (2013)

2.4. Climate—Pattern Analysis

I assessed whether pattern deviance from each of the above spatial analyses co-varied with climate across the measurement periods. I accessed climatic data from the Parameter elevation Regression on Independent Slopes Model dataset within a c. 800 m x 800 m area containing the study site geographic location (PRISM Climate Group, 2011); variables included precipitation, minimum temperature, maximum temperature, mean temperature, minimum vapor pressure deficit (VPD), and maximum VPD monthly for the years from 1938—2017. These data were then aggregated as seasonal averages, and then averaged over the years between measurement periods (i.e., summer precipitation associated with the measurement period of 2018 was the average monthly precipitation from June to August, averaged over the years 2010 through 2017). Prior to 1974, climate data were binned in intervals of 9 years, the average timespan between the measurement periods. I then reduced the dimensions using principal component analysis after centering and scaling by standard deviation. Only the first principal component (PC1) was used for subsequent analyses. PC1 explained 57% of the variation in seasonal climate and can be interpreted as a gradient of seasonal, climate harshness. Large positive values in PC1 corresponded to low precipitation, elevated temperature, and vapor pressure deficit across seasons (Table 2.2).

Table 2.2. Principal component climate and season correlations

Correlations between seasonal climate variables and PC1.

Climate variable	Spring	Summer	Fall	Winter
Precipitation	-0.61	-0.90	-0.79	-0.20
Temperature$_{min}$	0.44	0.71	0.82	0.60
Temperature$_{mean}$	0.66	0.85	0.94	0.63
Temperature$_{max}$	0.77	0.85	0.89	0.49
Vapor pressure deficit$_{min}$	0.34	0.58	0.73	0.65
Vapor pressure deficit$_{max}$	0.73	0.90	0.95	0.67

I used a form of linear regression to determine whether climate harshness (PC1) related to the observed regeneration patterns. There was however a lag between tree seedling establishment and observation. Given that environmental conditions at the time of germination and over the subsequent c. 5 years (P. Fornwalt, pers. comm.) are critical years for potential recruitment, it was tenuous to relate the current deviance of ingrowth tree patterns to very recent climate. In other words, the patterns for a given measurement period were more likely related to the climate experienced during trees' germination; this corresponded to a lag of 1 to 3 periods given the frequency of remeasurements of the study site. I thus used a finite distributed-lag model for the pattern deviances of A1—A4. Finite distributed-lag models regress the current value of a response to accumulations of specified lagged values of predictor variables (Davidson et al. 1985). In this study, this distributed-lag regression followed the form:

$$u'_{0,t} = \alpha + \beta_0 PC1_{t-1} + \beta_1 PC1_{t-2} + \beta_2 PC1_{t-3} + e_t, \tag{4}$$

where $u'_{0,t}$ was the deviance of an empirical function at measurement period t, α was the intercept, and β, lag weights for PC1 over lags of *t-1* through *t-3*. Lag weights were estimated using ordinary least squares. For exploratory purposes, I also applied Eq. 4 to predict regeneration density (trees ha^{-1}). For regressions associated with A5 and A6, I used simple, ordinary least squares regression. No attempts to correlate to lagged climate was necessary because these analyses concerned the mortality of ingrowth which had occurred during the current measurement period.

2.3 Results

2.3.1 Stand Development

The continual accrual of trees concomitant with growth of overstory trees led to greater stocking through time. Sizes of overstory trees were initially distributed bimodally with two peaks at approximately 15 cm and 35 cm DBH (Figure 1). This corresponded to the distinction of small from large trees at a 20 cm DBH breakpoint. Over time, the overstory trees increased from an average of 26 cm in 1974 to 32 cm DBH in 2018. Meanwhile, the proliferation of ingrowth over the measurement periods led to a shift in size distribution. Regeneration rates (ratio of newly observed regeneration to overstory trees) averaged 22.5% (± *19.5% s.d.*) over the periods. This produced a transition from a bimodal age structure to a multi-aged structure.

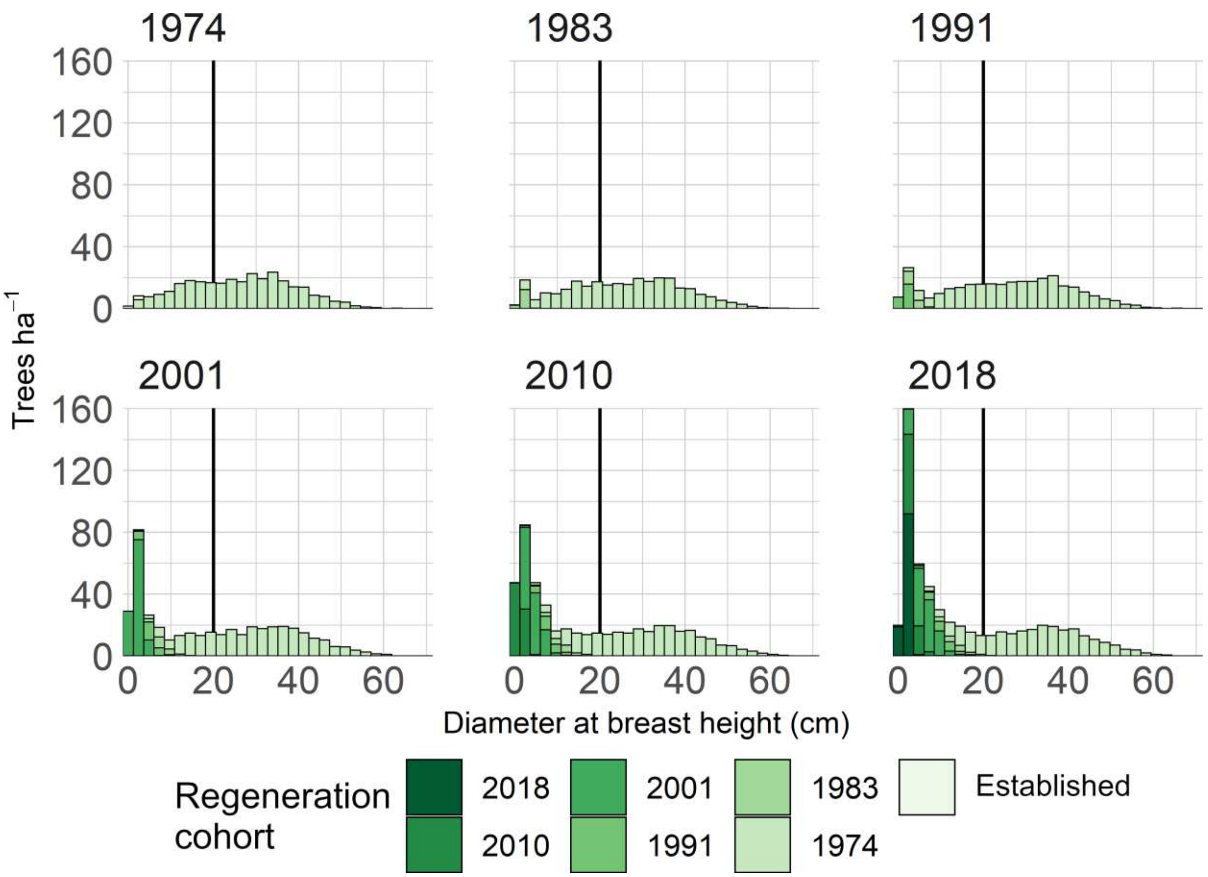

Figure 2.1 Tree size distributions

Change in tree size distribution by regeneration cohort, with a vertical line at 20 cm diameter at breast height separating small from large established trees.

As shown in Figure 2.2, both basal area and trees per hectare increased between each measurement period with a sole exception in 1983, attributable to some beetle-caused overstory mortality. Whereas there were an initial 297 trees ha^{-1} measured and 19.5 m^{2} ha^{-1} of basal area, stocking increased to 586 trees ha^{-1} totaling 24.3 m^{2} ha^{-1} of basal area, with ingrowth accounting for 19% of this change in basal area. By 2018, ingrowth had comprised 56% of all trees, though only 4% of the total basal area.

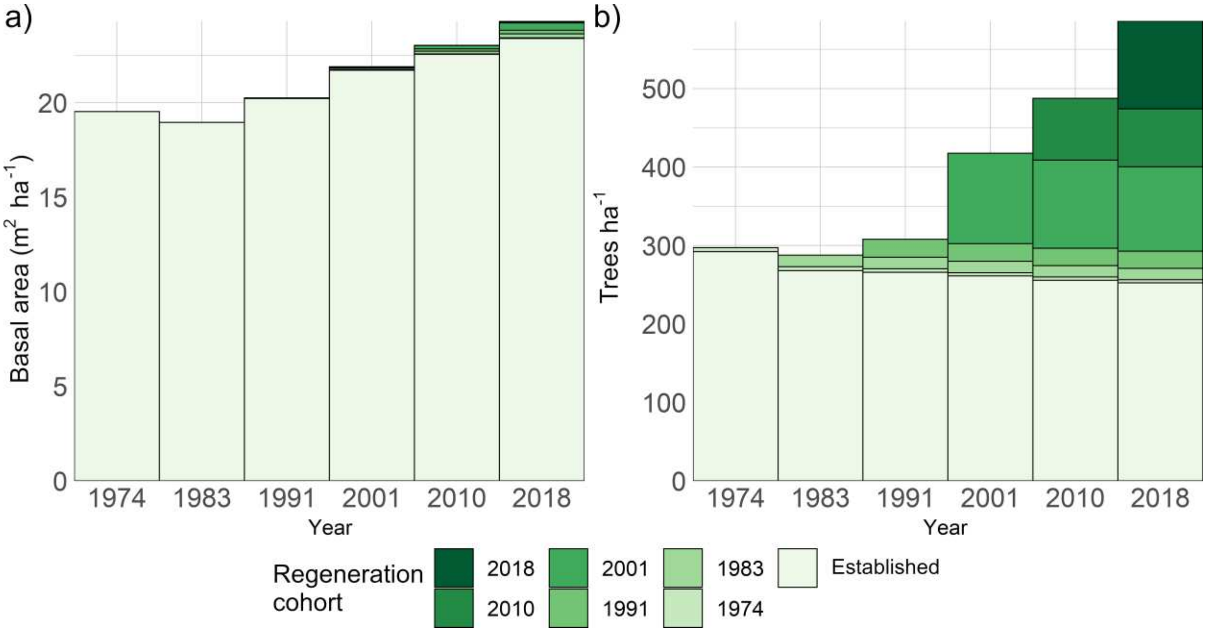

Figure 2.2 Tree density distribution

Change in tree density by a) basal area and b) trees per hectare over measurement periods, by regeneration cohort.

Mortality trends varied between previously established and ingrowth trees. Over the 44 years, 16% of the overstory trees died; the mortality rate (ratio of killed overstory trees to living overstory trees) averaged 1.5% (± 0.5%) over all periods, though was greater (8%) in 1974 due to mountain pine beetles. Ingrowth mortality rates (ratio of living ingrowth to recently dead ingrowth) averaged 2.6% (± 1.3%). Most mortality of ingrowth occurred within just one cohort; 73% of dead ingrowth observed over the duration of the study had both established in the period of 1991—2001 and perished by 2010.

2.3.2 Spatial Stand Structure

Initial data exploration by visual examination of stem-maps showed patchy distributions of overstory trees and clustered locations of spatial regeneration in openings (Figure 2.3). Open space present in the initial inventory in 1974 had largely been filled with successive cohorts of regeneration by 2018, creating a mosaic of trees either present before 1974 or those ingrown trees which had recruited during the study period.

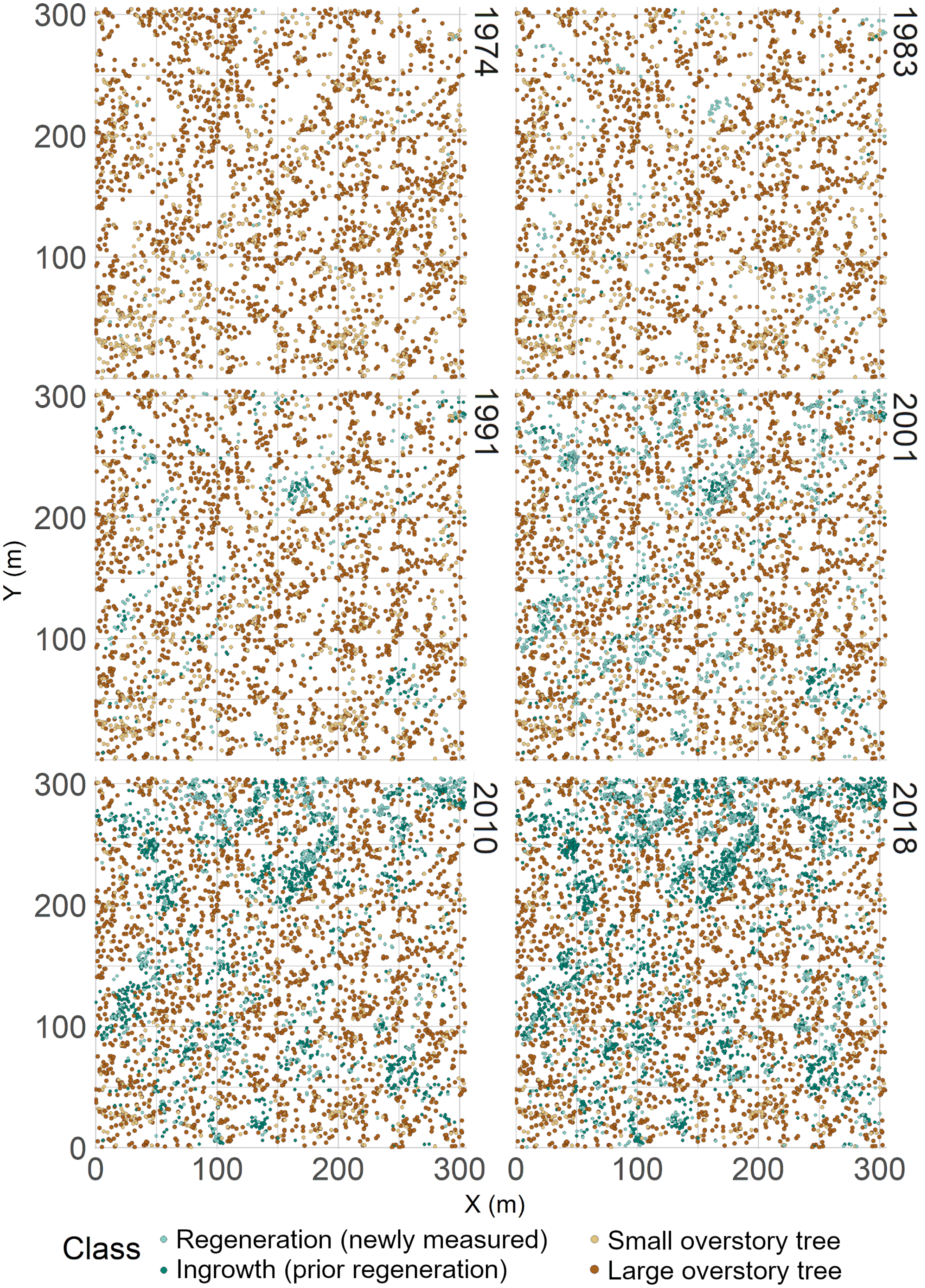

Figure 2.3 Stem-maps by year

Stem-maps of each measurement period including tree locations colored by class, including large (>= 20 cm diameter at breast height), small (< 20 cm diameter at breast height), ingrowth (trees appearing over the duration of the study), and regen (newly measured ingrowth trees).

2.3.3 Spatial Patterns of Tree Regeneration

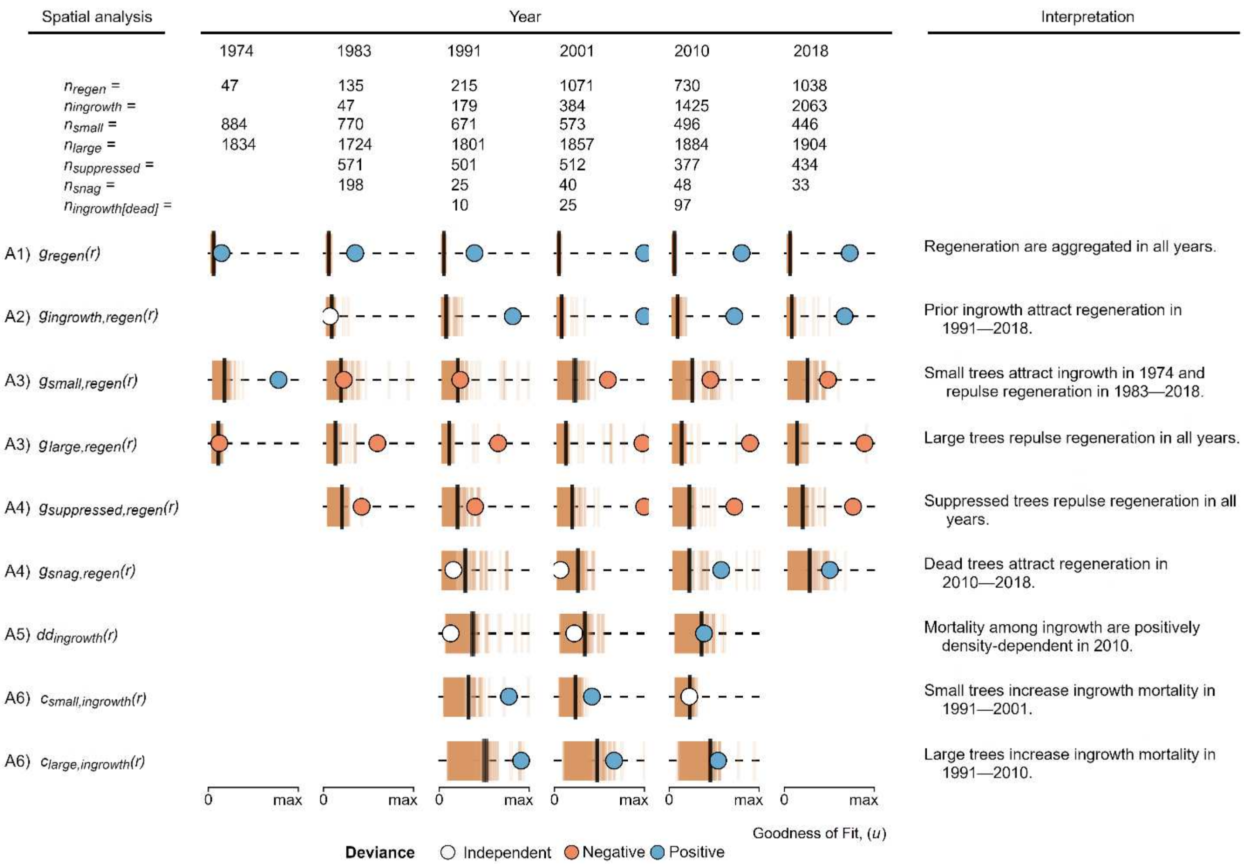

Figure 2.4 Point pattern analyses goodness-of-fit

Goodness of fit (u) for nine empirical point patterns (colored points) to address components of the six hypotheses (rows) in each time period (columns). Salmon-colored lines denote range of simulated null patterns, with the black line indicating the 95th percentile. Significant deviations occur when points are to the right of the black line with greater deviations at higher u values; points are colored to reflect direction of deviance.

Spatial patterns of regeneration locations at scales of 0 to 15 m displayed significantly non-random patterning among most analyses with substantial variation in deviance across observation periods (Figure 2.4). Tree regeneration were aggregated at every period (Analysis A1). In periods from 1991 to 2018, I observed attraction between regeneration and ingrowth (A2). There was significant attraction in the 1983 period between regeneration and ingrowth, yet only at scales < 1 m (Figure 2.5), therefore goodness of fit over the entire range of 0—15 m was insignificant. In all periods, regeneration exhibited repulsion from large trees (A3). Small trees attracted regeneration in 1974 and were repulsive in periods 1983 to 2018 (A3). Regeneration was repulsed from suppressed overstory trees in all periods (A4). Regeneration was independent of snags in periods 1991 and 2001 but attracted to snags in periods 2010 and 2018. Mortality rates of ingrowth within 15 m of other ingrowth were 3%, 2%, and 5% of ingrowth in periods 1991, 2001, and 2010, respectively (A5). This positive density-dependence deviated from chance only in the 2010 period. In periods 1991, 2001, and 2010, mortality rates of ingrowth near small trees were 30%, 7%, and 19% respectively (A6). This risk was significantly greater than chance in periods 1991 and 2010. In periods 1991, 2001, and 2010, mortality rates of ingrowth near large trees were 37%, 4%, and 11% respectively. In all periods this was significantly greater than chance.

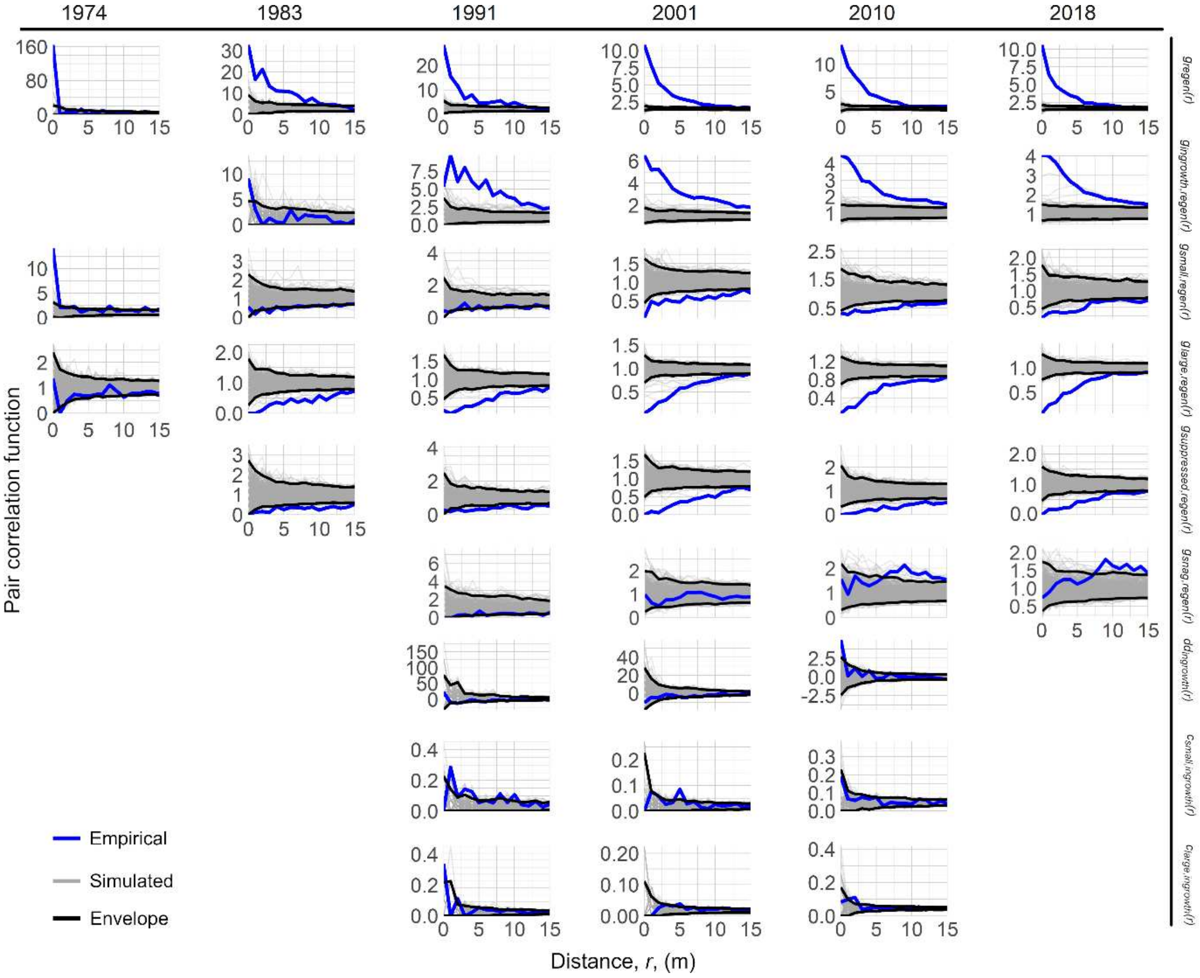

Figure 2.5 Point pattern analyses

Spatial point pattern analyses in the study (rows) at scales from 0 to 15 m in each time period (columns). Significant deviations occur when the empirical line deviates outside of the envelope of simulations. See text for explanation of analysis names.

The results from these statistical analyses are apparent on visual inspection (Figure 2.6). Some analyses did not include all measurement periods: suppressed trees were not detectable until remeasurement in 1983; I waited to measure the spatial correlation of regeneration with the locations of snags killed at least two measurement periods prior. No spatial analyses of regeneration mortality occurred until a sufficient sample size was reached ($n = 10$ at 1991) and time has not yet passed to detect mortality since 2018.

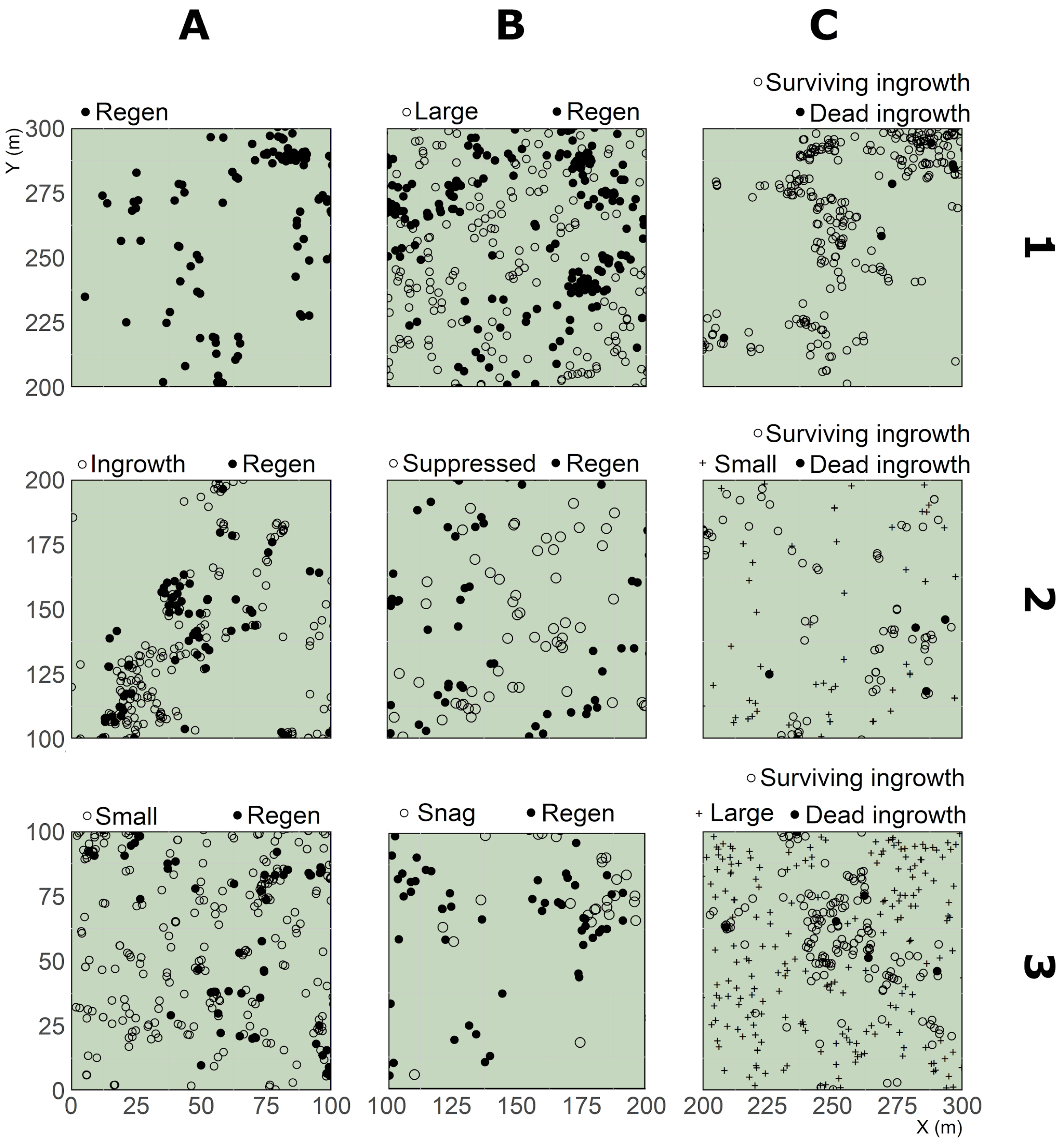

Figure 2.6 Point patterns of regeneration

Division of the study site in 2010 into nine 1-ha subsets highlighting the locations of points used for each of the nine point pattern analyses; these showcase findings of: (A1) aggregation of newly mapped tree regeneration; (A2) attraction of regeneration to prior ingrowth; (A3) moderate repulsion of regeneration from small trees; (B1) severe repulsion of regeneration from large trees; (B2) repulsion of regeneration from suppressed small + large trees; (B3) attraction of regeneration to snags (standing dead small + large trees); (C1) positive density-dependent ingrowth mortality; (C2) risk of regeneration mortality independent of small tree proximity; (C3) risk of regeneration mortality increasing with large tree proximity.

There are correlations among point patterns, indicating synchronicity of patterns across time. Measurement periods with greater regeneration aggregation, $g_{regen}(r)$, occur in periods with greater regeneration density (trees ha^{-1}), and greater repulsion from small trees, $g_{small,regen}(r)$, large trees, $g_{large,regen}(r)$, and suppressed trees, $g_{suppressed,regen}(r)$ (Absolute Pearson's correlations > 0.98). Meanwhile, measurement periods with low self-thinning, as measured by $dd_{ingrowth}(r)$, tend to have greater risk of mortality when near small trees, $c_{small,ingrowth}(r)$ (Pearson's correlation = 0.94), and large trees, $c_{large,ingrowth}(r)$ (Pearson's correlation = 0.95). The only patterns that were not highly correlated (Pearson's correlation < 0.90) with another pattern were $g_{snag,regen}(r)$, the spatial correlation of regeneration and snags, and $g_{ingrowth,regen}(r)$, the spatial correlation of regeneration and prior ingrowth.

2.3.4 Climate—Pattern Analysis

I found evidence to indicate climate potential drives tree regeneration point patterns (Analysis A8). Intra-period climatic conditions correlated strongly with tree regeneration density and regeneration aggregation (Table 2.2). When the lag-regressed values of PC1 were low, signaling moderated climate with lower temperatures and more precipitation, more trees established ($R^2 = 0.97$, p = 0.046; Figure 2.7a), preferring to establish in clusters ($R^2 = 0.99$, p = 0.011; Figure 2.7b) and ingrowth that established in prior years ($R^2 = 0.72$, p = 0.637; Figure 2.7c). In contrast, periods with higher values of lag regressed PC1, i.e., harsher climatic conditions, found regeneration establishing closer to both small ($R^2 = 0.82$, p = 0.253; Figure 2.7d) and large overstory trees ($R^2 = 0.91$, p = 0.135; Figure 2.7e). There was a strong correlation indicating that regeneration is repelled from suppressed overstory trees when climate was moderate ($R^2 = 1.00$, p = 0.035; Figure 2.7f). Regeneration tended to establish near snags under moderate climate, but this trend was not consistent across all periods ($R^2 = 1.00$, p = 0.035; Figure 2.7g).

The spatial patterns of regeneration mortality followed similar trends. Under moderate periods of climate, I found less density-dependent mortality among ingrowth ($R^2 = 0.81$, $p = 0.290$; Figure 2.7h). Conversely, ingrowth mortality was heightened near small ($R^2 = 0.85$, $p = 0.254$; Figure 2.7i) and large overstory trees ($R^2 = 0.83$, $p = 0.268$; Figure 2.7j) under moderated climate.

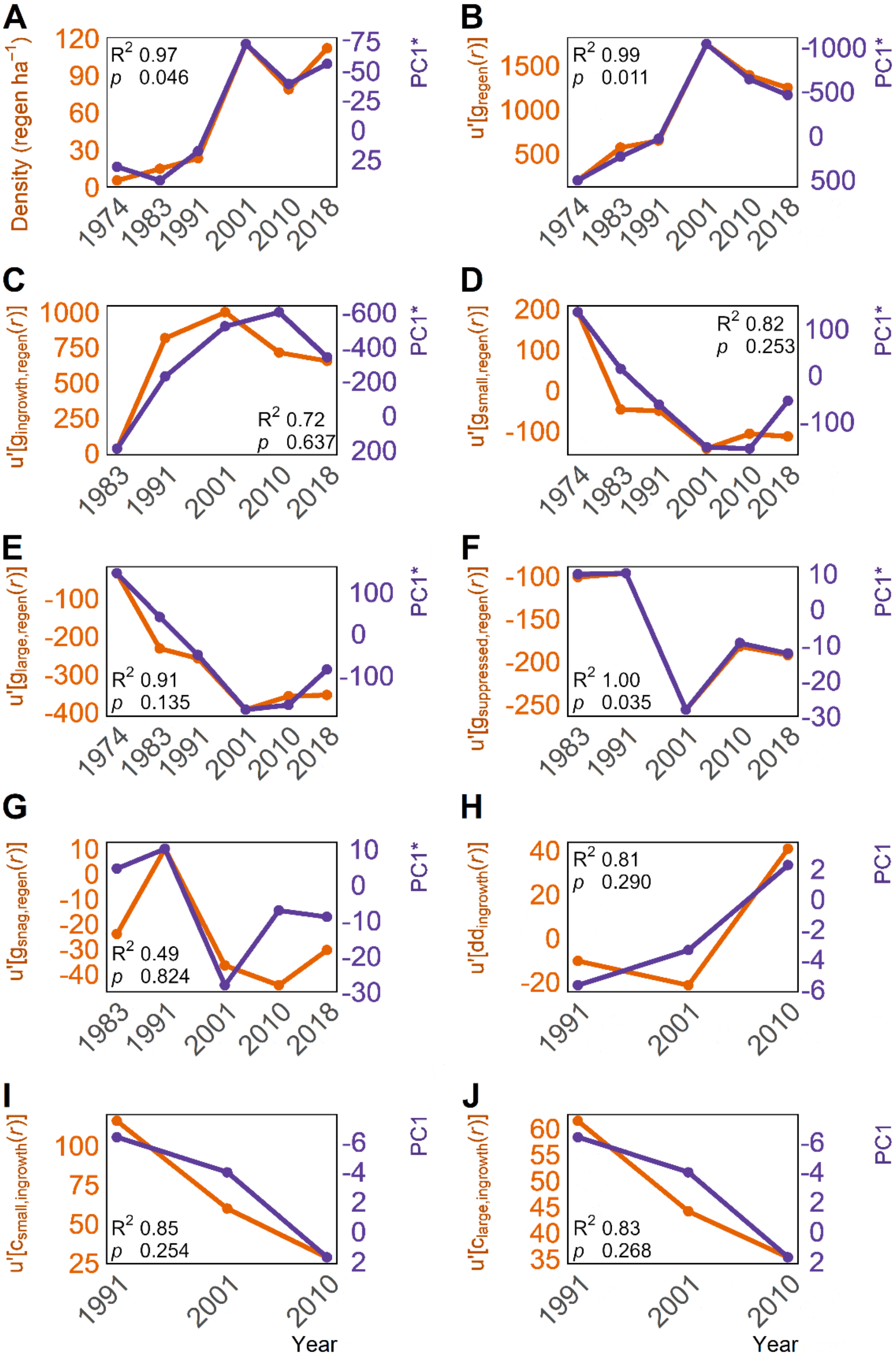

Figure 2.7 Point patterns and climate

Summary of lag regression fits fit to regeneration density (a) and deviances of spatial patterns (b—j) against climate harshness (PC1). The left y-axis displays the observed values whereas the right y-axis displays either raw PC1 values, or if denoted as PC1*, lag-weighted values of PC1 based on lag-regression fits (see text for details). Larger values of PC1 indicate climate harshness.

Table 2.3 Lag-regressions

Summary of lag-regression models of regeneration density and deviances of point patterns on climate harshness (PC1).

Pattern deviance $u'_{0,t}$	Parameter [lag]	β	SE	t	p	R2	Model p
Density (regen ha^{-1})	Intercept	423.44	60.70	6.98	0.0199	0.97	0.047
	PC1 [1]	-47.55	19.21	-2.48	0.1317		
	PC1 [2]	-5.91	17.62	-0.34	0.7692		
	PC1 [3]	-105.52	17.36	-6.08	0.0260		
$g_{regen}(r)$	Intercept	738.79	36.56	20.21	0.002	0.99	0.0107
	PC1 [1]	-104.54	11.57	-9.04	0.012		
	PC1 [2]	-19.19	10.61	-1.81	0.212		
	PC1 [3]	-109.65	10.45	-10.49	0.009		
$g_{ingrowth,regen}(r)$	Intercept	343.14	311.56	1.10	0.469	0.72	0.637
	PC1 [1]	-47.35	68.79	-0.69	0.616		
	PC1 [2]	-66.25	74.92	-0.88	0.539		
	PC1 [3]	-38.17	51.80	-0.74	0.596		
$g_{small,regen}(r)$	Intercept	2.14	37.85	0.06	0.960	0.82	0.253
	PC1 [1]	17.91	11.98	1.50	0.273		
	PC1 [2]	14.99	10.98	1.36	0.306		
	PC1 [3]	7.92	10.82	0.73	0.540		
$g_{large,regen}(r)$	Intercept	-221.21	29.65	-7.46	0.018	0.91	0.135
	PC1 [1]	18.91	9.38	2.02	0.182		
	PC1 [2]	14.91	8.61	1.73	0.225		
	PC1 [3]	13.65	8.48	1.61	0.249		
$g_{suppressed,regen}(r)$	Intercept	-136.31	30.24	-45.08	0.014	1.00	0.035
	PC1 [1]	11.50	0.67	17.23	0.037		
	PC1 [2]	-3.63	0.73	-4.99	0.126		

	PC1 [3]	16.51	0.50	32.83	0.019		
$g_{\text{snag,regen}}(r)$	Intercept	-19.22	24.38	-0.79	0.575	0.49	0.824
	PC1 [1]	2.97	5.38	0.55	0.678		
	PC1 [2]	-1.49	5.85	-0.26	0.841		
	PC1 [3]	3.64	4.05	0.90	0.534		
$dd_{\text{ingrowth}}(r)$	Intercept	19.51	14.47	1.35	0.406	0.81	0.290
	PC1 [0]	7.29	3.57	2.04	0.290		
$c_{\text{small,ingrowth}}(r)$	Intercept	45.04	10.99	2.65	0.230	0.85	0.254
	PC1 [0]	-9.95	4.19	-2.37	0.254		
$c_{\text{large,ingrowth}}(r)$	Intercept	40.11	5.39	7.45	0.085	0.83	0.268
	PC1 [0]	-2.97	1.33	-2.23	0.268		

2.4 Discussion

In a ponderosa pine stand over 44 years without active management and with minimal disturbance, the results presented here indicate the locations of tree regeneration are not spatial random; these locations are likely driven by biotic interactions, which, moreover, are modulated by climate. The spatial arrangement of trees in a forest stand is an integration of multiple processes such as regeneration and mortality dynamics, and effects of climate, disturbances, and management activities. A point pattern analytic approach to analyze tree spatial arrangement holds promise to elucidate the drivers of regeneration establishment locations (Fajardo et al. 2006; Malone et al. 2018) and further concepts of development of stand complexity (Stoyan and Penttinen 2000; Boyden et al. 2005; Larson and Churchill 2012).

A key advantage of this study was that regenerating trees were censused every c. 9 years. Although tree locations are dynamic through time, most investigations use a “frozen” approach (Herben and Hara 2003; Velázquez et al. 2016) making use of a single inventory of a mapped community to retroactively interpret past tree interactions. This approach is not ideal as it flattens the pattern-shaping processes over time (Comas and Mateu 2007). In contrast, longitudinal designs such as in this study are suited for investigating long-term dynamical processes such as recruitment (e.g. Lutz et al., 2014). By finding that specific tree patterns are correlated over time, I strengthen suggestive links between pattern and process. Additionally, a correlation with climate implies interactions between overstory and regenerating trees are modulated, creating plasticity of regeneration niches spatially.

2.4.1 Prescence of Large Trees Broadly Determines Regeneration Niche Preference

The spatial preferences of tree regeneration, over the duration of the whole study, were likely driven primarily by the presence of large trees. First, periods of greater aggregation within regeneration co-occur with periods of greater repulsion away from overstory trees. Additionally, the repulsion of regeneration away from suppressed trees, where competition is heightened, and increased mortality rates of regeneration near overstory trees were especially indicative of competition. This suggests that periods of heightened competition from the overstory confine successful establishment to gaps. Second, I observed colonization of canopy gaps, as indicated by the attraction of tree regeneration to snags. Gap creation, whether through disturbances such as harvesting (Sánchez et al. 2009), tree competition (Vacek and Lepš 1996), or, in this study, mountain pine beetle, provides greater availability of light and nutrients for shade-intolerant tree species (York et al. 2007). Third, large trees repulsed regeneration more than small trees; the interactions of saplings with larger trees tend to be more negative than interactions with medium-sized trees (Fajardo et al. 2006) because larger trees utilize a greater share of abiotic resources per capita (Nguyen et al. 2016). The importance of large trees for impacting ponderosa pine regeneration locations, however, does not negate contributing influences arising from fine-scale edaphic or topographic variability (Abella et al. 2013). These sources of niche modification are more apparent, and likely more consequential, where the overstory has been completely removed such as after stand-replacing fires (Ziegler et al. 2017b). The results here reify models of stand dynamics which emphasize the regulatory role of large trees (Lutz et al. 2012).

Larson and Churchill (2012)’s review of tree spatial patterns identified many commonalities regarding spatial structure across dry forests in the western US. Findings of clustered small trees segregated from larger, older trees has been observed frequently, whether stand structure was old-growth or responding to a partial harvest in decades past, and whether the overstory was ponderosa pine dominated or mixed conifer (Moeur 1993; Sánchez et al. 2009; Lydersen et al. 2013; Schneider et al. 2016; Iniguez et al. 2019). There remains a question as to how generalizable this pattern is; whereas the aforementioned studies found trees to have filled in gaps over time, North et al. (2004) found tree regeneration to disprefer gaps in a mixed conifer Sierra Nevada forest and suggested high temperatures in gaps precluded establishment. And in some forests, dense shrub communities can establish in openings (Knapp et al. 2013), outcompeting tree regeneration (Erickson and Harrington 2006). Further research of large, mapped plots over time are needed to investigate patterns of forest dynamics (Lutz et al. 2018); the compilation of such efforts will help separate the degree to which aspects of spatial forest dynamics are idiosyncratic or can be distilled into common heuristics.

2.4.2 Climatic Conditions Finely Tunes Regeneration Niche Preference

Though the patterns in this study suggest a net negative interaction of overstory trees on tree regeneration, this does not mean overstory trees had not benefitted tree regeneration. The canopy gaps in this study represented middling conditions wherein competition was lessened, but the proximate canopy still moderated microclimatic conditions. In this study, 99.6% of tree regeneration occurred within 14 m of an overstory tree; this is within the zone of influence of larger trees, as identified by prior research from Boyden and Binkley (2016) in the same plot as this study. Regenerating trees in very large open spaces devoid of any canopy shading may be subject to excessive surface temperatures and evaporation (North et al., 2004). Experimental plantings of ponderosa pine and other conifers in the Sierra Nevada demonstrate that the advantage of being in open space diminishes quickly asymptotes with distance from the overstory. This has led researchers to categorize openness according to distance from the overstory in order to capture the degree to which trees moderate the immediate growing environment (Lydersen et al. 2013; Matonis and Binkley 2018; Iniguez et al. 2019). For example, Iniguez et al., (2019) discriminate between gaps and openings where growing conditions are moderated in the former but not the latter. The authors point out that identifying a distance-based distinction between gaps and openings is subjective. Further investigations are needed to identify how the balance of overstory-attenuated microclimates against overstory competition affects ponderosa pine establishment and survival.

The relationships between climate and patterns of tree regeneration indicate that the net negative interactions from the overstory are dynamic and may spur development of diverse tree group structures. As climate became harsher, moisture stress in open areas likely increased. This led to greater density-dependent mortality within ingrowth but less mortality of ingrowth near the overstory. Additionally, the net repulsion from overstory trees likely lessened as canopy shading mitigated moisture and temperature stresses. In other words, the range of preferred conditions for establishment and survival contracted away from open spaces and towards canopy edges. This was manifested by a lessening in the tendency for regeneration to cluster with each other segregated from the overstory (Figure 2.9). This trend, evocative of the stress-gradient hypothesis, has been demonstrated by contrasting comparatively xeric and mesic ponderosa pine and Douglas-fir stands in northwestern Montana (Fajardo et al. 2006). Over time, tree regeneration which established during wetter periods will lead to development of even-aged tree groups (Cooper 1960) whereas drier periods may produce tree groups of mixed ages (White 1985). This study demonstrates that the stress gradient hypothesis can be applied to explain spatial regeneration dynamics in dry forests and leads to divergent tree group structuring.

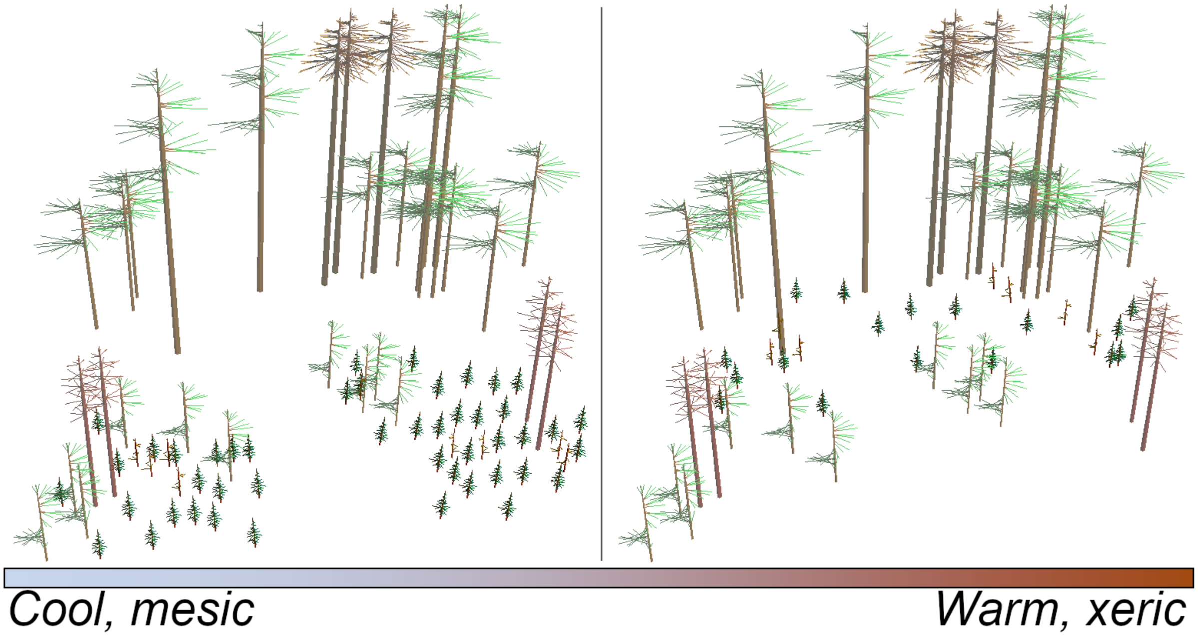

Figure 2.8 Demonstration of tree patterns

Conceptual figure of climatic mediation of tree regeneration spatial patterns. Locations of regeneration shift as conditions became warmer and more xeric, realized as: lower density; lower aggregation; less attraction to snags and recent ingrowth; less repulsion from overstory trees, including suppressed trees; less density-dependent mortality within regeneration; and greater regeneration mortality near overstory trees.

2.4.3 Silvicultural Implications for Future Forests

The trajectory of stand development observed here echoes a common theme: dry forests in the western US have infilled, leading to homogenization (Hessburg et al. 2005; Sánchez et al. 2009; Schneider et al. 2016). In this site, background mortality and the endemic mountain pine beetle event killed only 1 overstory tree ha^{-1} yr^{-1}. Meanwhile, 6.6 trees ha^{-1} yr^{-1} were recruited.

As of 2018, stocking consisted of 486 trees ha^{-1} with 24.3 m^2 ha^{-1} of basal area, far greater than the pre-settlement (1860 AD) average of 97 trees ha^{-1} or 6.3 m^2 ha^{-1} of basal area for similar forests in the Front Range region (Battaglia et al. 2018). Higher fuel connectivity associated with greater stocking increases the risk of high severity fire. This can result in high fire-caused mortality and sparse, homogeneous residual overstories with little seed availability to ensure forest recovery (Ziegler et al. 2017b; Stevens-Rumann and Morgan 2019); in contrast, fire severity is lower in heterogeneous forests with lower fuel connectivity (Kane et al. 2019; Koontz et al. 2020). In the upcoming century with greater expected wildfire activity (Williams et al. 2012), complexity-oriented silvicultural treatments which seek to create heterogenous forest structures are argued to bolster resistance and resilience to disturbances such as fire (Larson and Churchill 2012; Puettmann et al. 2015; Ziegler et al. 2017a; Fahey et al. 2018).

These complexity-oriented treatments employ variable retention harvesting, creating heterogeneity of residual trees. For example, the Individuals, Clumps and Openings framework (ICO) emphasizes emulating historical forest structure, namely a mosaic of isolated trees, groups of trees, and gaps (Churchill et al. 2013b). These treatment designs are aligned with the autecological spatial dynamics of ponderosa pine for two reasons. Firstly, this study suggests the persistence of edges and gaps benefits continual tree recruitment, by providing both open areas to regenerate as well as climate moderation, sustaining an all-aged forest structure. ICO-like treatments in similar forests produce areas of greater light conditions over spacing-based treatments (Cannon et al. 2019) benefitting ponderosa pine establishment. Enhanced light conditions also counteract undesirable compositional shifts towards shade-tolerant species occurring in many western US forests (Battaglia et al. 2018). Maintaining an all-aged forest structure enhances resilience, especially against mortality agents which favor larger and older trees (Baker and Williams 2015; Briggs et al. 2017), e.g. mountain pine beetle (Negrón and Popp 2004). However treatments as currently implemented are often not creating sufficiently sized edges and gaps (Briggs et al. 2017; Matonis and Binkley 2018). A silvicultural emphasis on edge and gap creation would enhance biological and structural diversity (Dickinson 2014; Kane et al. 2014; Briggs et al. 2017; Matonis and Binkley 2018).

Secondly, the ICO framework incorporates removal of ladder fuels (Churchill et al. 2013b). Fire modeling studies have confirmed that spatial segregation of small trees from overstory trees in historical and heterogeneous forests reduces fire severity (e.g., Ziegler et al., 2021). Given that tree regeneration in this study was repelled by—and mortality higher near—larger trees, ladder fuel removal would capture eventual mortality while lowering the potential for crown fire transition. Briggs et al. (2017) caution however, that forest managers should weigh fire hazard concerns against benefits of multi-storied tree groups, especially habitat provisioning (e.g., Youtz et al. 2008). Further, my results indicate tree regeneration will establish nearer to the overstory under a warming and more stressful climate in the 21st Century. My results demonstrate that retaining some all-aged groups will ensure the ingrowth in these groups will be buffered against heat and drought stress.

Close proximity of trees in dense patches can lead to heightened interactions, resulting in locally intense self-thinning (Suzuki et al. 2008). This study shows that climate can synergistically interact with the arrangement of local tree neighborhoods to increase risk of mortality, as suggested by Lutz et al. (2014). Most tree regeneration perished in the 2002-2010 period with mortality concentrated in denser patches of regeneration. This climatic period contained the strongest megadrought since the 16th Century (Williams 2012). As drought frequency and severity are expected to trend upwards, climate-adaptive silvicultural strategies may benefit from thinning some regeneration patches.

2.4.4 Limitations and Future Opportunities

The duration of this study captured the shift from a largely two-aged and two-sized stand to an uneven-aged stand, characterized by a reverse sigmoid shaped size distribution (O'Hara 2014). This shift occurred in the late 20th Century, whereas little regeneration occurred over the early to mid-20th century. This lack of early 20th Century regeneration has been observed elsewhere in the Colorado Front Range (Baker et al. 2007). Consequently, this study encompassed the majority of tree regeneration over the last century.

However, the inferential strength of this study would be improved both by more frequent observations and inclusion of seedlings. In the exploratory analyses, I found that the correlations between climate and spatial patterns, with exception of the patterns between ingrowth and regeneration, and between snags and regeneration, was high ($R^2 \geq 0.81$). Yet the statistical power was low, owing to low sample sizes of observation periods and degrees of freedom. More frequent observations aided by advances in lidar (light detection and ranging) can increase sample sizes while reducing effort to map trees (e.g., Kane et al., 2019). As a result, more frequent observations may be possible. In this study, increasing the sample size of observation periods would have aided inferential ability. Furthermore, it was necessary to summarize climate variables within the same temporal periods as the periodic observations, and these periods were marked by significant intra-periodic variability (Figure 2.10). More frequent observations would increase degrees of freedom, sample size, and increase the precision of climate as a predictor. By addressing these factors, future studies could establish a more robust climate—spatial pattern linkage.

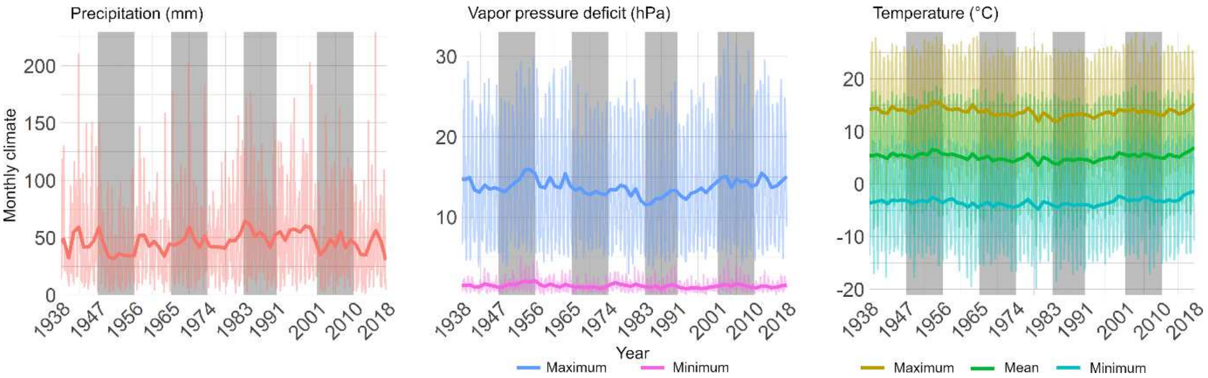

Figure 2.9 Climatic variability over years

Interannual PRISM climate at the study location point pattern; alternative grey and white vertical backgrounds represent individual periods.

2.4.5 Extending Point Pattern Analyses for Comparative Purposes

In spatial point pattern analysis (SPPA), studies use complete spatial randomness (CSR), spatial independence, or random labelling (depending on the structure of the data and desired hypothesis test) as a null model (Velázquez et al. 2016) for the basis of determining an observed spatial pattern. 'No difference' as a null hypothesis has been levied against traditional, frequentist hypothesis testing; likewise, spatial null models which assume no spatial structure of the data are often described as trivial and uninteresting. Reasons given are that an overwhelming compilation of SPPA research rarely demonstrate, and even *a priori* assumptions of investigators rarely assume, plant communities are randomly assembled (Velázquez et al. 2016). Inference-making with SPPA via simulation envelopes or goodness-of-fit measures is typically trinary—in the case of CSR as the null model, uniformity, randomness, or aggregation—and stops short of assessing effect size. This study however demonstrates that a null of randomness or no difference provides a baseline against which empirical patterns can be compared.

Moreover, I submit studentization and scalar transformation per Myllymäki et al. (2015), as employed here, can elevate the usefulness of perceived trivial null models. This simplification of complex data structures (e.g., aggregating data from Appendix Figure A1 to Figure 5) generates effect sizes and permits comparison-making, an underused but promising use of SPPA (Fajardo et al. 2006; Velázquez et al. 2016). This approach avoids an view of states like aggregated or random as mutually exclusive categories and reframes spatial patterns as occupying a gradient of spatial correlation.

2.5 Conclusions

Heterogeneous forest structures develop over extended periods of time from shifting distributions of regeneration niches. This case study suggests those niches in ponderosa pine forests in the Southern Rockies are driven largely by competition from the overstory, but also with a modicum of facilitation during droughts. In the absence of historically frequent disturbances such as fire, continued canopy closure will continue to decrease the availability of gaps. This will challenge successful recruitment in similarly situated ponderosa pine-dominated forests as well as mixed conifer dry forests. The results here offer evidence to support the use of variable retention harvesting methods. Emphasizing gap creation can enhance opportunities for recruitment, supporting a mixture of age classes and therefore long-term viability.

The analyses connecting climate to spatial regeneration patterns was exploratory in nature and provided hypotheses for more confirmatory experiments and studies. Meanwhile, forest managers must implement silvicultural strategies today in anticipation of growing conditions in the future. Whether the same spatial patterns of regeneration in ponderosa pine forests of the Southern Rockies extend to the future will likely become increasingly tenuous over time as climate deviates from the range I observed in this study. Rather than regenerating into openings, creating distinct tree groups, harsher climatic periods may enhance the ‘nurse’ effect from the overstory, leading to greater abundance of multi-aged tree groups. This will create characteristically different assemblages of tree groups, requiring forest and fire managers to adjust their silvicultural planning and fuels management.

CHAPTER 3 – TREE REGENERATION SPATIAL PATTERNS IN PONDEROSA PINE FORESTS FOLLOWING STAND-REPLACING FIRE: INFLUENCE OF TOPOGRAPHY AND NEIGHBORS

3.1 Introduction

Disturbances, management, and ecological processes imprint their signatures on the spatial pattern of forest structure throughout forest development. Interpreting these spatial patterns while using other sources of information such as species' silvics provides insights into forest stand dynamics (Stoyan and Penttinen 2000). One ecosystem where studies of spatial patterns have led to an improved understanding of stand dynamics is in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.)-dominated forests of western North America. In many of these forests, relatively frequent, low- to mixed-severity fires historically shaped structure and composition, creating and maintaining generally open, uneven-aged stands consisting of a mosaic of individual trees, tree groups, and openings (Larson and Churchill 2012). These mosaics have been characterized as aggregated at sub-hectare scales and with heterogeneous spatial patterns of tree sizes (e.g., within a group, interior trees were often smaller than peripheral trees) (Pearson 1950; Larson and Churchill 2012). Fires responded to and reinforced these spatial patterns (Larson and Churchill 2012) and these fire-dependent patterns regulated elements of forest dynamics including demography (Boyden et al. 2005), mortality (Boyden et al. 2005), tree growth (Pearson 1950) and regeneration (Fajardo et al. 2006).

As the density and spatial arrangement of tree locations and sizes affect forest dynamics (Bače et al., 2015; Donato et al., 2012; Ziegler et al., 2017a), understanding patterns of initiating stands is critical for anticipating the consequences of altered fire regimes (Hansen et al. 1991;

Tepley et al. 2014). Many ponderosa pine forests are experiencing greater occurrence and extent of high-severity, stand-replacing fires due, in large part, to a century of fire exclusion, past land uses, and changing climate (Brown et al. 2004; Stephens et al. 2014; Hessburg et al. 2016). Because of distance-limited seed dispersion, large stand-replacing patches often beget sparse post-fire tree regeneration, generating concern that forest developmental pathways may be altered by shifts towards greater high-severity fire (Chambers et al. 2016; Rother and Veblen 2016). Such changes will have long-lasting repercussions for forest structure and composition (Chambers et al. 2016; Rother and Veblen 2016).

Recent syntheses of stand development suggest that severe, stand-replacing fires induce spatially complex forest structures (DellaSala et al. 2014; Tepley et al. 2014). Patterns of sparse stand regeneration are hypothesized to be especially heterogeneous, influenced by large and fine-grained variability in growing environments (Donato et al. 2012; Bače et al. 2015). Competition is thought to largely influence patterns (Donato et al. 2012), resulting in the spatial segregation of trees into monospecific groups (Pielou 1962) and diminished growth between competing neighbors (Das et al. 2011). Other studies, however, suggest that positive interactions may be more important as neighbors ameliorate moisture stress in the absence of canopy cover (Donato et al. 2012; Redmond et al. 2015). Positive interactions would form heterospecific groups in contrast to competitive interactions (Pielou 1962). As much as tree interactions inform spatial patterns, abiotic influences on resource availability are also likely to be important, reflecting niche preferences and promoting fine-scale aggregation (Bonnet et al. 2005; Getzin et al. 2008). For example, the higher evaporative demand on southwestern aspects or lower soil moisture retention on steep slopes inhibit regeneration less so than on northeastern or shallower slopes (Rother and Veblen 2016). Moreover, sparsely regenerating stands may also develop a heterogeneous spatial arrangement of tree sizes due to biotic interactions and differential growth rates across abiotic gradations (Donato et al. 2012; Bače et al. 2015). How patterns of regenerating trees manifest is therefore contingent on the prevailing growing environment and requires examination of the roles of biotic and abiotic factors such as tree interactions and topography (Donato et al. 2012).

Further, tree regeneration patterns are modulated by traits of species composing the regeneration (Urza and Sibold 2017). For example, in ponderosa pine-dominated forests, wind is an important disperser of ponderosa pine and Douglas-fir *(Pseudotsuga menziesii* (Mirb.) Franco) seeds; the heavier seed size of ponderosa pine may not disperse as far as lighter Douglas-fir seeds (Vander Wall 2003; Chambers et al. 2016; Rother and Veblen 2016). In contrast, lodgepole pine *(Pinus contorta* Dougl. ex Loud.) cones are often serotinous (Alexander 1966) which could result in concentrated seed dispersal around dead parent trees. However, lodgepole pine seeds are also light and easily wind-dispersed (Vander Wall 2003). Quaking aspen (*Populus tremuloides* Michx.) sprouts clusters of ramets around preexisting genets and does not primarily rely on wind dispersion to regenerate (Shepperd 1993). Once regeneration occurs, species' tolerance to heat, light, and moisture availability, which vary by abiotic and biotic environmental conditions, can influence establishment and growth (Urza and Sibold 2017). These differential traits make it pertinent to examine tree regeneration patterns using a species-specific approach.

The overarching aim was to identify the spatial patterns of tree regeneration in ponderosa pine-dominated forests following stand-replacing fire and ascertain how tree patterns are responding to topographic variation and tree interactions. I conducted this study in ponderosa pine forests given their wide geographic range in western North America and the interest of managers in buffering post-fire resiliency of dry forests globally (Stephens et al. 2014). Specifically, I (1) assessed the spatial patterns of tree locations and heights; (2) examined whether species interactions, in a beneficial or negative manner, were shaping these patterns; and (3) explored the influence of topographic gradations on these patterns. This study's results further an ecological understanding of forest recovery and may inform forest management decision making within these and similar dry forests.

3.2 Materials and Methods

I studied ponderosa pine forests following three wildfires in the western USA: the 2000 Bobcat Gulch Fire (Colorado Front Range), the 2002 Hayman Fire (Colorado Front Range), and the 2000 Jasper Fire (Black Hills of South Dakota; Figure 3.1). Within the fire footprints, elevation ranged from ~1700 to 2500 m, mean annual precipitation from 48 to 58 cm, and temperature from 5.2 to 7.8 °C (Brown et al. 1999). Aside from ponderosa pine, three other species were abundant. Quaking aspen occurred within all three burned areas, often in moister sites (Peet 1981). Douglas-fir was common on northerly aspects within the Bobcat Gulch and Hayman Fires (Peet 1981). The third, lodgepole pine, occurred on northerly aspects in the Bobcat Gulch Fire (Peet 1981).

These forests historically experienced fires with a range of severities from low to moderate to high with the latter being infrequent and tied to climatic anomalies (Brown and Sieg 1999; Brown et al. 1999; Fornwalt et al. 2016). The mixture and frequency of severities were significantly spatially variable over landscapes, influenced by complex topography, and over decades, influenced by broad-scale climatic oscillations (Brown and Sieg 1999). Though there is some debate as to the relative historical portion and patch sizes of fire severities across these landscapes (Fule et al. 2014), it is generally accepted that high-severity fires were not historically as common in extent or occurrence as today (Hessburg et al. 2016).

3.2.1 Data Collection

I established six randomly located 4-ha (200 m × 200 m) plots in stand-replacing patches (i.e., 100% tree mortality) of each fire, for a total of 18 plots (Figure 3.1). I excluded areas that were inaccessible (i.e., not on public land or >4 km from a road) or that experienced post-fire logging or planting. I placed three plots per fire adjacent to, and three plots at least 200 m from, living residual forest, permitting statistical accounting of distance–regeneration density relationships. Sampling occurred 11 to 15 years post fire to allow time for tree establishment (Shepperd et al. 2006).

In each plot, I recorded locations, species, and heights of all post-fire regenerating trees ≥15 cm tall (Figure 3.1). Where conspecifics of similar height were densely clustered, I recorded the cluster's centroid, radius, number of individuals, and their average height. Clusters were small with a median count of five trees and radius of 0.5 m. I then assigned random coordinates to clustered trees within their cluster's radius. I considered only those species with a sufficient sample size (≥20 individuals in any plot), leaving ponderosa pine and quaking aspen across all fires, Douglas-fir in the Hayman, and Bobcat Gulch fires, and lodgepole pine in the Bobcat Gulch Fire. After filtering, regeneration counts ranged from three trees to 1704 trees per 4-ha plot, averaging forty-three trees ha^{-1} across the sampled population (Table 3.1).

I calculated three topographic measurements within each plot using 10-m resolution digital elevation models (USGS 2016): aspect, percent slope, and topographic position index (TPI) (Tagil and Jenness 2008). I cosine-transformed azimuthal aspect to a range from zero (southwest) to two (northeast). I measured TPI as the difference in elevation between a location and its surrounding neighborhood, defined as a 10-m radius in this study. I used base tools in ArcGIS 10.3 (ESRI, Redlands, CA, USA) with the Geomorphology and Gradient Metrics toolbox (Cushman et al. 2010) for these calculations.

In ArcGIS 10.3, I also measured the distance from residual forest canopy using supervised classification (see Chambers et al. (2016) for method details) on 1-m resolution aerial imagery (USGS 2016). I joined topographic measurements and distance from residual forest canopy to each 4-ha plot (Table 3.1).

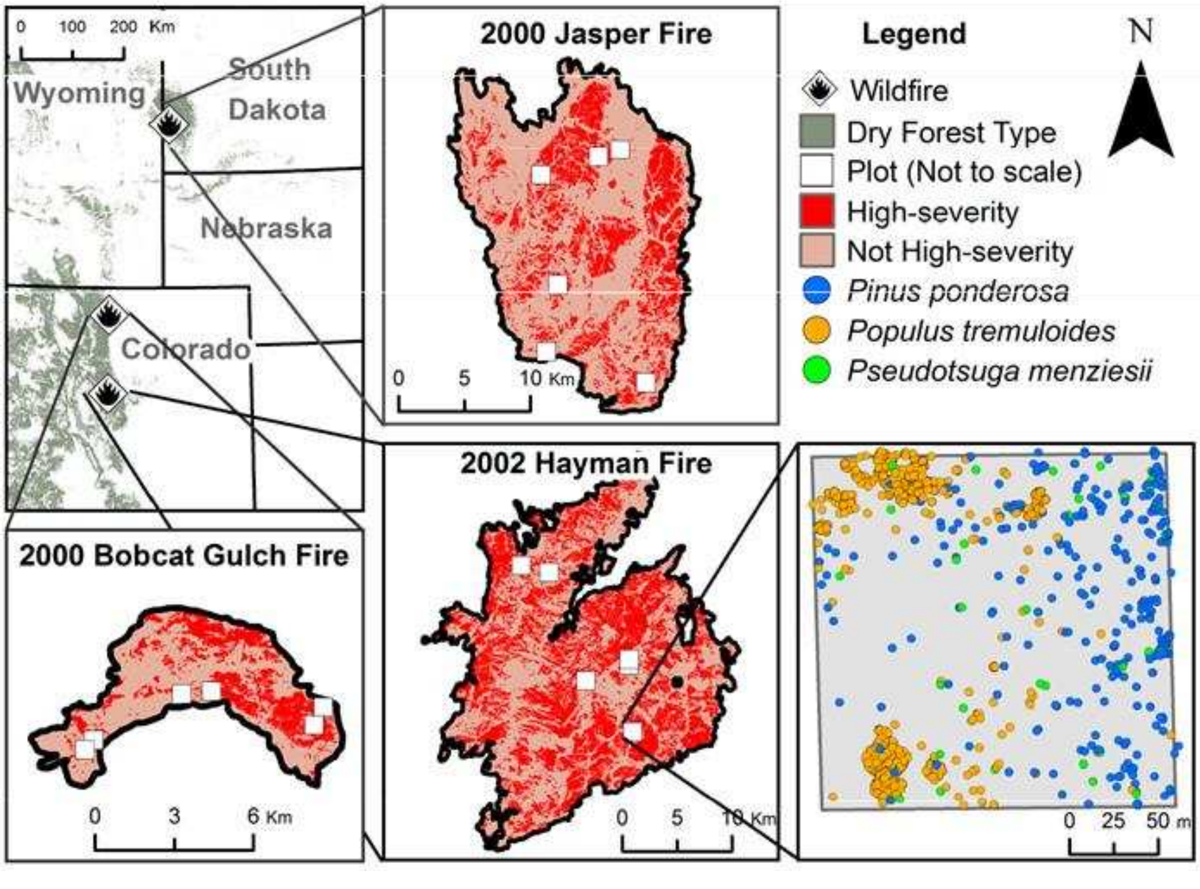

Figure 3.1 Study location

Locations of sampled fires and 4-ha plots within high-severity areas, as well as an example plot of mapped tree regeneration, by species, for illustration.

Table 3.1 Regeneration properties

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

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

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

3.2.2 Patterns of Regenerating Tree Locations

To assess spatial patterns of each species, I tested whether trees were distributed randomly (i.e., complete spatial randomness or CSR), uniformly, or aggregated using the distance-dependent univariate pair correlation function, g(r) (Wiegand and Moloney 2013). This function describes the density of mapped points at distance, r, from any arbitrary point, relative to expectation under CSR (Wiegand and Moloney 2013). Therefore, when observed statistics of g(r) are greater than expected, tree patterns are aggregated; similarly, lower values than expected suggest uniformity.

I randomly distributed points under a null model 999 times to evaluate for departure from CSR.

The null model, an inhomogeneous Poisson process, distributed points under non-constant intensity (points per unit area). Intensity was parameterized by an Epanechnikov smoothing kernel at a bandwidth of 15 m and resolution of 1 m (Wiegand and Moloney 2013). I chose an inhomogeneous over a homogeneous Poisson process to account for intensity gradients in the observed data (Wiegand and Moloney 2013). Treating each plot as a replicate, I pooled observed statistics together and null statistics together using ratio estimation (Wiegand and Moloney 2013). I then tested goodness-of-fit of pooled observations about the pooled null expectation (Wiegand and Moloney 2013; Baddeley et al. 2015) over a range of distances, 0 to 15 m ($\alpha = 0.05$ for all hypothesis tests). The upper limit was selected a priori following recommendation that tests should mirror the scale at which trees' spatial correlation structures generally manifest; this is often near 15 m (Wiegand and Moloney 2013).

I then explored interspecific interactions with the bivariate pair correlation function, $g_{1,2}(r)$. This statistic is like $g(r)$, except it considers only the number of species 2 points located at distance, r, from species 1 points (Wiegand and Moloney 2013). The statistics' interpretation depends on choice of the null model (Goreaud and Pelissier 2003); the null model was independence. The toroidal shift method is often used to simulate independence (Goreaud and Pelissier 2003); an alternative method is preferred when point patterns display significant inhomogeneity (Wiegand and Moloney 2013). I simulated independence by randomly displacing species 2 locations within a 15-m radius while holding species 1 locations fixed. This preserves broad spatial structures of species locations, while removing small-scale correlations (Wiegand and Moloney 2013). Using this analysis, I could determine whether species were located independent of one another, attracted to one another (i.e., statistics above the null expectation), or repulsed from one another (i.e., statistics below the null expectation). The former implies beneficial interactions while the latter, negative interactions (Pielou 1962). The procedure for handling replication and goodness-of-fit testing for departure from the null model was otherwise identical to the above univariate analysis.

Last, I explored the influence of topography on tree locations, while accounting for the effect of distance from residual forest canopy. I fit an inhomogeneous Cox process model, a weighted generalized linear model with a log-link and Poisson error distribution (Baddeley et al. 2015), to estimate the intensity of each species at each location. Models were a function of distance from the residual forest canopy, each of the topographic covariates and, as a random effect, the identity of each plot's fire. To identify statistical significance of topography, I compared this full model to a reduced model with no topographic covariates using the likelihood-ratio test. I assessed these models with a two-step process. For each covariate, I multiplied its range of observations by its estimated coefficient. This is the log-scale relative magnitude of each covariate. Transforming to linear scale yields the factor change in intensity from the lowest to highest observed value of each covariate (Baddeley et al. 2015). Next, I examined model performance; I assessed goodness-of-fit of the observed g(r) from the univariate analysis against 999 realizations of the fitted models. Here, I did not pool across plots; significant deviation from the fitted point process in any one plot constituted an incomplete description of the observed pattern. I performed point process modelling in R (v3.2.3, R Core Team 2016, Vienna, Austria) with Spatstat

(v1.46-1; Baddeley et al., 2015).

3.2.3 Patterns of Regenerating Tree Heights

I assessed the patterns of each species' tree heights with the univariate mark correlation function, $k_{mm}(r)$ (Wiegand and Moloney 2013). This function measures the relationship, formalized using a suitable test function, between marks of pairs of points, m_1 and m_2, separated by r. I used the test function $f(m_i, m_j) = m_i m_j$ using tree heights of any arbitrary pair of points, i and j, as marks (Wiegand and Moloney 2013). The test function statistics were normalized by the square of all tree heights; therefore, $k_{mm}(r) < 1$ when neighboring trees at r are shorter than, and $k_{mm}(r) > 1$ when neighboring trees are taller than the mean height of all trees. The former implies negative interactions while the latter, beneficial interactions (Suzuki et al. 2008; Das et al. 2011).

I then explored the influence of heterospecific proximity on each species' tree heights using the bivariate r-mark correlation function, $k_{1m2}(r)$. In this analysis, the test function yields the identity of species 2's height at r from species 1 normalized by the mean of species 2's heights (Wiegand and Moloney 2013); $k_{1m2}(r) < 1$when species 2 trees at r from species 1 trees are shorter than the mean height of all species 2 trees, and $k_{1m2}(r) > 1$ when trees are taller than the mean.

Goodness-of-fit tests and plot replication procedures were identical to those used for the above pair correlation functions. For both $k_{mm}(r)$ and $k_{1m2}(r)$, I simulated null models of independence using 999 random permutations of a species' heights. I performed both the univariate and bivariate analyses for pair correlation and mark correlation functions in Programita (Wiegand and Moloney 2013) using Ripley's edge correction scheme (Wiegand and Moloney 2013).

Finally, I examined the influence of topography on tree heights. I regressed, with mixed-effects general linear models, species' (log) heights on distance from residual canopy and the topographic factors with the identity of each plot's fire as a random effect. Mirroring the Cox process modelling approach above, I compared the full model against a reduced (i.e., intercept-only) model with a likelihood-ratio test and calculated the relative magnitude of each factor. I used marginal-R^2 (variance explained by fixed-effects only) (Nakagawa and Schielzeth 2013) as an indicator of model fit. I met general linear modelling assumptions.

3.3 Results

3.3.1 Patterns of Regenerating Tree Locations

All species had aggregated spatial patterns, with aggregation greatest at smaller scales (Figure 3.2). In particular, deviance from CSR among lodgepole pine ($p = 0.025$) and Douglas-fir ($p = 0.003$) trees occurred at very small scales, from 0 to 2 m and 0 to 4 m, respectively. Aggregation of ponderosa pine ($p = 0.001$) and quaking aspen ($p = 0.001$) extended farther, out to 9 m. These findings reflect the clustering apparent on initial visual inspection of mapped plots (e.g., Figure 3.1).

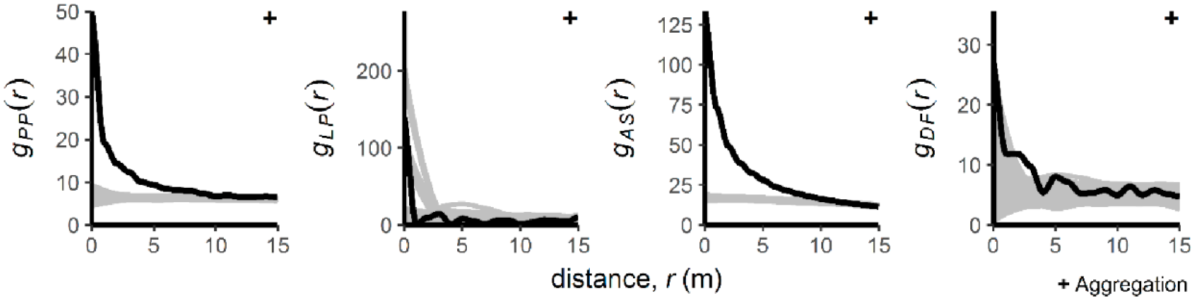

Figure 3.2 Univariate point patterns

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

In addition, interspecific spatial interactions were found to shape tree patterns for half of all species pairs. In every pairwise species association involving ponderosa pine, I detected a pattern of attraction ($p = 0.001$ to 0.019). The pattern of attraction was most clear at scales up to 4 m (Figure 3.3). Pairs of species not involving ponderosa pine, however, were spatially independent of each other ($p = 0.059$ to 0.800). In no species pair was repulsion evident.

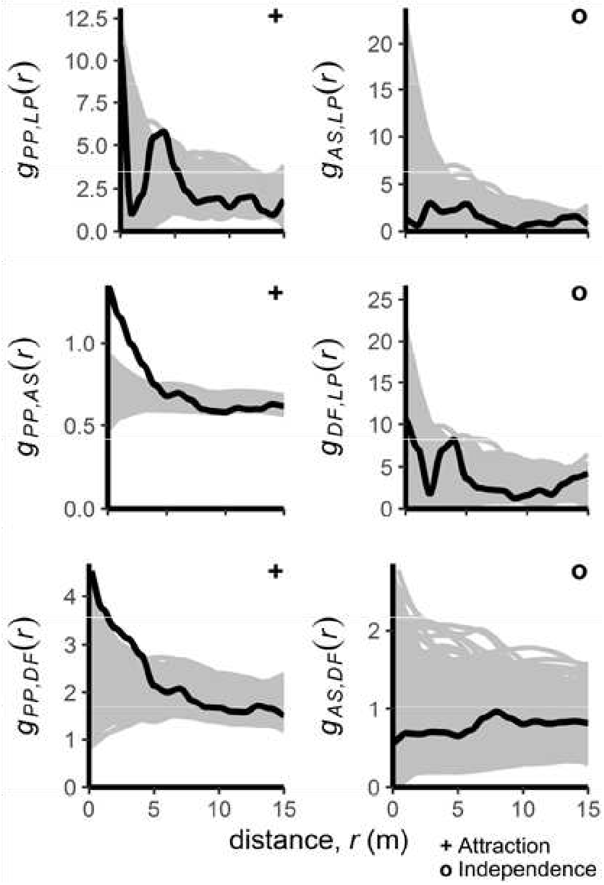

Figure 3.3 Bivariate point patterns

Patterns of replicated bivariate pair correlation functions of post-fire tree regeneration (black lines) among 999 simulations of independent marking (grey lines). Symbols indicate goodness-of-fit interpretations of potential departure of observations from independence. See Figure 3.2 for species key.

The Cox process models indicated that topography also influenced spatial patterns of all species. Topography and distance from residual canopy, together, explained variance in tree locations more than the latter alone (*p*-values < 0.001). Relative magnitudes of covariates show that slope, primarily, and aspect, secondarily, were most influential among conifers (Table 3.2). Ponderosa pine abundance was greatest on southwestern aspects and shallow slopes, whereas the other conifers were more abundant on northwestern aspects and steeper slopes. Quaking aspen locations were most strongly driven by topographic position with more individuals in swales (i.e., low TPI). Last, I found distance from residual forest canopy to be negatively related to densities of all conifers. Assessing the fit of these models, the observed g(r) was similar to the simulated statistics of the Cox process models at distances of 4–15 m; however, the models underpredicted tree densities at smaller distances, as corroborated by plot-wise goodness-of-fit tests (*p*-values < 0.005).

Table 3.2. Cox point process model fits

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

Covariate	**β**	**SE**	**t**	**p**	**Relative magnitude**
		Ponderosa pine (*Pinus ponderosa*)			
(Int.)	-3.549	0.083	-42.798	< .001	
Distance	-0.006	<0.001	-17.769	< .001	119.744
Aspect	-0.317	0.058	-5.504	< .001	1.793
Slope	-0.059	0.006	-10.266	< .001	13.348
TPI	-0.050	0.070	-0.709	.478	1.587
		Lodgepole pine (*Pinus contorta*)			
(Int.)	-12.536	1.478	-8.438	< .001	
Distance	-0.004	0.002	-1.855	.064	24.294
Aspect	0.669	0.500	1.339	.181	3.811
Slope	0.102	0.029	3.474	.001	630.665
TPI	0.110	0.327	0.336	.737	2.706
		Quaking aspen (*Populus tremuloides*)			
(Int.)	-5.637	0.492	-11.453	< .001	
Distance	0.001	<0.001	3.656	< .001	2.220
Aspect	0.193	0.062	3.101	.002	1.471
Slope	-0.026	0.011	-2.306	.021	5.172
TPI	-0.883	0.057	-15.496	< .001	2955.452
		Douglas-fir (*Pseudotsuga menziesii*)			
(Int.)	-9.674	1.474	-6.564	< .001	
Distance	-0.007	0.001	-6.108	< .001	265.845
Aspect	0.580	0.190	3.048	.002	3.190
Slope	0.094	0.018	5.107	< .001	380.372
TPI	-0.116	0.138	-0.845	.398	2.857

3.3.2 Patterns of Regenerating Tree Heights

I mostly found positive autocorrelation of tree heights (Figure 3.4). When ponderosa pine, lodgepole pine, and quaking aspen were within 15 m of a conspecific, they were taller than expected by random chance (*p*-values of 0.001, 0.036, and 0.001, respectively). Heights of ponderosa pine and lodgepole pine exceeded expectation at distances up to 4 m, while quaking aspen heights were greater than expected across the distance range evaluated (0–15 m). Douglas-fir was the only species for which I did not detect departure from independent marking (p = 0.135).

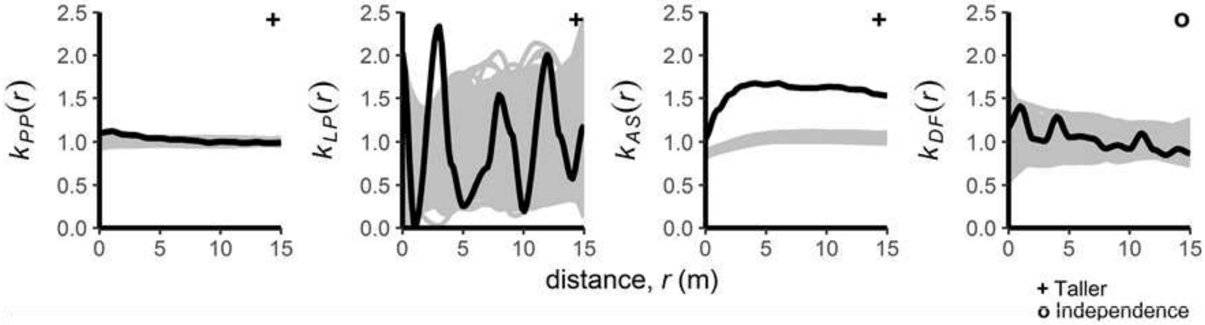

Figure 3.4 Univariate height spatial patterns

Patterns of replicated univariate mark correlation functions of post-fire tree regeneration heights (black lines) among 999 simulations of independent marking (grey lines). Symbols indicate goodness-of-fit interpretations of potential departure of observations from independence. See Figure 3.2 for species key.

Species associations influenced tree heights in just under one-third of species pairs (Figure 3.5). Among three pairs, trees of one species near another species were shorter than expected by chance. This included both quaking aspen and Douglas-fir around ponderosa pine, across the full range of distances observed (p = 0.001). In addition, ponderosa pine was shorter when near Douglas-fir (p = 0.049), particularly at distances <2 m from a Douglas-fir. However, in each of these instances, the effect size was small; proximity to heterospecifics conferred about a ~5% decrease in tree height. In just one species pair did I find a positive relationship: Douglas-fir trees within 5 m of quaking aspen were significantly taller (p = 0.030). Here again, the effect size was relatively small.

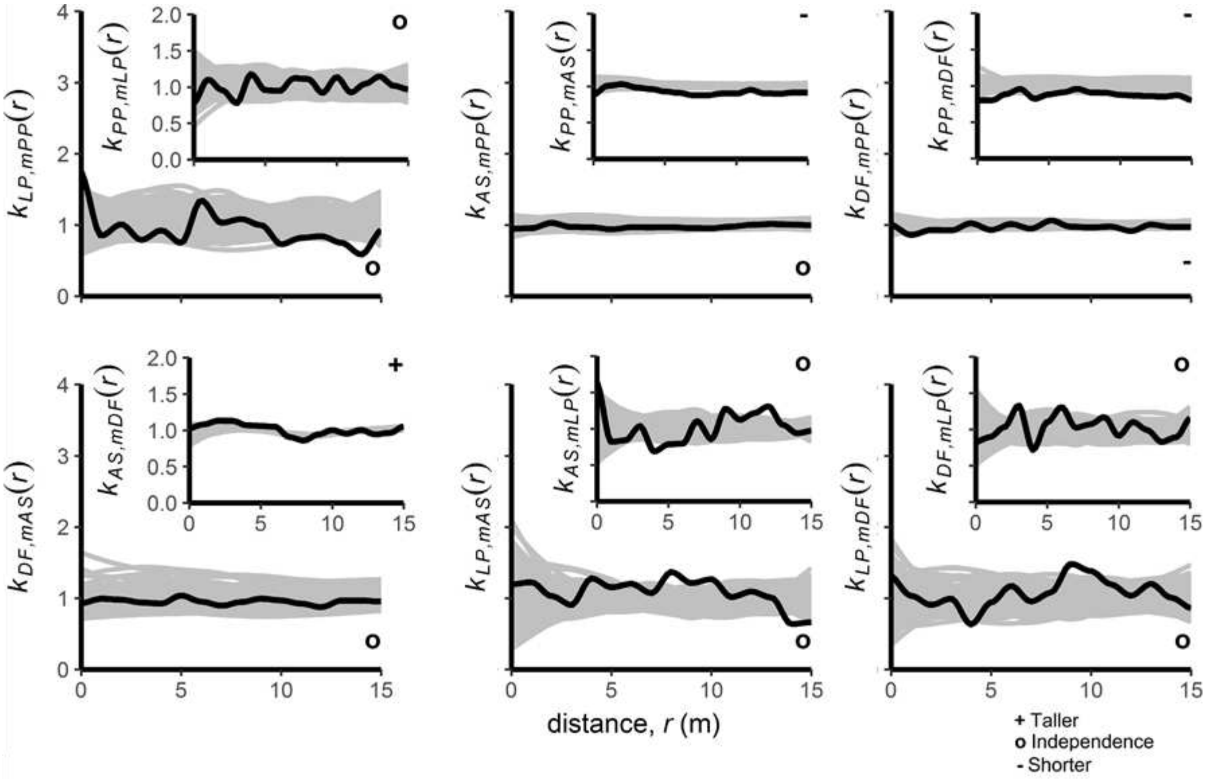

Figure 3.5 Bivariate height spatial patterns

Patterns of replicated bivariate mark correlation functions of post-fire tree regeneration heights (black lines) among 999 simulations of independent marking (grey lines). Symbols indicate goodness-of-fit interpretations of potential departure of observations from independence. See Figure 3.2 for species key.

Topographic variability minimally influenced tree heights. The full model of tree heights performed better than a reduced model, only for ponderosa pine ($p = 0.004$) and quaking aspen ($p < 0.001$). However, full models were only able to explain 2.1% of the variability in ponderosa pine heights and 15.9% of the variability in quaking aspen heights (Table 3.3). Full models were no better than reduced models for lodgepole pine ($p = 0.861$) and Douglas-fir ($p = 0.249$).

Table 3.3. General linear model fits on regeneration height

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

Covariate	β	SE	t	p	Rel. Mag.
		Ponderosa pine (*Pinus ponderosa*); (marginal-$R^2 = 0.021$)			
Intercept	-0.760	0.151	-5.030	< .001	
Distance	0.001	< 0.001	3.110	.002	1.595
Aspect	-0.026	0.026	-0.998	.318	1.054
Slope	-0.006	0.004	-1.565	.118	1.352

TPI	0.048	0.025	1.930	.054	1.294
Lodgepole pine (*Pinus contorta*); (marginal-$R^2 = 0.271$)					
Intercept	-0.178	0.671	-0.264	.793	
Distance	0.003	0.001	1.995	.054	3.652
Aspect	-0.153	0.273	-0.562	.578	1.348
Slope	-0.004	0.013	-0.327	.745	1.177
TPI	-0.054	0.148	-0.364	.718	1.192
Quaking aspen (*Populus tremuloides*); (marginal-$R^2 = 0.159$)					
Intercept	-1.153	0.210	-5.502	< .001	
Distance	< 0.001	< 0.001	2.333	.020	1.445
Aspect	-0.112	0.014	-8.037	< .001	1.251
Slope	0.046	0.003	17.861	< .001	9.648
TPI	-0.143	0.011	-13.118	< .001	2.397
Douglas-fir (*Pseudotsuga menziesii*); (marginal-$R^2 = 0.021$)					
Intercept	-1.319	0.127	-10.349	< .001	
Distance	0.001	< 0.001	1.656	0.099	1.421
Aspect	0.233	0.067	3.497	0.001	1.592
Slope	-0.005	0.003	-1.635	0.104	1.305
TPI	-0.005	0.063	-0.082	0.935	1.025

3.4 Discussion

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

Further, observed patterns stand in contrast to other studies of conifer regeneration, wherein density was one to two orders of magnitude greater during stand initiation (Donato et al. 2009; Pauchard et al. 2016). Those studies found relatively simpler patterns and no effect of topography nor biotic interactions on those patterns. This may indicate that the mechanisms controlling early stand development may be contingent on regeneration density (Donato et al. 2012).

Moreover, topography and tree interactions acted on spatial patterns of regeneration at different scales. Specifically, topography, after accounting for seed dispersal limitation, explained tree location patterns at scales greater than ~4 m, whereas tree interactions explained both location and size patterns at scales less than ~4 m. This separation of scales may result from trees modifying their immediate growing environment. For example, Nguyen et al., (2016) noted a larger separation scale of 15 m for larger trees within mature forests. If the separation scale relates to tree size, I expect that topography might diminish in influence as this sites' trees grow.

3.4.1 Intraspecific Spatial Patterns

The observed intraspecific aggregation among all species supports the idea that aggregation is the predominant pattern in ponderosa pine-dominated forests (Larson and Churchill, 2012; Ziegler et al., 2017a). After stand-replacing fire, both topography and intraspecific interactions played roles in formation of aggregation. At coarser scales, topography was explanatory in ways specific to species. On flatter and southwestern hillsides, I found greater abundance of ponderosa pine. Meanwhile, other conifers were more abundant on steeper and northwestern slopes, and quaking aspen were common in swales. At finer scales, I suggest that both species-specific regeneration strategies and intraspecific facilitation generated aggregation. Species-specific regeneration strategies may promote aggregation of both quaking aspen and lodgepole pine because both bear adaptions—resprouting and serotiny respectively, which yield ramets and seedlings, respectively—centered around parent trees (Alexander 1966; Shepperd 1993). In contrast, ponderosa pine and Douglas-fir lack in-situ seed sources following stand-replacing fire (Oliver and Ryker 1990). Rather than a species-specific regeneration strategy, I suspect that improved fitness nearer to conspecifics (Stoll and Prati 2001) resulted in increased survival of regeneration due to beneficial interactions. As facilitatory effects can increase with proximity, this selection for aggregation may play upon itself, inducing a positive aggregating feedback (Losapio et al. 2017).

Through the analysis of tree height patterns, I found size hierarchies at small scales. That is, trees were taller in denser, rather than sparser, neighborhoods. Accumulating evidence from tropical and temperate forests suggest that such size hierarchies develop early during secondary succession (Ehle and Baker 2003; Suzuki et al. 2008). These size hierarchies are often attributed to resource inequity (Weiner and Solbrig 1984); if resource inequity across abiotic gradients regulates local densities, as the results suggest, conspecifics should be not just more numerous but taller in suitable areas (Pielou 1960). However, Suzuki et al. (2008) and Stoll and Prati (2001) demonstrated that, even in otherwise homogeneous environments, tree interactions sufficiently produce unequal growing conditions and lead to size hierarchies. Given that I found little relationship between topography and tree heights *and* that size hierarchies occurred at finer scales than topographic-related tree density, the results support the latter cause of size hierarchies: denser neighborhoods can improve growth as intraspecific facilitation improves resource conditions. This interpretation warrants evaluation using controlled studies to verify the general and species-specific means of tree pattern regulation. This is especially pertinent because interactions among different abiotic and biotic factors can induce analogous patterning (Getzin et al. 2008).

3.4.2 Interspecific Spatial Patterns

Facilitation may have also shaped patterns of regeneration among heterospecifics. Unlike other species, ponderosa pine was more abundant on southwestern aspects, exposing individuals to greater moisture stress and posing a survival risk (Rother and Veblen 2016). This is counterintuitive, though it may be that survival was greater where individuals were near nurse trees. Patterns of spatial attraction to all other species may explain the existence of ponderosa pine on southwestern slopes. Spatial attraction via facilitation has also been identified among conifers following low- to moderate-severity fires in ponderosa pine forests (Callaway 2007). In addition, Fajardo et al., (2006) demonstrated that, as water availability decreased, ponderosa pine trees were more apt to establish nearer to Douglas-fir. In contrast, other conifers and quaking aspen were not attracted to other species in this study. Presumably, this is because these species were more abundant in northeasterly aspects and swales which confer less moisture stress. This study adds to accumulating evidence that regeneration of ponderosa pine may especially depend on facilitation in harsh (e.g., post stand-replacement) environments (Fajardo et al. 2006).

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

3.4.3 Limitations and Future Research Directions

Although this study has provided insights into the potential roles of topography and tree interactions in the pattern of regeneration following high severity fires, the interpretation of the results is constrained by several limitations. Previous research has suggested that the rate and pattern of tree regeneration in ponderosa pine forests is influenced by a number of complex interacting phenomena, including the spatial variability in solar radiation, temperature, precipitation, soil edaphic factors, herbivory, regeneration mechanisms, and the caching and perching behavior of wildlife (Bonnet et al. 2005; Wild et al. 2014; Chambers et al. 2016). This study's design indirectly accounted for the abiotic processes using topographic surrogates. Although a number of studies have shown a strong correlation between topographic variables and abiotic attributes including temperature, moisture and soil edaphic factors, the lack of direct measurement limits the ability to discern the exact mechanisms controlling regeneration pattern. As an alternative approach to directly measuring these abiotic factors, I could have included additional variables that are known to influence the fine scale patterns of temperature and moisture such as the presence of stumps and coarse woody debris (Bonnet et al. 2005; Wild et al. 2014; Chambers et al. 2016). Given the fine-scale variability of such factors (Vakili et al. 2016), I would expect that their inclusion would have resulted in increased resolution and understanding of regeneration pattern at scales under 4 m. Further research that aims to better understand the influence of various mechanisms across scales could shed additional light on how environmental conditions affect regeneration patterns and stand initiation following large, severe wildfires.

In addition, ponderosa pine recruitment and establishment is highly dependent on inter-annual climate (Shepperd et al. 2006). Because of this dependency, this study may provide limited understanding for regeneration following future large, severe fires or for the longer-term trajectory on these study sites. Specifically, changes in moisture regimes following the fire event could lead to changes between facilitation and competition among species. For example, previous research has suggested that as moisture stress increases, the degree of aggregation and interspecific attraction may increase (Fajardo et al. 2006); whereas, others have indicated that facilitative relationships may reverse to competitive ones (Holmgren and Scheffer 2010), inducing negative density-dependent patterns (Pielou 1962). Measurements of spatial patterns in multiple burned areas under varying climatic conditions could further help determine how plastic spatial patterns are in response.

3.4.4 Ecological and Management Implications

Anticipating how current patterns of tree regeneration may influence future forest dynamics is complex and fraught with uncertainty. However, building on prior research, I hypothesize that the current predominance of beneficial tree interactions may beget greater competition in the future (Donato et al. 2012; Wright et al. 2014). Within conspecifics, size hierarchies may lead to within-patch self-thinning of smaller, poorer competitors and relaxation of aggregation towards a more random or even uniform forest structure (Shepperd 1993; Boyden et al. 2005; Suzuki et al. 2008). The two-way competition, indicated by patterns of tree height between ponderosa pine and Douglas-fir, could produce eventual mortality of poorer competitors (Donato et al. 2012), though field studies demonstrate that fairly equal competitors can coexist in proximity despite mutually-inhibiting growth (Fajardo et al. 2006; Das et al. 2011). Conversely, the slightly shorter stature of quaking aspen near ponderosa pine hints at one-way competition; in many coniferous forests, competition drives mortality of quaking aspen, producing interspecific spatial repulsion (Peterson and Squierst 1995). The long-term persistence of quaking aspen may therefore depend on spatial refuges isolated from conifers. Thus, the facilitatory processes during regeneration may have established conditions for competitive forest dynamics.

Given that future patterns of forest structure and ecosystem function are conditioned on prior events (Stoyan and Penttinen 2000), forest managers can adopt strategies post-fire to influence desired pathways of stand development. These strategies can accelerate spatially-complex forest structure desired in many ponderosa pine forests (Donato et al. 2012). I found that patterns of regeneration exhibited some features of desired and historical conditions, such as tree grouping

(Larson and Churchill 2012), spatially-heterogeneous tree size patterns (Donato et al. 2012), and environmental-specific distributions of tree species (Peet 1981). Yet, the observed tree densities 11 to 15 years post fire were lower than average historical tree densities reported for ponderosa pine forests in the Front Range and Black Hills (100–140 trees ha^{-1}) (Brown and Cook 2006; Brown et al. 2015). If managers choose to augment natural regeneration, patterns of naturally recovering landscapes can inform efforts to address deficiencies (Turner et al. 2003) and enhance recovery (Beschta et al. 2004). Plantings should reinforce local patterns of fine-scale heterogeneity (Hessburg et al. 2016), such as those I found, leveraging both topographic gradients and presence of facilitatory woody plants (DellaSala et al. 2014).

3.5 Conclusions

The findings here lend empirical evidence to models of forest development which state that stand initiation, where sparse, is likely to be spatially heterogeneous and resulting patterns may, in part, be due to topographic conditions and tree interactions. In addition, the observed patterns indicate that facilitation dominated over competition during the initial decade of establishment of these ponderosa pine-dominated forests. This seemingly contrasts with models of early stand development which state tree competition, and not facilitation, is largely responsible for forming spatially complex forest structure (Donato et al. 2012; Bače et al. 2015); however, these models of forest development generalize stand initiation over the first few decades. It may be that competition increases during the latter half of stand initiation. In summary, the results lead us to suggest that, in addition to density-dependency, general models of early forest development may need to account for temporally dynamic and scale-dependent roles of the abiotic environment and tree interactions.

Finally, heterogeneous forests tend to have more rapid successional dynamics than homogeneous forests (Getzin et al. 2008). If post-fire actions emulate, rather than overwrite, the complex patterns of reinitiating forests, ecologically based forest management may encourage faster development of desired, complex forest structure.

CHAPTER 4 – PYRIC TREE SPATIAL PATTERNING IN HISTORICAL AND CONTEMPORARY MIXED CONIFER FORESTS, CALIFORNIA, USA

4.1 Introduction

Drier mixed conifer forests of western North America have long been shaped by frequent fire. These fires mediated heterogeneous, uneven-aged forest structures at fine scales through partial and periodic tree mortality, stimulating fire-adapted understory plants, and creating temporally and spatially variable conditions for tree regeneration (Show and Kotok 1924; Larson and Churchill 2012; Knapp et al. 2013). Consequently, forest structure was patterned into complex mosaics composed of scattered individual trees, groups of trees, and canopy openings occupied by understory plants or regenerating trees (Larson and Churchill 2012). Formation of tree groups was spurred by conditions such as small gaps with higher light availability, patchy distributions of mineral soil exposed by fire (Larson and Churchill 2012), microclimate amelioration by neighbors and nurse trees (Fajardo et al. 2006), and zoochoric seed caching (Vander Wall and Joyner 1998). Canopy openings were likely a product of either localized agents of tree mortality, unfavorable microsite conditions for tree regeneration such as shallow soils (North et al. 2004), or resource competition with nontree species (Abella et al. 2013).

Historical fire behavior and effects likely varied at fine scales in response to heterogeneously patterned forest structure and composition. Surface fuels accumulate in groups with more tree basal area (Banwell and Varner 2014), and local crowding within tree groups increases the probability of intertree fire spread (Contreras et al. 2012). This may have led to a clustered pattern of tree mortality, especially in areas with dense tree groups (Larson and Churchill 2012; Hood et al. 2018; Lutz et al. 2018). Alternatively, fire severity may increase in openings due to drier and windier microclimates (Bigelow and North 2012) and the contribution of greater understory cover to surface fuel loads (Matonis and Binkley 2018; Stephens et al. 2021). Thus, locations of higher severity patches may have been dispersed and in areas with lower tree stocking. Inferences regarding fine-scale pyric regulation of forest structure are often based on comparisons of tree spatial patterns in contemporary, fire-suppressed forests against historical forests or contemporary forests with intact fire regimes (e.g., Fry et al., 2014; Schneider et al., 2016). However, the lack of direct fire observation in these and other studies makes it difficult to understand the pattern–process interactions driving pyric regulation. Even when measurements are made before and after fires on individual sites, it is challenging to separate fire effects from other co-occurring processes such as density-dependent competition (Yu et al. 2009); but see Furniss et al., 2020).

Recently, physics-based fire modeling has been suggested as an ideal approach to test conceptual models of fire-mediated forest dynamics (Lutz et al. 2018) because simulations allow for a high degree of experimental design and control (Larson and Churchill 2012; Parsons et al. 2017; Hoffman et al. 2018a; Lutz et al. 2018). This line of inquiry has explored the feedback between heterogenous fuel arrangements and consequent fire behavior across stands (Hoffman et al. 2012; Linn et al. 2013; Parsons et al. 2017) and distance-dependency of tree-to-tree crown fire spread (Contreras et al. 2012). However, relatively few studies have used physics-based fire modeling to explore how fire interacts with forest structure patterns within stands (e.g., Ritter et al., 2020). Furthermore, an explicit comparison of how pattern–process interactions may differ between historical and contemporary forests is lacking.

An increased understanding of fine-scale fire-structure interactions can guide fuel hazard reduction treatments. This knowledge is particularly pertinent for forest restoration treatments that emulate historical forests' qualities, expressly creating a heterogeneous structure composed of single trees and tree groups (Tuten et al. 2015; Knapp et al. 2017; Ziegler et al. 2019). Over a century of fire exclusion, as well as unregulated grazing and logging, have increased tree densities, reduced the number and size of openings, favored shade-tolerant species, and decreased heterogeneity of the over and understory (Figure 4.1; Iniguez et al., 2019). Changes in forest structure and composition have resulted in greater and more uniform canopy and surface fuel loads (Lydersen et al. 2013; Fry et al. 2014; Matonis and Binkley 2018) and increased fire behavior (Hessburg et al. 2005). If the spatial patterns of trees influence the distribution of fire effects, the loss of fine-scale structural variability may be dampening the pattern–process relationship once present in historical forests (Hessburg et al. 2005; Parsons et al. 2017). Although forest restoration treatments seek to restore such relationships (Addington et al., 2018; Larson and Churchill, 2012; Tuten et al., 2015; Ziegler et al., 2017a), treatments leaving evenly spaced trees continue to be implemented (Underhill et al. 2014; Puettmann et al. 2015; Stephens et al. 2021), based on aspatial fire hazard reduction principles (Larson and Churchill 2012). Even within some variable retention harvesting methods, specifications often implement spacing-based targets within tree groups (Tuten et al. 2015). A greater understanding of how fine-grained forest overstory and understory structure interacts with fire to mediate tree patterning can help aid the design and evaluation of restoration-based silvicultural approaches (Knapp et al. 2017; Lutz et al. 2018). Additionally, this information may provide insight into the link between pattern and process at fine spatial scales and its stability over a century of forest change.

In this study, I examined the spatial dynamics of fire-caused mortality across a time series in a mixed conifer forest, which historically experienced frequent fire. I leveraged data from three large (~4 ha) forest plots that were stem-mapped immediately before harvesting in 1929, approximating forests before EuroAmerican settlement characteristics, and again in 2008, representative of contemporary long-unburned forests with a history of logging. I used a physics-based fire model to simulate fire spread in each of the two time periods and then estimated fire-caused mortality based on species and tree size. I hypothesized that mortality would be clustered and density-dependent in the historical period due to pre-existing spatial variability typical of historical forests; I further hypothesized the residual forest structure would retain a mosaic of tree groups of diverse sizes. In contrast, I expected that mortality patterns would be more random and density-independent because the 2008 counterpart plots were comparatively homogeneous with continuous canopy as opposed to discrete tree groups (Lydersen et al. 2013). Such random mortality patterns might then leave behind a less variable distribution of tree group sizes. I recognize that factors in addition to tree mortality—namely spatially variable regeneration dynamics driven by spatially variable abiotic conditions—also contributed to the historical pattern.

4.2 Materials and Methods

4.2.1 Study Area

I used three large plots of the permanent "Methods of Cutting" study established in 1929 in the Stanislaus-Tuolumne Experimental Forest of the central Sierra Nevada. The study sites have a Mediterranean climate, with warm, dry summers and cool, moist winters (Knapp et al. 2013). The sites are on a northwest aspect, at an elevation from 1,805 m to 1,840 m above sea level, and on deep, well-drained gravelly loam soil (Knapp et al. 2013; Lydersen et al. 2013).

Figure 4.1 Study site photograph

Photographs of the mixed conifer forest in one of this study's plots contrasting low canopy cover and a heterogeneous overstory and understory in 1929 (left) versus high canopy cover and a homogeneous overstory and understory in 2007 (right photograph).

These plots, named MC9 (4.3 ha area), MC10 (3.8 ha), and MC11 (4.3 ha), were originally designed to investigate regeneration and growth rates following silvicultural prescriptions in a mixed conifer forest dominated by Abies concolor Lindl. ex Hildebr., *Pinus lambertiana* Douglas, *Calocedrus decurrens* Florin, *P. ponderosa* ex. Lawson, and *P. jeffreyi* Balf., in order of abundance. Locations, species, heights, and diameter at breast height (dbh) of trees ≥ 9.1 cm dbh were recorded in 1929 prior to partial harvesting. The understory fuels were mapped into broad cover type patches (rock, tree regeneration, understory shrubs by dominant species, and the remainder assumed to be forest litter). Stem mapping of trees ≥ 10 cm dbh in MC9 and MC10 occurred again in 2008. In 2007, I remapped only 3.4 ha in MC11 because a road had built through it. For brevity, I refer to the 2007 and 2008 measurements as the 2008 measurement period. Additional information on the history of these plots and prior research is provided in Hasel et al., (1934), Knapp et al., (2013), Knapp et al., (2013), and Lydersen et al., (2013).

Prior work from Knapp et al., (2013) and Lydersen et al., (2013) have examined the forest structures in 1929 and 2008, placing these sites in the context of historical reference conditions, and contemporary conditions among similar forests. Results from these studies suggest the two sampling periods were representative proxies for pre-EuroAmerican and once-logged contemporary forests in mixed conifer forests of the Sierra Nevada. It is worth noting the historical median and maximum fire return intervals were six years and forty years, respectively; the last fire occurred in 1889, forty years before sampling (Knapp et al. 2013). Forest structure sampled in 1929 therefore represented the upper end of the historical range of variability regarding fire frequency. Consequently, the exclusion of smaller trees from sampling in 1929 may have overlooked tree regeneration establishing during the longer fire-free interval; meanwhile, few trees were likely omitted in 2008 because tree regeneration was sparse at that time (Knapp et al., 2013; Figure 4.1).

4.2.2 Fire Behavior Modeling

I simulated fire behavior with the Wildland-urban interface Fire Dynamics Simulator. Using a computational fluid dynamics approach, numerical solutions are solved in a domain composed of discretized voxels over a series of time steps (Mell et al. 2007, 2009). This approach allows for the representation of vegetation and fire behavior over three-dimensional space and time. I simulated fire spread in six instances (each of the three plots over two time periods), using the respective stem maps and accompanying understory cover type. Each of the understory cover types was crosswalked to a standard surface fuel model (Scott and Burgan 2005). The four cover types mapped initially in 1929, included conifer litter, tree regeneration, *Chamaebatia foliolosa* (Benth.) shrubs, and shrubs of other species, represented by standard surface fuel models timber-litter 3 (TL3), timber-litter 1 (TL1), grass-shrub 2 (GS2), and shrub 2 (SH2), respectively. Because understory vegetation had almost entirely disappeared by 2008 as gaps in the forest filled with trees, I simulated those surface fuels as a homogenous layer of TL3.

I simulated relatively high fire weather conditions because more severe burning conditions were expected to elicit tree mortality. Furthermore, high to extreme fire weather conditions are associated with a majority of burned area in western U.S. wildland fires (Finney and McAllister 2011). Wind speeds entering the domain were set at 5.07 m/s at 6.1 m above ground level. Surface and crown fuel moistures were simulated at 5% and 100%, respectively. These values represent the 99.9th and 14.5th percentile for the wind speed and 1-hr dead downed woody fuel moisture, respectively, compared to data from 2011–2019 at the nearby Pinecrest 2 remote automated weather station (National Weather Service ID #043615). Appendix S1 gives technical detail on the design and further parameterization of the simulations.

I calculated gross and per-tree crown consumption (percent dry mass lost) from simulation results. I used these results to estimate mortality following Parsons et al., (2018); I applied tree mortality likelihood equations from Hood et al., (2007) using dbh, tree species, and, in lieu of percent crown volume scorched, crown consumption. Trees with a mortality likelihood ≥ 50% were designated fire killed.

4.2.3 Point Pattern Analyses

I used a framework of point pattern analyses to examine stand scale spatial patterns of trees before each fire, and the spatial dynamics of projected mortality following each fire. All statistical inferences were made using an $\alpha = 0.05$. Point pattern analyses were conducted in Programita ver. 2018 (Wiegand & Moloney, 2013). I used tidyverse ver. 1.2.1 (Wickham et al., 2019) for data wrangling, and cowplot ver. 1.0.0 (Claus & Wilke, 2019) and ggthemes ver. 4.2.0 (Arnold, 2019) for data visualization, in R ver. 3.6.1 (R Core Team, 2019).

4.2.4 Mark Correlation Functions

I used mark correlation functions to describe the spatial structure of tree sizes, aiding interpretation of fire effects. Mark correlation functions yield statistics of an appropriate test function averaged over all pairs of trees at distance r apart. I first used the r-mark correlation function (Illian et al., 2008), termed $k_{\mathrm{dbh}}(r)$ here, whose test statistic was the average tree dbh located r away from another tree. By comparing the empirical statistics to a null model of random labeling where dbh is randomly shuffled among tree locations, I could assess whether trees distanced r away from another tree were smaller or larger than the mean aspatial tree dbh. In addition, I used a mark variogram, $\gamma_{\mathrm{dbh}}(r)$, to assess whether tree sizes were spatially correlated. The test function $\frac{1}{2}\,(\mathrm{dbh}_i - \mathrm{dbh}_j)^2$ described the semivariance in tree dbh between two trees, i and j, located r distance apart. I compared the empirical statistics to a null model of random labeling to determine whether dbh between trees located r distance apart were more or less variable than expected by chance.

4.2.5 Pair Correlation Functions

The first pair of univariate pair correlation functions described the patterns of living trees, both before fire, $g_{\mathrm{all}}(r)$, and after fire, $g_{\mathrm{alive}}(r)$. Univariate pair correlation functions measure the average number of points, that is, trees, at distance r from a point, normalized by dividing by the expected number of points. The empirical pair correlation functions are compared to a set of functions realized from a null model. In these analyses, I used an inhomogeneous Poisson point process model. This null model randomly distributed points using an intensity field parameterized by an Epanechnikov smoothing kernel at a bandwidth of 20 m and a resolution of 1 m. I chose an inhomogeneous over a homogeneous Poisson process to account for intensity gradients in the observed data. Any values above or below expectation reflected those trees were spatially distributed as aggregated or uniform patterns, respectively.

The next pair of pair correlation functions described the patterns of estimated fire-killed trees. Bivariate pair correlation functions count the average number of type 2 points at distance r from a type 1 point, normalized by the density (points per area) of type 2 points (Wiegand & Moloney, 2013). Here, the types were the labels of alive or dead. First, I calculated the difference $g_{\mathrm{dead,dead}}(r)–g_{\mathrm{alive,dead}}(r)$, concisely referred to here as $g_{\mathrm{cluster}}(r)$; $g_{\mathrm{dead,dead}}(r)$ measured the relative density of fire-killed trees near fire-killed trees and $g_{\mathrm{alive,dead}}(r)$, the relative density of fire-killed trees near surviving trees. Thus, $g_{\mathrm{cluster}}(r)$ estimated whether fire-killed trees were more, less, or equally common around surviving trees than around other fire-killed trees. The null expectation was zero, whereas higher values indicated clustering of mortality, and lower values indicated the dispersion of mortality. Second, I measured density dependence of mortality with the difference $g_{\mathrm{dead,dead+alive}}(r)–g_{\mathrm{alive,dead+alive}}(r)$. This compared the relative density of all trees near a dead tree minus the relative density of all trees near a surviving tree. The null expectation was zero; higher and lower values indicated a bias toward mortality in areas of higher or lower density, respectively. For the null models of g_{cluster} (r) and $g_{\mathrm{dens.dep}}(r)$, I randomly labeled points' types, alive or dead, rather than moving points because the locations of survival or mortality are conditioned on the spatial pattern of trees before a fire (Goreaud & Pelissier, 2003).

Monte Carlo methods were used to create realizations for assessing the departure of empirical statistics from a null model. I generated 399 simulations of the respective null models for each point pattern analysis over a range of *r* from 0 to 15 m. The range of *r* should reflect the scale that spatial correlations are expected to manifest a priori, often 0—15 m among trees (Wiegand & Moloney, 2013). A simulation envelope can be constructed from the 2.5th to 97.5th percentile statistic for each distance *r* followed by a comparison of the empirical statistic against the envelope (Wiegand & Moloney, 2013). However, standardization is recommended to make formal inference without inflated Type I Error (Wiegand & Moloney, 2013). Therefore, I first studentized the empirical and null correlation functions to *z* scores, constructed maximal global envelopes from the 2.5 to 97.5 percentiles, and then back transformed those functions' statistics to their original scale (Myllymäki et al., 2015). Under this approach, a deviation at any distance r from the envelope constituted a statistically significant deviation for the set of *r* from 0 to 15 m (Wiegand & Moloney, 2013). Last, I then averaged mark correlation functions and pair correlation functions across distance *r* from 0 to 15 m to produce a single statistic to compare the strength of departure from null models across time periods. The implementation of point pattern analyses here followed best practices laid out in Velázquez et al., (2016); I accounted for edge effects.

4.2.6 Modeling Fire Effects on Within-stand Structure

I assessed whether fires produced different outcomes in the distributions of tree group size (number of trees per group) in 1929 versus 2008. Tree groups were identified following the approach whereby trees within a group are within a limiting distance, here 6 m, from another member tree (e.g., Lydersen et al., 2013). First, I compared the median group sizes with a Wilcoxon signed rank test, and second, the variation of group sizes with a modified signed-likelihood ratio test for equality of coefficients of variation (SLRT). I modified *p* values with a Bonferroni correction to account for multiple comparisons across the three plots. Third, I used Sankey diagrams to visualize how trees' group sizes changed due to fires. For this, I binned groups into size classes: single trees, 2–4, 5–9, 10–19, and 20+ trees per group.

4.3 Results

4.3.1 General Forest Structure and Fire Behavior

Forest structure differed substantially between 1929 and 2008 in all three plots (Table 4.1). Despite trees being on average considerably smaller in 2008 than 1929, basal areas were higher in 2008 because tree density was greater. Furthermore, the canopy base height in 1929 was twice as tall on average as in 2008. Tree sizes were less randomly distributed in 1929 than in 2008. In 1929, the dbh of trees within 15 m of each other was smaller (26.6 cm averaged across plots) than the average dbh of all trees (33.1 cm averaged across plots; Figure 4.2a). Further, the semivariance of those trees' dbh within 15 m of another averaged 0.51 across plots (Figure 4.2b). In contrast, the dbh of trees within 10 m of each other in 2008 averaged 27.4 cm, while the average dbh of all trees was 28.7 cm (Figure 4.2a). In addition, the semivariance of those trees' dbh within 15 m of another averaged 0.82 across plots (Figure 4.2b). These results show that trees closer to one another tended to be similar in size and relatively smaller. This pattern was much more pronounced in 1929 than in 2008.

Table 4.1. Forest structure and mortality

Summary of stand structure, within and across species, by plot and measured year, as well as canopy consumption and predicted mortality.

Plot	**Pre-fire forest structure**	**Mortality (% pre-fire stocking)**

	Trees ha^{-1}	Basal area (m^2 ha^{-1})	QMD (cm)	Canopy base height* (m)	Rate of spread (m s^{-1})	Canopy consumption (%)	Trees ha^{-1}	Basal area (m^2 ha^{-1})
				1929				
MC9	307	54.8	47.8	1.4	0.64	27	53	17
MC10	300	52.0	47.2	1.4	0.58	27	62	16
MC11	434	30.1	42.2	1.4	0.49	26	57	16
				2008				
MC9	846	38.0	32.1	0.7	0.65	90	97	84
MC10	723	72.2	35.8	0.7	0.66	90	97	84
MC11	680	66.1	35.4	0.8	0.57	78	88	62

*Canopy base height expressed as the tenth percentile crown base height

Fire behavior and effects predictions were numerically higher in 2008 than in 1929. Averaged across plots, rates of spread were 0.57 m/s and 0.63 m/s in 1929 and 2008, respectively. Canopy consumption tripled from 1929 to 2008, averaging 26% and 78% in 1929 and 2008. Last, mortality estimates rose from 57% of trees in 1929 (16% of basal area) to over 94% of trees (77% of basal area) in 2008.

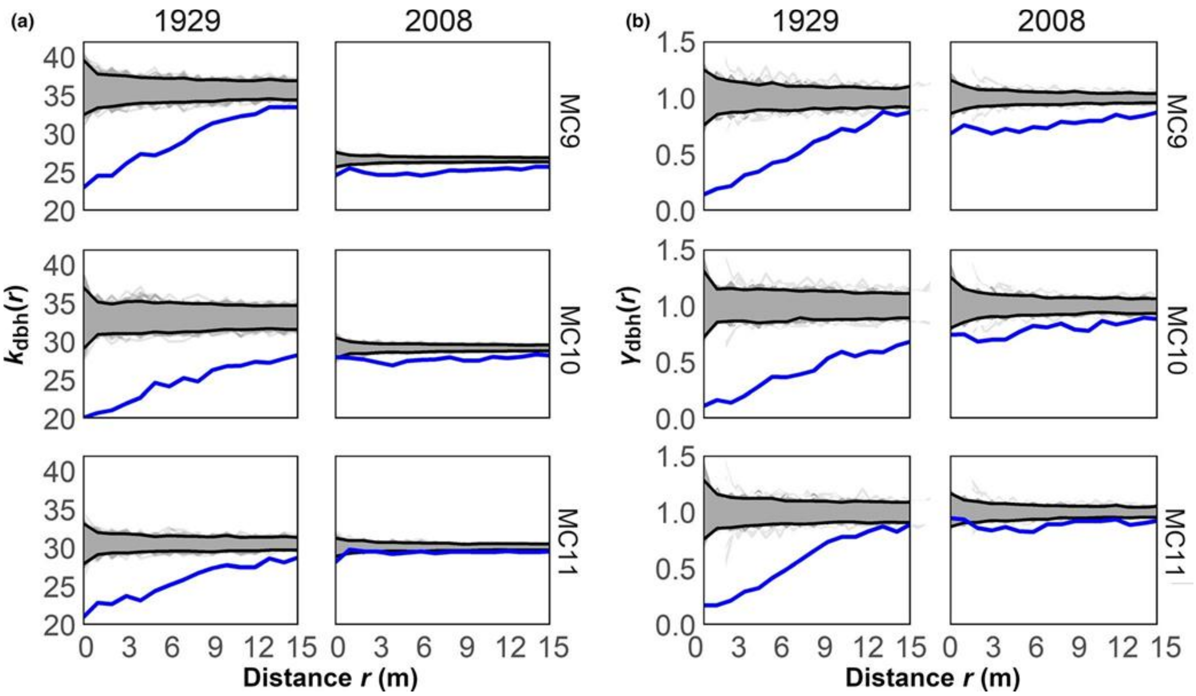

Figure 4.2 Spatial structure of tree DBH

Mark correlation functions describing the spatial structure of tree diameter at breast height (dbh) in 1929 and 2008 for each plot (MC9, MC10, MC11) where (a) shows the r-mark correlation function, $k_{dbh}(r)$, which is the average dbh at distance *r* from another tree and (b) shows the mark variogram, $\gamma_{dbh}(r)$ which is the correlation of dbh between trees at distance *r* apart. Blue lines are the empirical functions, while gray lines are simulated functions of null models generated via random labeling and black lines are the 95th percentile confidence envelopes.

4.3.2 Fire Effects on Tree Spatial Patterns

Spatial and aspatial distributions of surviving and fire-killed trees were markedly different across time periods. Whereas tree mortality and survival were arranged in a patchy mosaic in 1929, only scattered trees were estimated to survive in 2008 (Figure 4.3a). In both time periods, larger trees were more likely to survive (Figure 4.3b); across plots, in 1929, the average surviving tree ranged from 46.3 to 56.7 in 1929 and 59.8 cm to 81.2 cm dbh in 2008.

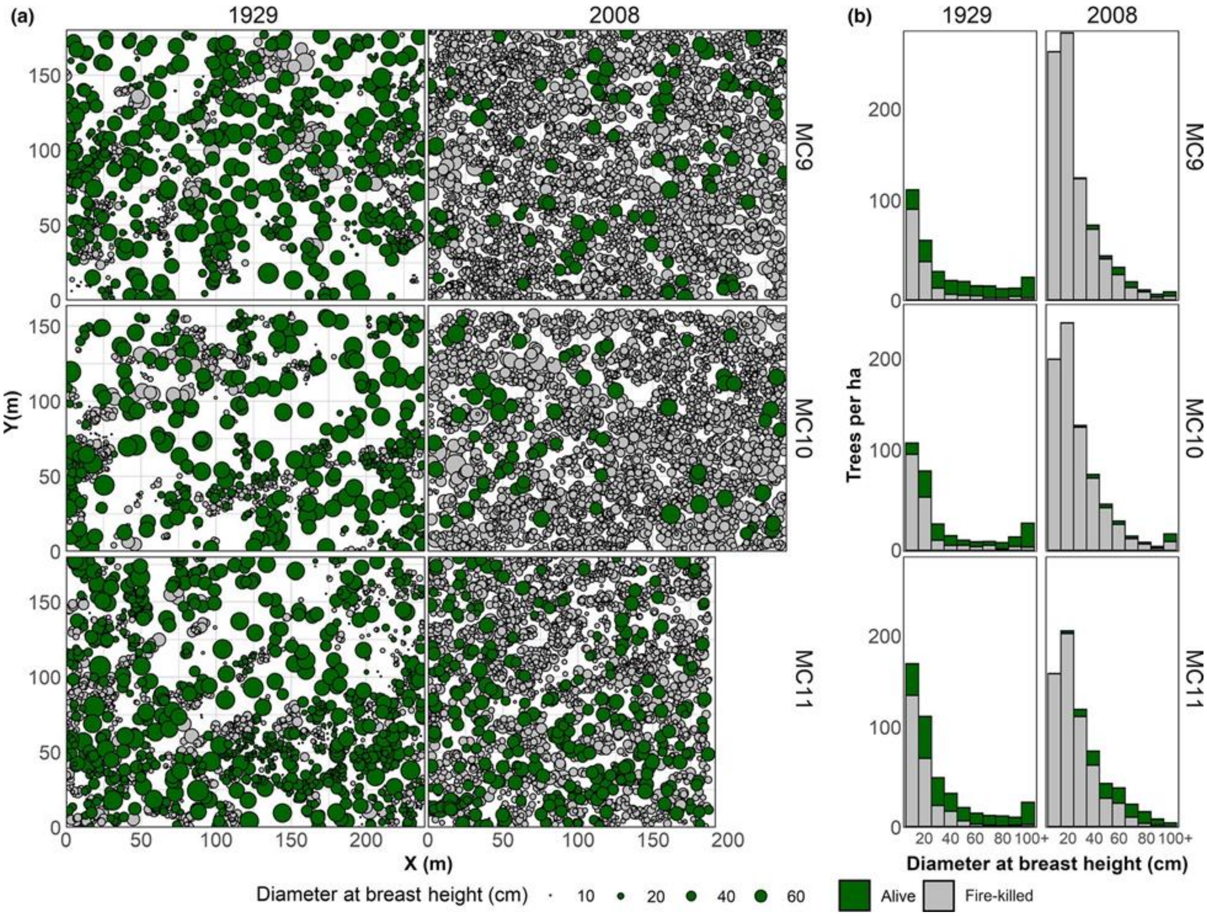

Figure 4.3 Study site stem-maps and DBH distributions

The locations of killed and surviving trees, by plot and year (a), and (b) histograms of trees by size

Simulated fires markedly altered the spatial patterns of trees in 1929. Trees were initially aggregated; as a measure of aggregation magnitude, z scores of $g_{\text{all}}(r)$, averaged across r, ranged from 5.4 to 7.6 across sites (Figure 4.4a). Aggregation was present postfire but diminished; r-averaged z scores of $g_{\text{alive}}(r)$ ranged from 1.8 to 2.4 (Figure 4.4b). Mortality was not randomly distributed (Figure 4.4c), with clustering of fire-killed trees ($g_{\text{cluster}}(r)$; r-averaged z: 3.1— 9.6). Further, dead trees had more neighbors than surviving trees ($g_{\text{dens.dep}}.(r)$; Figure 4.4d), indicating mortality was density-dependent (r-averaged z: 3.1—6.4).

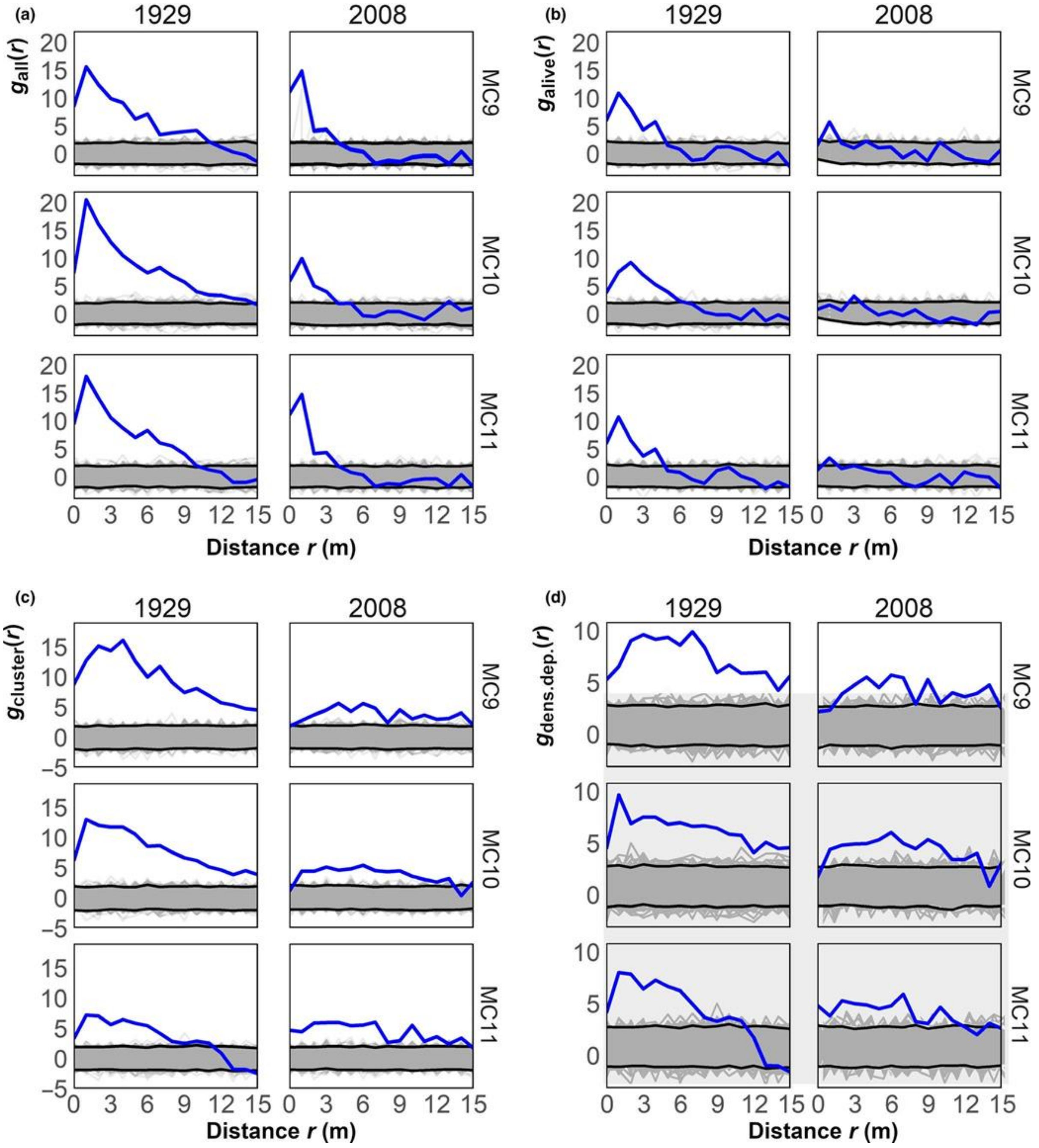

Figure 4.4 Spatial patterns of living and fire-killed trees

Standardized effect size of four points pattern statistics within plots in 1929 and 2008. The functions describe the spatial pattern of all trees before a simulated fire ($g_{all}(r)$); (a), the pattern of residual trees ($g_{alive}(r)$); (b), the clustering of killed trees ($g_{cluster}(r)$); (c), and the density dependence of killed trees ($g_{dens.dep}(r)$); (d). Blue lines are the empirical functions, while gray lines are simulated functions of null models generated via random labeling, and black lines are the 95th percentile confidence envelopes.

Trees were less aggregated in 2008 ($g_{all}(r)$ r-averaged z: 1.8—2.2; Figure 4.4e). Fires also dampened residual aggregation, measured by $g_{alive}(r)$ (Figure 4.4f; r-averaged z: 0.2—0.8). The spatial distributions of the fire-killed trees were less clustered (Figure 4.4g; r-averaged z: 3.7—4.3), as measured by $g_{\text{cluster}}(r)$. These killed trees were also in locations of higher tree density ($g_{\text{dens.dep.}}(r)$; r-averaged z: 3.1—3.3). Compared to 1929, the magnitude of all measures—tree aggregation before and after a fire, and clustering and density dependence of fire-killed trees—were all lower 2008.

4.3.3 Fire Effects on Tree Groups

Before fire, tree groups were more numerous and larger in 2008 than in 1929 (Figure 4.5). In 1929, there were between 114 and 129 groups per hectare. Groups with multiple trees amounted to 41% to 49% of all tree groups, constituting 75% to 85% of all trees and 41% to 53% of the stand basal area. In contrast, there were between 160 and 186 groups per hectare in 2008. Between 56% to 65% of these groups were multitree groups, with 88% to 93% of all trees and 85% to 91% of the stand basal area. The mean group size (inclusive of single trees) before fire was significantly smaller in 1929 (2.4–3.5 trees per group) than in 2008 (3.7–5.3 trees per group; Wilcox tests p values ≤ 0.03). The coefficient of variation (CV) of pre-fire tree group size in 1929 versus 2008 differed in MC9 (CV of 1.57 and 2.08, respectively; SLRT $p = .03$), but not in MC10 (CV of 2.26 and 1.72, respectively; SLRT $p = .14$), nor in MC11 (CV of 1.54 and 1.37, respectively; SLRT $p = .72$).

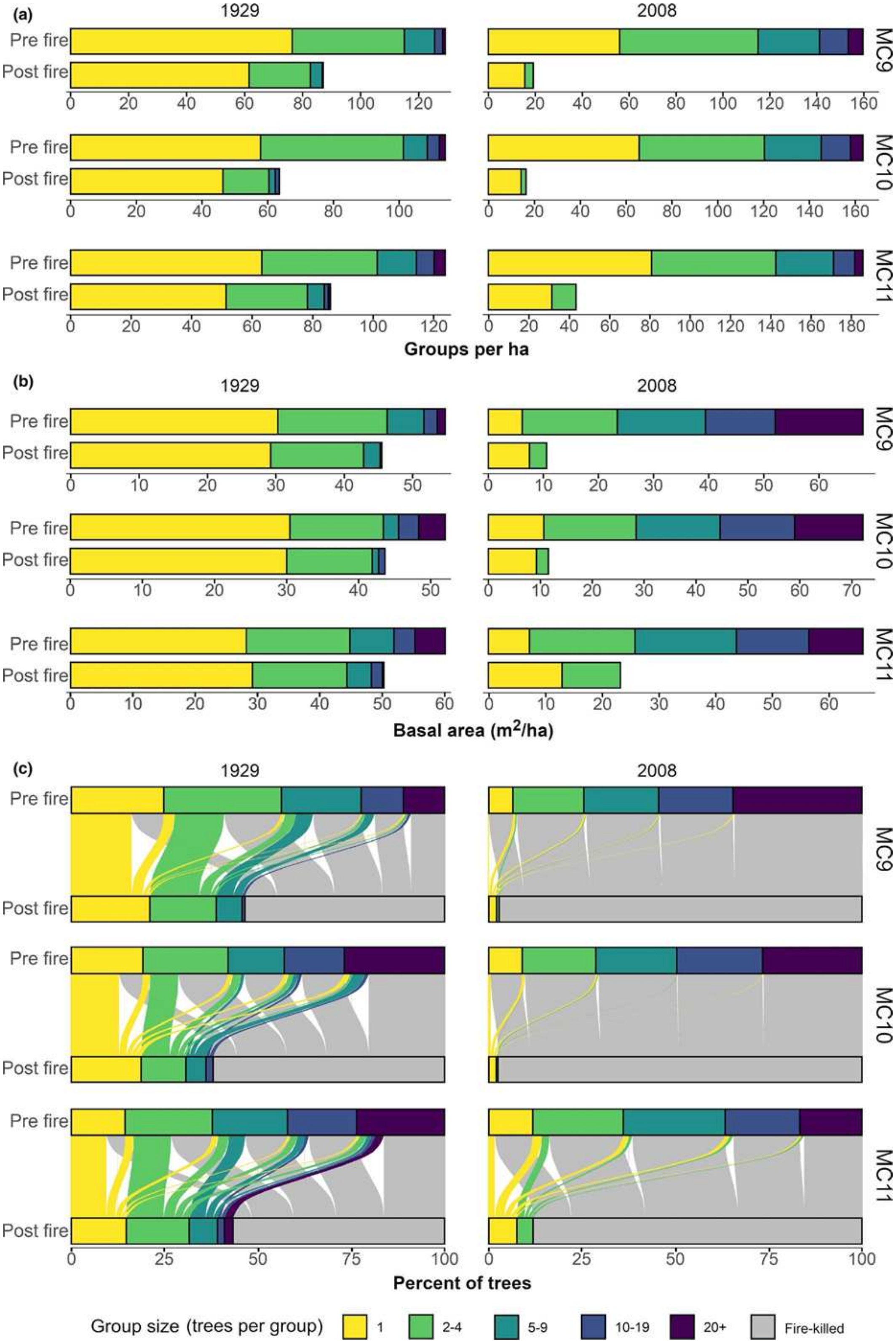

Figure 4.5 Tree group size distributions

Change in tree groups per hectare (a), basal area by tree group (b), and flow of trees between tree group sizes (c), following simulated fire.

After fire, tree groups were fewer in number, smaller in size, and less variably sized in 2008 than 1929 (Figure 4.5). Plots in 1929 had 64 to 87 groups per hectare. Twenty-seven percent to 40% of groups, across plots, had multiple trees, accounting for 57% to 71% of trees and 31% to 43% of the basal area. After fire in 2008, there were 16 to 44 groups per hectare, with 13% to 28% of groups as multitree groups. These multitree groups made up 26% to 36% of trees and 20% to 44% of basal area. Residual tree groups averaged 1.5–1.9 and 1.1–1.3 trees per group in 1929 and 2008, respectively. The difference in group sizes between periods was supported by Wilcoxon tests in MC10 ($p = .01$) and MC11 ($p < .01$) but was not significantly different in MC9 ($p = .07$). Further, residual tree groups were less variable in size in 2008 (CV from 0.32 to 0.46) than 1929(CV from 0.79 to 1.16; SLRT, p values < 0.01).

The effect of fires on tree group size distributions differed greatly between time periods. In 1929, trees within larger groups were more likely to be killed (Figure 4.5c). For example, approximately two thirds of all single trees survived, providing the bulk of single trees postfire, but less than half of trees in groups of 2 to 4 trees persisted. Fires, therefore, had the effect of splitting larger tree groups into smaller residual groups (Figure 4.6). In 2008, however, a large majority of trees were killed regardless of their respective tree group size (Figure 4.5c), and residual single trees and groups of 2–4 trees were derived from a mixture of all pre-existing group sizes (Figures 4.5c and 4.6).

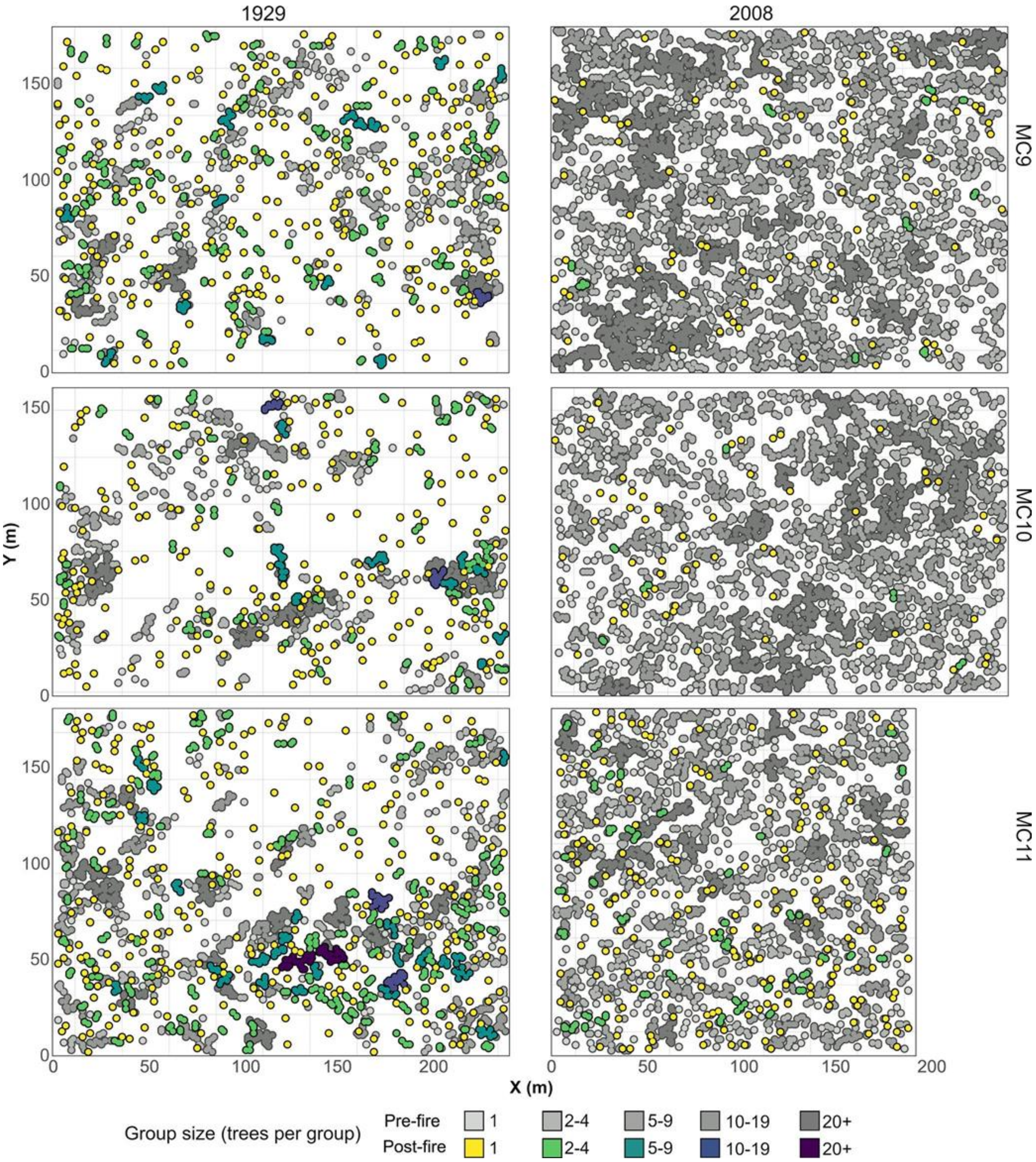

Figure 4.6 Tree group shifts following fire

Mapped change in distribution of trees, by tree group size class

4.4 Discussion

Fine-scale heterogeneity in forest structure is increasingly recognized as a salient characteristic of forests that historically experienced frequent fire (Larson and Churchill 2012;

Puettmann et al. 2015; Clyatt et al. 2016). This heterogeneity is thought to have been a self-reinforcing pattern–process relationship with low to moderate severity fire (Bonnicksen and Stone 1980; Larson and Churchill 2012). The modeling results here based on the historical data support this interpretation and point to a strong local fuel control on fire effects. Simulated fires in 1929s forest condition maintained qualitative and quantitative characteristics typical of forests adapted to frequent fire. Specifically, trees predicted to survive these fires were arranged in an aggregated pattern (Figure 4.3b) consisting of both single trees and groups of up to twenty trees (Figure 4.5). This mirrors the patterns of trees reconstructed in many frequent-fire forests of western North America before EuroAmerican settlement (Larson and Churchill 2012). Clyatt et al., (2016) found that most (~73% to 99%) trees in this region were historically single trees or in small groups of 2 to 9 trees. I found fewer single trees or trees in small groups (64% on average) in the historical period before fire, whereas 94% of trees were single or in small groups after simulated fires. Though this shift was large— greatly reducing larger (10+ trees) groups and increased the relative abundance of single trees—the postfire forest structure fell within the historical range of variability reported by Clyatt et al., (2016).

Simulated fires in the contemporary forest condition produced quite different patterns of surviving trees than those based on the historical forest condition. As has been identified in many other studies in frequent-fire forests (e.g., Iniguez et al., 2019; Sánchez et al., 2009), tree establishment and growth over decades without fire at this study site contributed to many more trees that were arranged in a more homogeneous condition (Lydersen et al. 2013). This coupling of higher tree density and greater homogeneity resulted in a relatively continuous tree canopy layer, which was quite different from the broken, clumpy tree canopy layer in the 1929 condition (Figure 4.3). After fire, no tree groups had more than four trees, and 64% to 82% of all trees were single trees. The shift from trees occurring mostly in large tree groups before fire to single trees after fire has been observed elsewhere in contemporary Sierra Nevada forests in patches of high severity (Kane et al. 2019). This pattern occurred because the surviving larger, more fire-resistant, trees were dispersed rather than clustered, a common characteristic among the largest trees in many frequent-fire forests (Boyden et al. 2005; Larson and Churchill 2012). Consequently, the results suggest high-severity fires in overstocked, contemporary forests are more likely to yield random patterns of sparse residual trees rather than rectify the trend toward homogenization over fire-free decades.

Spatial patterns of predicted mortality from fire can be largely attributed to local arrangements of differently sized trees. In 1929, fire-killed trees were generally smaller, highly clustered, and density-dependent. This pattern is facilitated by the spatial segregation of trees by size class, leading to clustered mortality among smaller trees, which tend to be near each other (Figure 4.2). This pattern of clustered density-dependent fire-caused tree mortality has been observed in similar Sierran mixed conifer forests (Kane et al. 2019) and dry *Pinus sylvestris* (L. var. mongolica Litv.) forests in China (Yu et al. 2009). In contrast, fire-killed trees in 2008 were widespread, not clustered, and less density-dependent than in 1929. These differences are due to a combination of intermixed tree sizes, which is related to the dispersion of small trees, as well as higher tree stocking, larger tree groups, and fewer canopy interspaces (Figures 4.2 and 4.5). First, small tree dispersion provides numerous points for surface to crown fire transition to occur. Second, the increased stocking and presence of large tree groups reduces local convective cooling, facilitating both crown fire transition and spread (Ritter et al. 2020). These results suggest that the fire-mediated patterns of tree mortality have been significantly altered since historical times and that these altered patterns are produced by more severe fires resulting from greater tree densities and altered tree arrangements.

Simulated fires in both periods involved the same fire weather scenario, which by most standards would be considered high fire danger (Bradshaw et al., 1984). Interestingly, despite this fire danger level, the forests in the historical period maintained their salient structural characteristics, that is, large live trees arranged in a heterogeneous mixture of groups and individuals (Larson and Churchill 2012). Meanwhile, simulated fires in the contemporary period produced historically ahistorical forest structures with relatively random and sparse overstories. Though clustered tree regeneration may recover aspects of spatial heterogeneity at some time after fire (Ziegler et al., 2017b), the overall stocking would likely be well under the natural range of variation for these forests (Safford and Stevens 2017). This is somewhat counter to findings from studies that reported restorative effects from actual wildfires in long fire-excluded forests (Churchill et al. 2013a; Jeronimo et al. 2019; Kane et al. 2019). However, these differences are likely explained by the variation in fire weather in actual wildfires and pre-fire fuel structures, which are likely more variable than fuel models indicate. While finding of divergent postfire outcomes between historical and contemporary forests is not new (Brown et al. 2008; Taylor et al. 2014), the findings here are novel because they explicitly account for differences in the spatial patterns of trees. In doing so, I demonstrated a considerable impact of forests with lower densities and heterogeneous tree arrangements, including sizeable horizontal and vertical fuel gaps, on mitigating fire-caused tree mortality. Furthermore, these findings serve as quantitative evidence supporting the assertion that historical forests' heterogeneity made them relatively resistant to fire, even under high fire weather conditions (Safford et al., 2012; Show & Kotok, 1924; Stephens et al., 2016).

The lack of canopy gaps in the contemporary period coupled with overall smaller trees allowed for higher intensity fires, which translated to greater predicted tree mortality. These findings can be incorporated in forest restoration strategies that seek to balance seemingly competing objectives, such as high tree canopy cover versus lower forest density (e.g., USFS, 2019). These findings suggest that forest restoration efforts that attempt to mimic historical tree patterns by retaining clumps of high local tree cover, while also creating gaps and isolated individual trees provide a structure that helps reduce wildfire hazard.

4.4.1. Limitations and Directions for Future Research

Virtual experimentation permitted us to simulate potential fire behavior in historical and contemporary forests. This approach overcame a common limitation of using pattern analysis alone to retrospectively infer the effects of processes like fire (McIntire and Fajardo 2009; Lutz et al. 2018). However, the single set of burning conditions I simulated was narrower than the daily and seasonal variation of fire weather and climate within and across fire seasons. Previous research identified that the interaction between fire behavior and the spatial arrangement of fuels depends on burning conditions (Linn et al. 2013; Parsons et al. 2017). Had I simulated fires under more moderate burning conditions, I might expect fires in 2008 yield more heterogeneous forests, similar to the findings of heterogeneity after fire following actual, moderate fires by Kane et al. (2019). Furthermore, the variability in fire weather over a fire's duration and topographic complexity would be expected to promote heterogeneous residual forest structure. Additional research is needed to understand the mediation of forest structural patterns under a broader set of burning conditions and its implications on the use of prescribed fires and managed wildfires for stand and landscape restoration.

This study design purposefully excluded impacts from secondary agents of fire-caused mortality, whose effects on tree spatial patterns can confound the effects from direct fire damage (Yu et al. 2009). However, the approach I used to predict tree mortality (Parsons et al. 2018), while strictly accounting for the effects of direct fire damage, relies on substituting crown consumption for crown scorch in empirical tree mortality equations. This substitution, as well as additional mortality following delayed ecophysiological processes (Hood et al. 2018), may have led to an underprediction of tree mortality, as well as altered patterns of tree mortality (Furniss et al., 2019). Because higher severity fires lead to greater homogeneity of forest structure (Kane et al. 2019; Koontz et al. 2020), any underprediction of tree mortality may have led to overestimated tree spatial heterogeneity after a fire. Additionally, advancements in tree mortality predictive models have incorporated species-specific response curves relating crown damage to risk of mortality (e.g., Hood and Lutes, 2017); these model forms outperform the predictive models from Hood et al. (2007) used here (Grayson et al., 2017), but methodologies to apply these mortality models to output from physical heating models are still in development (Hood et al. 2018). I echo calls for continued research connecting heating and physical damage from fire to tree mortality (Hood et al. 2018; O'Brien et al. 2018). Such efforts will increase the applicability of physics-based fire models (Parsons et al. 2018).

Finally, it is important to recognize that fires are not the only exogenous agents shaping tree patterns at fine scales. In frequent-fire forests of the United States, agents such as wind, ice/snow, lightning, animals, bark beetles, and defoliators also shape forest structure (Lundquist and Negron 2000). Their impacts on tree patterns differ from fire. For example, while creating clustered mortality patterns similar to fire (Addington et al. 2018), mountain pine beetles (*Dendroctonus ponderosae*) preferentially attack moderate to larger individual trees. Since larger trees tend to be aggregated, as in this study, tree mortality patterns resulting from mountain pine beetle may appear as less density dependent. Adding further complexity, the impacts of these disturbances are also conditioned on the tree patterns resulting from preceding disturbances (Lundquist and Negron 2000). Larson and Churchill (2012), for example, suggest that elevated surface fuel accumulation underneath tree groups, which experienced some previously mortality from insects or pathogens would increase the likelihood of fire-caused mortality. This milieu of biotic and abiotic agents of mortality, in addition to, and interaction with, patterns of fire-damaged trees, can produce wholesale shifts in patterns of residual living trees, legacy remnants, and tree mortality away from the immediate postfire patterns of live and fire-killed trees (Furniss et al., 2020). An increased understanding of overlapping disturbances on the formation and modification of tree spatial patterns will aid in the design of restoration treatments and the use of tree spatial patterns to interpret site history.

4.5 Conclusions

This study investigated patterns of tree mortality and the consequent patterns of surviving trees following simulated fires in a historical and contemporary mixed conifer forest of the Sierra Nevada. Mortality was biased toward smaller diameter trees in the historical period leading to clustered and density-dependent patterns of tree mortality, while maintaining a diverse range of residual tree groups characteristic of historical dry forests. In the long-unburned contemporary period, fire-caused mortality was widespread, resulting in sparse scatterings of trees and small tree groups after fire. Estimated tree mortality and patterns of residual trees were more random and less heterogeneous in the contemporary plots than in either their historical counterparts or the historical range of variability. This study suggests that high-severity fires in these, and similar forests, today are unlikely to reestablish the historically characteristic pattern–process linkages. Relying on fire alone to achieve these structural qualities likely requires multiple entries of prescribed fire (Collins et al., 2019) or a fortuitous occurrence of moderate severity wildland fire (Kane et al. 2019). Alternatively, mechanical thinning followed by prescribed fire may achieve these qualities more quickly while leaving less to chance (Knapp et al. 2017). Managed ecological processes and management activities which emulate the characteristics of historical forest structure may enhance resistance to modern wildfires imperiling future forests.

CHAPTER 5 – FINE-SCALE TREE ARRANGEMENT AFFECTS FUEL REDUCTION EFFECTIVNESS

5.1 Introduction

Forest fuel reduction treatments are a key management practice to reduce fire hazard and undesirable fire effects (Vaillant and Reinhardt 2017). Within dry forests of the western US in particular, these treatments seek to rectify changes to forests which have occurred due to a host of land use and land management practices occurring since the late 19th Century such as suppression of once frequent (intervals of < 35 yr.) fires (Covington and Moore 1994; Battaglia et al. 2018; Hessburg et al. 2019). These changes include increases in surface and canopy fuel loads, loss of early seral stands, and higher abundance of shade-tolerant tree species, among other changes. As a consequence, the potential for large and historically-uncharacteristic severe wildfires has been increasing (Fornwalt et al. 2016). Immediate impacts of such shifting fire regimes include societal and economic costs associated with smoke impacts and loss of life and property (Rocca et al. 2014). Extended impacts include risks of erosion leading to degradation of water quality and aquatic habitat in a severely burned landscape (Rhoades et al. 2011), and broad scale tree mortality as well as poor forest recovery where large severe patches hinder natural regeneration (Ziegler et al. 2017b). Climate change further increases the potential for severe fires by increasing the duration of the fire season and frequency of severe weather during which large fire growth can occur (Khorshidi et al. 2020). Furthermore, shifts in precipitation patterns can increase fuel loads available for burning and stress trees through drought, heightening susceptibility to fire-caused mortality (Malone et al. 2016; Stephens et al. 2018a). Annual moisture deficits, associated with climate change, has also been linked to increases in tree regeneration failures in recent decades (Stevens-Rumann et al. 2018). To mitigate these ecological, societal, and economic impacts of large, severe fires, fuel treatments use silvicultural techniques to alter the fuel complex, with the aim of reducing fire behavior and severity (Hoffman et al. 2018b).

Fuel treatments in dry forests of the western US are generally accepted as potentially effectual in reducing fire behavior and severity. This stems from a scientific understanding that fire behavior is driven by fire weather, topography, and the characteristics of fuels (Hoffman et al. 2018b), Of these, fuel treatments directly manipulate the latter. Fuel treatments are oriented around four objectives (Keyes and O'Hara 2002; Agee and Skinner 2005): reduce surface fuel loads, increase canopy base height, reduce canopy bulk density, and preserve larger fire-resistant trees. The reduction of surface fuel loads and lifting of the canopy base height reduce the likelihood of fire transition from the forest floor to the canopy while reduction in canopy bulk density dampens chance of crown fire spread. Fire modelling and case studies post fire demonstrate that silvicultural cuttings following these objectives reduce fire behavior and effects, especially when combined with prescribed or managed fires to reduce surface fuel loads (Fulé et al. 2012).

The application of silvicultural targets to achieve these objectives is often applied uniformly within stands (Larson and Churchill 2012; Stephens et al. 2021). This may be explicit through the use of thinning from below (i.e., low thinning) to raise the canopy base height, and distance-based specifications which seek to separate tree crowns (Dennis 1983; Johnson 2008; Johnson and Kennedy 2019; Alexander and Cruz 2020). Peterson et al. (Peterson et al. 2005), for example, propose that trees should be separated by the distance corresponding with the typical crown width of codominant trees. Even if prescriptions do not explicitly emphasize these two methods, simplified forest structures after treatment sometimes result from the use of aspatial silviculture and fire behavior planning tools and because of a legacy of density management practices used for timber production (Underhill et al. 2014; Churchill et al. 2017; Fahey et al. 2018; Lefevre et al. 2020).

Recently, there has been a greater scientific understanding that trees in many forests globally self-organize into spatially heterogeneous patterns (Puettmann 2009; Fahey et al. 2018). Prior to EuroAmerican settlement in dry forests of the western US, trees were arranged in complex mosaics with single, scattered individual trees and tree groups of diverse sizes situated among openings of various sizes (Larson and Churchill 2012; Lydersen et al. 2013). Spatially variable factors facilitated the development of tree groups, which included patchy exposure of mineral soil following frequent fires (Larson and Churchill 2012), the amelioration of microclimate by larger nurse trees (Fajardo et al. 2006), zoochoric seed caching, among other factors (Vander Wall and Joyner 1998). Canopy openings were produced following patchy tree mortality, resource competition with understory plants (Abella et al. 2013), or unfavorable microsite conditions for tree regeneration (North et al. 2004). These heterogeneous patterns produced habitat for wildlife with complex habitat requirements (e.g., northern Goshawk [*Accipiter gentilis*] (Youtz et al. 2008)), diverse composition of understory plants (Matonis and Binkley 2018), and longer retention of snow pack (Schneider et al. 2019). As many forest management projects seek to provide many ecological benefits and services in addition to fire hazard reduction, treatments at stand scales are increasingly designed to yield spatially complex rather than simple forest structure (Underhill et al. 2014; Puettmann et al. 2015).

It is commonly noted that the long-term persistence of relatively sparse heterogeneous forests historically points to their resilience despite recurring fires (Larson and Churchill 2012;

Reynolds et al. 2013b; Hessburg et al. 2015; Addington et al. 2018). Fire modeling work has shown that, by reducing canopy fuel, restoration treatments can reduce fire behavior, largely through reductions in canopy fuel load (Ziegler et al. 2017a). Similarly, fire modeling in a mixed-conifer forest measured in both 1929 and 2008 suggested that fire behavior is greater in the modern era because tree densities have since increased. But the investigators observed significant potential mortality in dense groups of trees in the 1929 scenario. This provides support to claim canopy consumption may be lower if trees had been separated rather than aggregated. Similar modeling from Contreras et al. (Contreras et al. 2012) and Hoffman et al. (Hoffman et al. 2012) suggest crown fire initiation and spread is less likely when tree crowns are lifted from the surface and farther separated. Additionally, higher rates of spread often occur after thinning due to higher midflame wind speeds (Reinhardt et al. 2008). This is typically not a concern because the thinned overstory is less able to support crown fire; however, large openings, such as after restoration treatments, entrain winds which increases both rate of spread and fireline intensity, increasing potential for crown fire initiation (Pimont et al. 2009; Hoffman et al. 2015a; Atchley et al. 2021).

The degree to which forest managers may find a tradeoff between ecological restorative (i.e., spatially heterogeneous) treatments and fire hazard reduction is an area of active research (Lutz et al. 2018; Stephens et al. 2021) though fraught with confounding factors. Recently, Ritter et al. (in press)'s modeled fire in a Black Hills (South Dakota, US) ponderosa pine forest following a conventional fuel treatment as well as a heterogeneous restoration treatment which left half the basal area as the conventional treatment. Though the authors found trivial difference between cutting methods, it is unclear to what degree the non-significant results were influenced by the arrangement of trees or by differences in canopy fuel load. Assessing any tradeoff between ecological restoration and fire hazard reduction requires consideration that forest stocking, given the relationship between fuel load and fire behavior can be more impactful than the arrangement of fuel itself (Hoffman et al. 2012; Parsons et al. 2017). Additionally, empirical study of wildfires in the Sierra Nevada (California, US) between 1984 and 2017 showed that areas (at a scale of 0.8 ha) with lower burn severity were correlated with variability in forest structure, but also with lower canopy and surface fuel loads and higher fuel moistures. Burning conditions such as fuel moisture warrant an additional consideration.

This study investigates the potential fire behavior following different possible fuel treatment cutting methods. To explore a potential tradeoff between homogenizing, conventional treatments and heterogeneous restoration treatments, the cutting methods spanned a range of post-cutting forest structures. These methods either retained tree groups at one end or distanced out individual trees on the other end. Additionally, cuttings either left small trees in place or targeted these for removal. To simulate cuttings, I manipulated lists of mapped trees previously collected in ponderosa pine (*Pinus ponderosa* ex. Lawson) forests of the intermountain western US. I used a three-dimensional, physics-based fire model to simulate fire behavior and assess midflame wind speed, rate of spread and canopy consumption both before and after cuttings. To control for other factors influential on fire behavior, I simulated hypothetical cuttings over a range of residual basal areas, surface fuel loads, wind speeds and fuel moistures. This research was motivated by two questions. First, how did fire behavior, controlling for retained basal area, vary across cuttings? Second, how importance was the cutting method relative to the other controls on fire behavior?

5.2 Materials and Methods

The experimental design was set up to examine compare potential reductions in fire behavior following six cutting methods that spanned a range of manipulations of horizontal and vertical arrangements of forest structure, crossed with varying levels of residual basal area (5, 10, and 15 m^2 ha^{-1}). Cutting methods included random, thin-from-below, distance-based, and variable-retention; I also included distance-based and variable retention cuttings each with thin-from-below. I conducted simulations at five sites after cutting, as well as before cutting to provide a pre-treatment baseline. Simulations spanned a range of surface fuel loads (0.4, 0.8, and 1.2 kg m^{-2}), surface fuel moistures (5%, 8%, and 11%), and open wind speeds (5, 10, and 15 m s^{-1} at 10 m above ground level) in order to quantify the relative importance of cutting methods and residual basal area relative to these factors which also significantly influence fire behavior.

5.2.1 Cutting Methods

I implemented each of the six cutting methods on five stem-mapped sites. These stem-maps, provided by Ziegler et al. (Ziegler et al. 2017a), describe the locations and characteristics of trees in ponderosa pine (*Pinus ponderosa* Lawson)-dominated forests in Colorado and Arizona. The data used included the (*x*,*y*) locations of trees and their respective crown width, crown base height, and tree height.

Cuttings included random, distance-based, variable retention, thin-from-below, distance-based with thin-from-below, and variable retention with thin-from below. I selected these cutting methods to separately manipulate the spatial separation or aggregation of crown fuel in the horizontal and vertical dimensions. Each cutting operated by sequentially removing, or retaining, trees until a basal area target of either 5, 10 or 15 m^2 ha^{-1} was met. The random cutting sampled trees to remove with equal weighting. The distance-based cutting sequentially removed trees nearest to another tree. The thin-from-below cutting sequentially removed trees with the smallest

DBH. To implement variable retention cuttings, I modified an algorithm previously described by Tinkham et al. (2017). This algorithm is similar to the ICO, or individuals, clumps, and openings silvicultural method developed by Churchill et al. (2013b). First, half of the basal area was removed by placing openings, eliminating all trees within circles of various sizes. Mimicking Churchill et al. (2013b), these openings sizes followed a frequency distribution of 24%, 40%, 20%, 10%, 5% and 1% for openings with radii of 0.75, 2.25, 3.75, 6.75, and 8.25 m, respectively. To place openings, I began by calculating a smoothed map of trees per m^{-2} with Gaussian kernel smoothing; these values were then inverted to provide weights. Thus, openings were more likely to be randomly placed in areas with lower tree density. In the second step, the algorithm designated groups of trees to retain. I desired to retain tree groups of various sizes at frequencies similar to historical ponderosa pine forests, as reported by Clyatt et al. (2016). Here, the desired share of basal area within tree groups of 1, 2 to 4, 5 to 9, 10 to 14 and 15 to 25 trees were set to 30%, 30%, 20%, 10%, and 10%, respectively. Starting the largest tree group size class, the algorithm randomly selected a tree, identified trees with 4 m of the focal tree, and trees within 4 m of those identified trees, ad infinitum. If enough trees to create a group were identified, that group was retained, provided no member tree was within 4 m of a previously retained tree. Once the basal area desired for a given tree group size class was met, the algorithm successively found tree groups of the next smallest group size class.

To ensure that the design of cutting scenarios produced differences in forest structure, I examined several attributes: trees per hectare; quadratic mean tree diameter at breast height (QMD); mean opening size; coefficient of variation of tree DBH within tree groups; and mean distance between neighboring trees. Discrete tree groups were identified as sets of trees wherein each member tree was within 4 m of another member tree. I calculated the mean opening size by first calculating all the area within the 4 ha-sites that were over 4 m from any trees; then I identified discrete contiguous openings and measured each openings' area (m^2). I measured these attributes after implementing each cutting scenario on each site at each level of residual basal area. I first tested whether the average values of these attributes, per cutting scenario and basal area, differed from pre-cutting using Dunnett's test for comparing several treatments with a control. I used an α of 0.05 for all statistical tests in this study. Second, I applied a Sidak-adjusted pairwise comparisons procedure to assess whether the least-squares means of these attributes varied between cutting scenarios, at each level of basal area. These least-squares means were the values predicted by a mixed-effects model, implemented with nlme v.3-1-152 (Pinheiro et al. 2021) in R to measure the estimators for each variable, y (Eq. 5.1); site was coded as a random variable while basal area (BA) and cutting methods were fixed variables.

$$y = BA + Cutting + BA \times Cutting + Site, \qquad \text{Equation 5.1}$$

5.2.2 Fire Simulations

I simulated fire behavior with the Wildland-urban interface Fire Dynamics Simulator v. 9977 (WFDS). This model choice facilitates the simulation of fire in a spatially complex and temporally dynamic environment (Hoffman et al. 2018a). Using a computational fluid dynamics approach, numerical solutions describing fuel, fire, and the atmosphere are solved over a series of time steps within a three-dimensional domain composed of voxels. Further model description of WFDS' approaches and evaluation of the model in the context of wildland fire can be found in the following references (Mell et al. 2007, 2009; Castle et al. 2013; Hoffman et al. 2015b, 2018a; McGrattan et al. 2015, 2020; Mueller et al. 2015; Terrei et al. 2019; Morandini et al. 2019; Sánchez-Monroy et al. 2019).

Each simulation in WFDS was set up identically except with regard to the factors under consideration in this study: open wind speed, surface fuel arrangement, surface fuel moisture, and list of trees. The domain was composed of 1 m^3 voxels and spanned spanning 900 m × 400 m × 90 m in the *x*, *y*, and *z* dimensions, respectively (Figure 5.1). Each plane along the boundaries had the following prescribed conditions. Wind entered at $x = 0$ m, wind entered; the speed at each height (*z*) followed a power law function, $u(z) = u_{20} \times \frac{z}{20}^{\frac{1}{7}}$, where the open wind speed, u_{20}, was defined either as 5, 10, or 15 m s^{-1}.

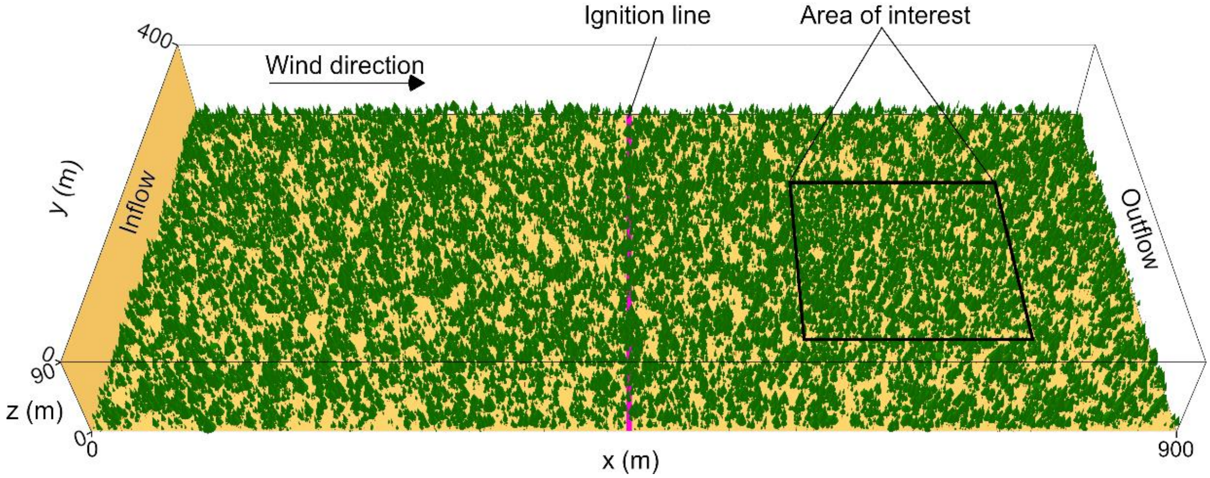

Figure 5.1 WFDS Simulation domain

Features of wildland-urban interface Fire Dynamics Simulator domains used in this study, including overall dimensions, wind direction, location of the initiating fire line, and area of interest.

Entering wind at x = 0 m followed a power law function, $u(z) = u_{20} \times \frac{z}{20}^{\frac{1}{7}}$, with speed, *u*, increasing with height above ground level, *z*, according to a defined 20-m wind speed, U_{20}, defined in this study as 6 m s^{-1}. Boundary conditions on lateral sides, $y = 0$ m and $y = 400$ m, and the and the ceiling, $z = 90$ m, were mirrored, i.e., free slip and no flux. The boundary condition at the outlet, z = 900 m, was open. The terrain along the ground, $z = 0$, was flat. All simulations ran for 2000 s (~33.3 min). A line fire at 448 to 450 m in the x dimension and from 70 to 330 in the y dimension initiated at 300 s and freely burned towards the outlet, passing through the 4-ha area of interest. This area of interest spanned from 600 m to 800 m in the *x* dimension and from 100 m to 300 m in the *y* dimension.

The area of interest contained the locations of trees either before cutting for one of the five given sites or retained after implementing a particular cutting for a given residual basal area. All tree crowns in the domain were represented as right circular cones defined by the tree height, crown base height, and crown width. The material properties I assigned to tree crowns included a surface to volume ratio of 4000 m^{-2} m^{-3}, drag coefficient of 0.159, bulk density of 0.5 kg m^{-3}, particle density of 520 kg m^{-3}, and foliar moisture content of 100%.

I included additional fictitious trees across the domain, outside the area of interest, to ensure that the wind field in the area of interest was well developed and typical of wind flows throughout a forest canopy (Figure 5.1). The tree locations outside of the area of interest were randomly placed after using the tree locations inside of the area of interest to fit a log-Gaussian Cox point process model (Baddeley et al. 2015). Thus, trees outside of the area of interest mimicked the spatial arrangements of trees inside the area of interest. I randomly sampled trees from the area of interest to attribute heights, crown base heights, and crown widths to these trees outside the area of interest.

There was a unique spatial arrangement of surface fuel to match (1) the respective arrangement of trees in a domain for a particular site, either before cutting or after simulating a specific cutting method to a given basal area, and (2) a median surface fuel load (0.4, 0.8, or 1.2 kg m^{-2}). All surface fuels were given the same fuel moisture, either 5%, 8%, or 11%. I distributed surface fuel heterogeneously to reflect the influence that canopy cover has on the composition and characteristics of the surface fuelbed locally. This process ensured that differing cutting methods or residual basal areas had identical median fuel loads even though their spatial distributions differed. First, I calculated the distances from any location to a tree using Spatstat (Baddeley et al. 2015) in R v4.1.1 (R Core Team 2016, Vienna, Austria), then inverted these distances, and last re-scaled these distances using a triangular distribution with a minimum of 0.2, maximum of 3.0, and median of either 0.4, 0.8, or 1.2. I used these values to assign fuel loads, reflecting an tendency for greater fuel loads to be present near trees and lesser fuel loads in openings in the sites (Banwell and Varner 2014; Matonis and Binkley 2018). Where the surface fuel load was 0.2 kg m^{-2}, I assigned a fuel bulk density of 2 kg m^{-3}, representing a grass-dominated fuelbed. For each surface fuel load increase of 1 kg m^{-2}, I increased fuel bulk density by 6.25 kg m^{-3} to account for a greater relative proportion by conifer needles. Surface fuels had a surface area to volume ratio of 5800 m^{2} m^{-3}, particle density of 510 kg m^{-3} and drag constant of 0.375.

5.2.3 Fire Behavior Analysis

This study had 200 simulations of fire behavior post cutting and 40 simulations of fire behavior before cutting. With six cutting methods, three residual basal areas, across five sites, and three levels each of open wind speed, surface fuel load, and surface fuel moisture, there were 2,430 possible simulations post cutting and 135 possible simulations before cutting. I used the C-optimized Fedorov’s exchange algorithm (Atkinson and Donev 1992) as implemented by the AlgDesign v1.2.0 package (Wheeler 2019) in R to reduce the number of simulations down to 200. This algorithm randomly selects combinations of levels of factors from a full factorial list of combinations with the goal of minimizing the variance of best linear unbiased estimators.

I calculated mean midflame wind speed, rate of spread (ROS), and canopy consumption (CC) after each of the 240 WFDS simulations. Midflame wind speed was calculated by averaging the streamwise wind speed across time in the area of interest at 2 m in height in the x direction for one minute, from 240 to 300 s prior to fireline initiation. Average rate of spread was calculated by averaging, across each location in the area of interest, the time of fire arrival in that location compared to the time of arrival 10 m downstream of the location. I calculated canopy consumption on a percentage basis using the dry mass of all tree crowns in the area of interest at the start of the simulation compared to the dry mass at the end.

The statistical analysis included calculations of marginal effects of the independent variables as predicted by mixed-effects models, the effect sizes for each independent variable, and last comparisons between cutting methods. The mixed-effects models on midflame wind speed used the form (Eq. 5.2),

$$U_2 = U_{10} + SFL + SFM + BA + Cutting + BA \times Cutting + Plot, \qquad \text{Equation 5.2}$$

which includes midflame windspeed (U_2), open wind speed (U_{10}), surface fuel load (SFL), residual basal area (BA), cutting scenario, and site. Site was a random variable. The mixed-effects models on fire rate of spread (ROS) and percent canopy consumption (CC) (Eq. 5.3),

$$\{ROS, CC\} = U_{10} + SFL + SFM + BA + Cutting + BA \times Cutting + Plot, \qquad \text{Equation 5.3}$$

also included surface fuel moisture (SFM). I present the mixed-effects model results with an analysis of deviance test to assess statistical significance of variables. I calculated the marginal effect of each fixed independent variable by averaging over other independent variables. Next, I measured the effect size of all variables with partial eta squared ($\eta2_p$) ; partial eta squared measures the proportion of total variance explained by each independent variable after accounting for the variation explained by all other variables. To contextualize the effect sizes, I categorized effect sizes as small, medium, and large $\eta2_p$ was larger than .0099, .0588, and .1379, respectively (Cohen 1969). Last, I applied Sidak-adjusted pairwise comparisons procedures to evaluate whether midflame wind speed, rate of spread, or canopy consumption, significantly differed between cuttings. If the interaction between cutting and basal area was significant, I conducted pairwise comparisons at each level of basal area.

5.3 Results

5.3.1 Effects of Cuttings on Forest Structure

Across sites, the initial basal areas across sites ranged from 22.6 m^2 ha^{-1} to 30.2 m^2 ha^{-1}. This equated to an average reduction of 43%, 62%, and 82% for the basal area targets of 15, 10, and 5 m^2 ha^{-1}, respectively. The differences in forest structure between cutting scenarios were apparent on initial visual inspection (Figure 5.2) and reflected in the pairwise comparisons.

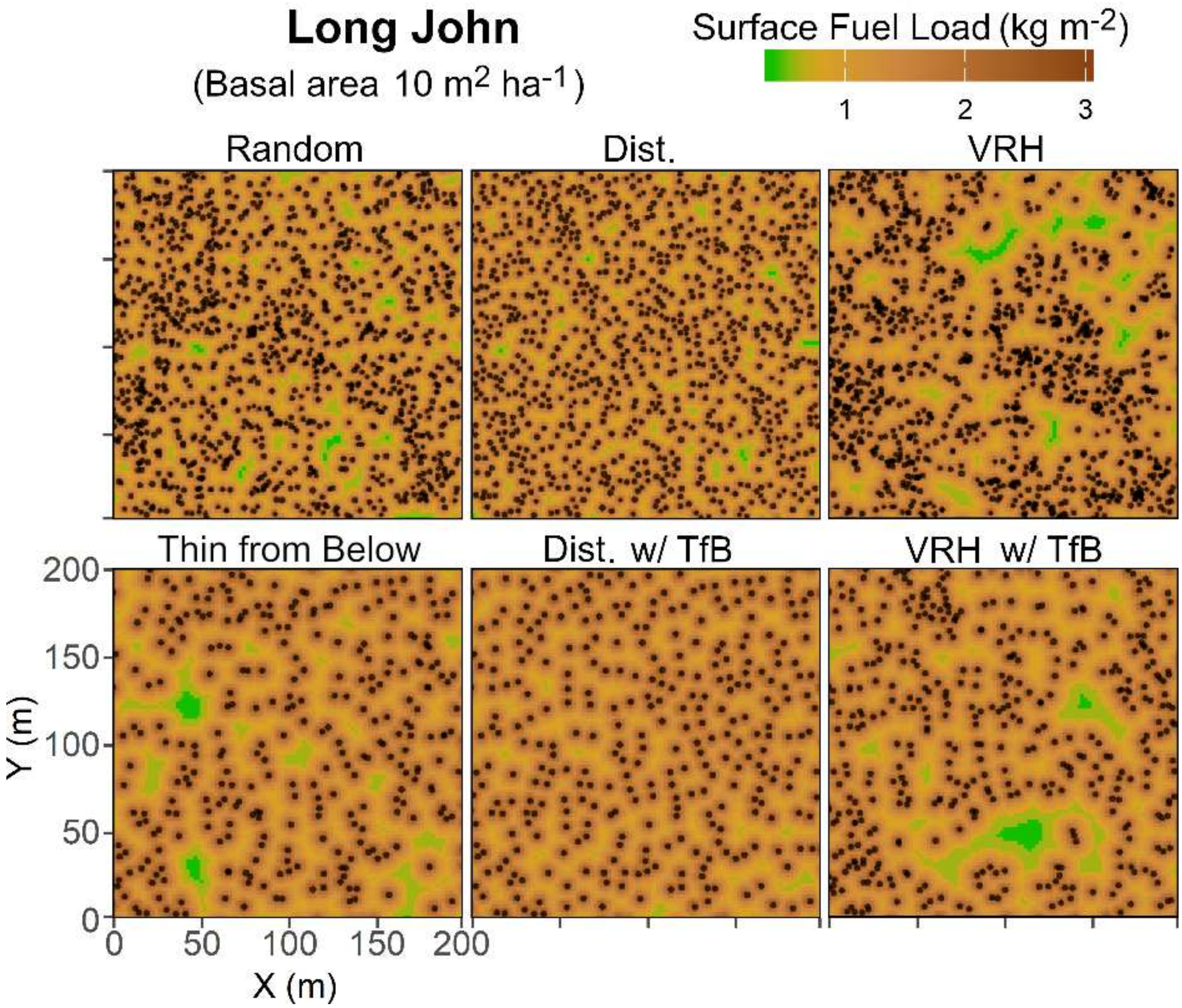

Figure 5.2 Demonstration of cutting scenarios

Example of simulated cuttings on one site, Long John, mapping the locations of residual trees (black dots) given a target basal area of 10 m^2 ha^{-1}, and the arrangement of surface fuel loads, given a spatial median of 1.2 kg m^{-2}.

Regarding aspatial measures of forest structure, cuttings significantly reduced trees per ha (Dunnett's test, all *p*-values < 0.010) from an initial 687 trees ha^{-1} before cutting. Trees per ha averaged 243, 152, and 73 at residual basal areas of 15, 10, and 5 m^2 ha^{-1}, respectively. Pairwise comparisons tests reflected that trees per ha were highest after random cuttings and variable retention harvests, followed by distance-based cuttings, and then any cutting scenario incorporating thinning from below (Figure 5.3a). Cuttings that did not include any thinning from below component had negligible effect on QMD (Dunnett's test, all *p*-values < 0.646), averaging between 22 and 29 cm. Those cuttings with any thinning from below increased QMD (Dunnett's test, all *p*-values > 0.001) to a level between 38 cm and 56 cm, raising QMD as less basal area was retained (Figure 5.3b).

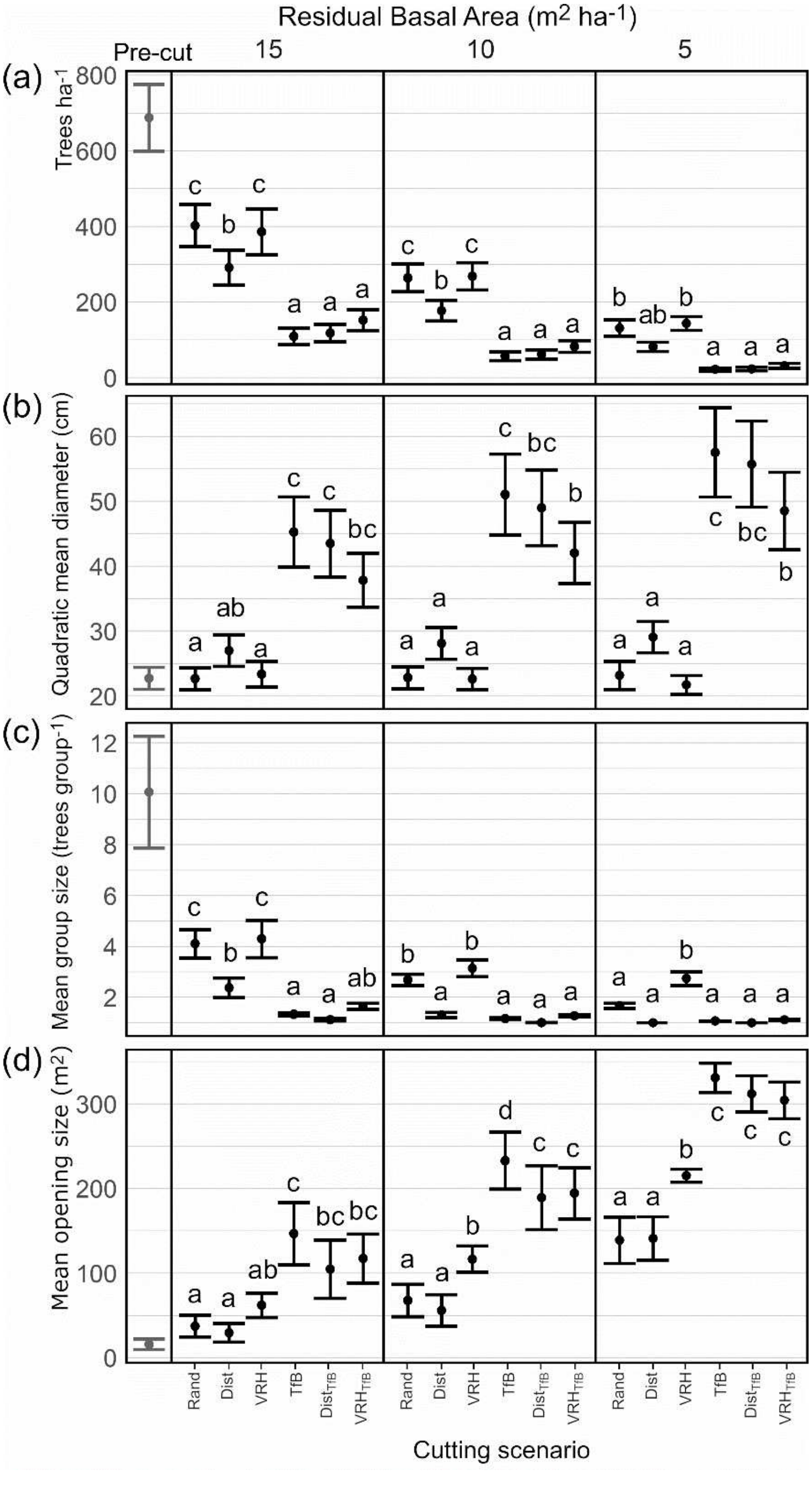

Figure 5.3 Impacts of cutting scenarios on forest structure

Average and standard error changes following simulated cuttings, on (a) tree density, (b) quadratic mean diameter, (c) mean size of tree groups, and (d) mean opening size, (e) coefficient of variation of tree diameter at breast height within tree groups, and (f) mean distance between neighbor trees, before cutting and at each level of residual basal area.

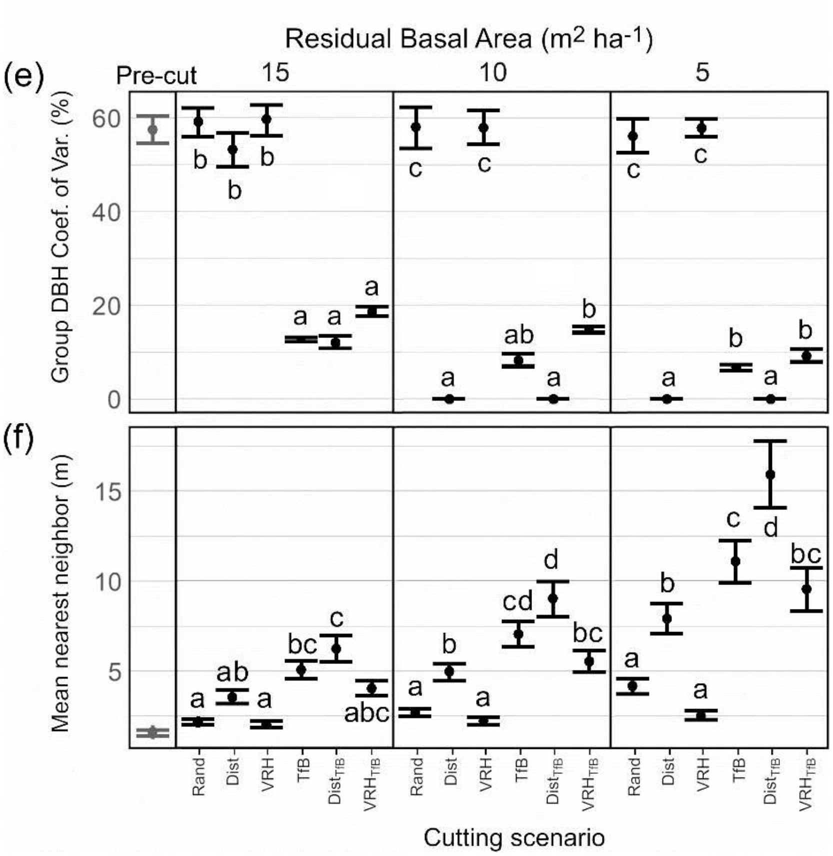

Figure 5.3 (cont.).

Regarding spatial elements of forest structure, all cutting scenarios reduced mean group size (Dunnett's test, all *p*-values < 0.001). While the average number of trees per group was ~10 before cutting, the lightest cuttings left ~4 trees per group after random and variable retention cuttings, ~2 trees per group after distance-based cuttings, and less than 2 trees per group in any of the cuttings including thinning from below. As less basal area was retained, the average tree group size after any cutting scenario fell further (Figure 5.3c). Cuttings reduced mean opening size (Dunnett's test, all *p*-values < 0.0341). Opening sizes were larger among cuttings incorporating thinning from below, followed by the variable retention harvest, and then the random and distance-based cuttings (Figure 5.3d). For example, the average opening size was as over 300 m^2, or 1/30th ha, after scenarios including thinning from below. This was twenty times larger than the average opening size before any cutting. In contrast, opening sizes averaged 215

m^2 after variable-retention and 140 m^2 after both random and distance-based cuttings. Additionally, only random and variable retention cutting scenarios maintained the variation of tree DBH within tree groups (Dunnett's test, p-values ≥ 0.504; Figure 5.3e) and the average distance between trees (Dunnett's test, p-values ≥ 0.703; Figure 5.3f).

5.3.2 Effects of Cuttings on Fire Behavior

All cutting scenarios increased midflame wind speed compared to pre-cutting (Dunnett's test, all p-values < 0.010). Before cutting, midflame wind speeds averaged 1.38 m s^{-1}, but ranged from 2.65 m s^{-1} to 3.39 m s^{-1} across cuttings. There were also significant differences between cuttings (Analysis of deviance, $\chi^2(df = 5) = 294.2$, $p < .001$) and pairwise comparisons identified two groups (Figure 5.4a). Those cutting scenarios which included either sole or partial thinning from below were similar with a midflame wind speed of ~3.31 m s^{-1} versus 2.66 m s^{-1} averaged across the random, distance-based, and variable retention cuttings (Figure 5.4b). Of all independent variables, open wind speed was the strongest determinant of midflame wind speed (Analysis of deviance, $\chi^2(df = 1) = 1468.9$, $p < .001$; Figure 5.4d). Residual basal area was the second most important variable (Analysis of deviance, $\chi^2(df = 1) = 291.6$, $p < .001$; Figure 5.4b); as residual basal area decreased from 15 m^2 ha^{-1} to 5 m^2 ha^{-1}, midflame wind speeds increased from 1.5 m s^{-1} to 4.4 m s^{-1} (Figure 5.4c). The effect of cutting did not depend on residual basal area (Analysis of deviance, $\chi^2(df = 5) = 3.3$, $p = .660$).

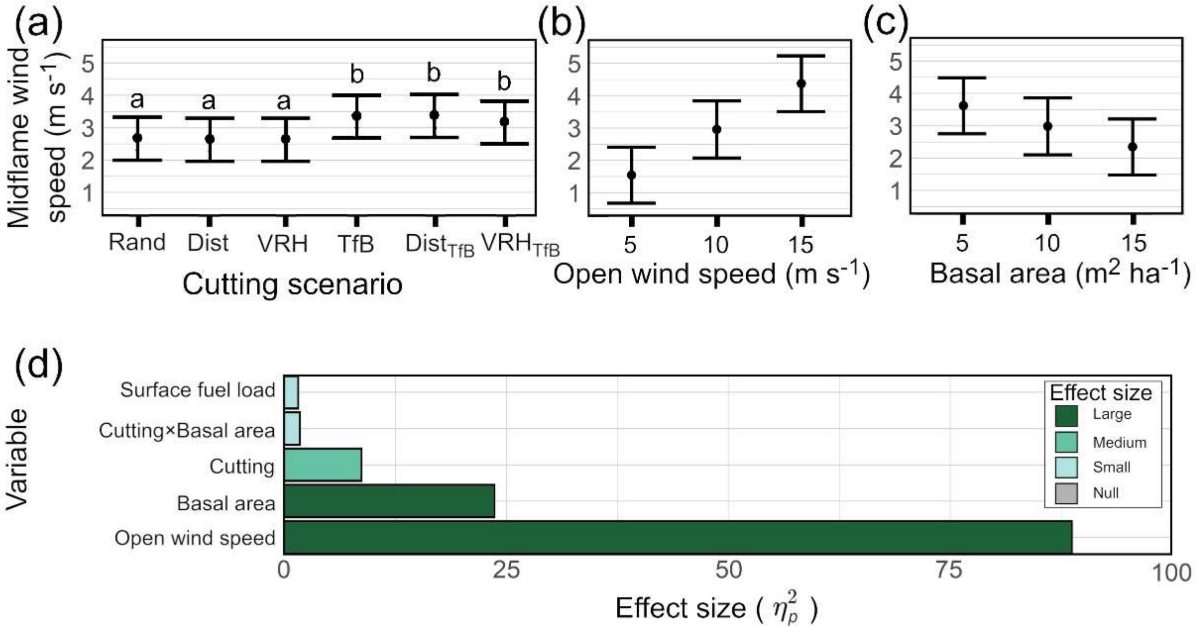

Figure 5.4 Cutting impacts on wind speed

Marginal effects of (a) cutting scenario, (b) open wind speed, and (c) basal area following mixed effects modelling on midflame wind speed, and (d) effect size of variables. Letters indicate significant differences between cuttings using pairwise comparison procedures.

Fire rate of spread (ROS) was lower after all cutting scenarios relative to pre-cutting (Dunnett's test, all *p*-values < 0.002). ROS averaged 0.67 m s^{-1} before cutting, and from 0.48 m s^{-1} to 0.53 m s^{-1} across cutting scenarios. ROS significantly differed between cutting methods (Analysis of deviance, $\chi^2(df = 5) = 24.6$, $p < .001$). Further, while there was no trend with respect to residual basal area (Analysis of deviance, $\chi^2(df = 1) = 3.4$, $p = .064$), I found that the differences between cuttings increased with lower residual basal area (Analysis of deviance, $\chi^2(df = 5) = 13.9$, $p = .016$; Figure 5.5a). At the highest basal area, 15 m^2 ha^{-1}, pairwise comparisons tests showed that ROS was not different between cutting scenarios, averaging 0.51 m s^{-1}. But when thinning to 5 m^2 ha^{-1}, ROS decreased to 0.47 m s^{-1} within distance-based and random cuttings. Meanwhile, ROS increased to 0.54 m s^{-1} after variable retention and thin-from-below cuttings. Thus, significant differences emerge between cutting scenarios at moderate and low residual basal areas.

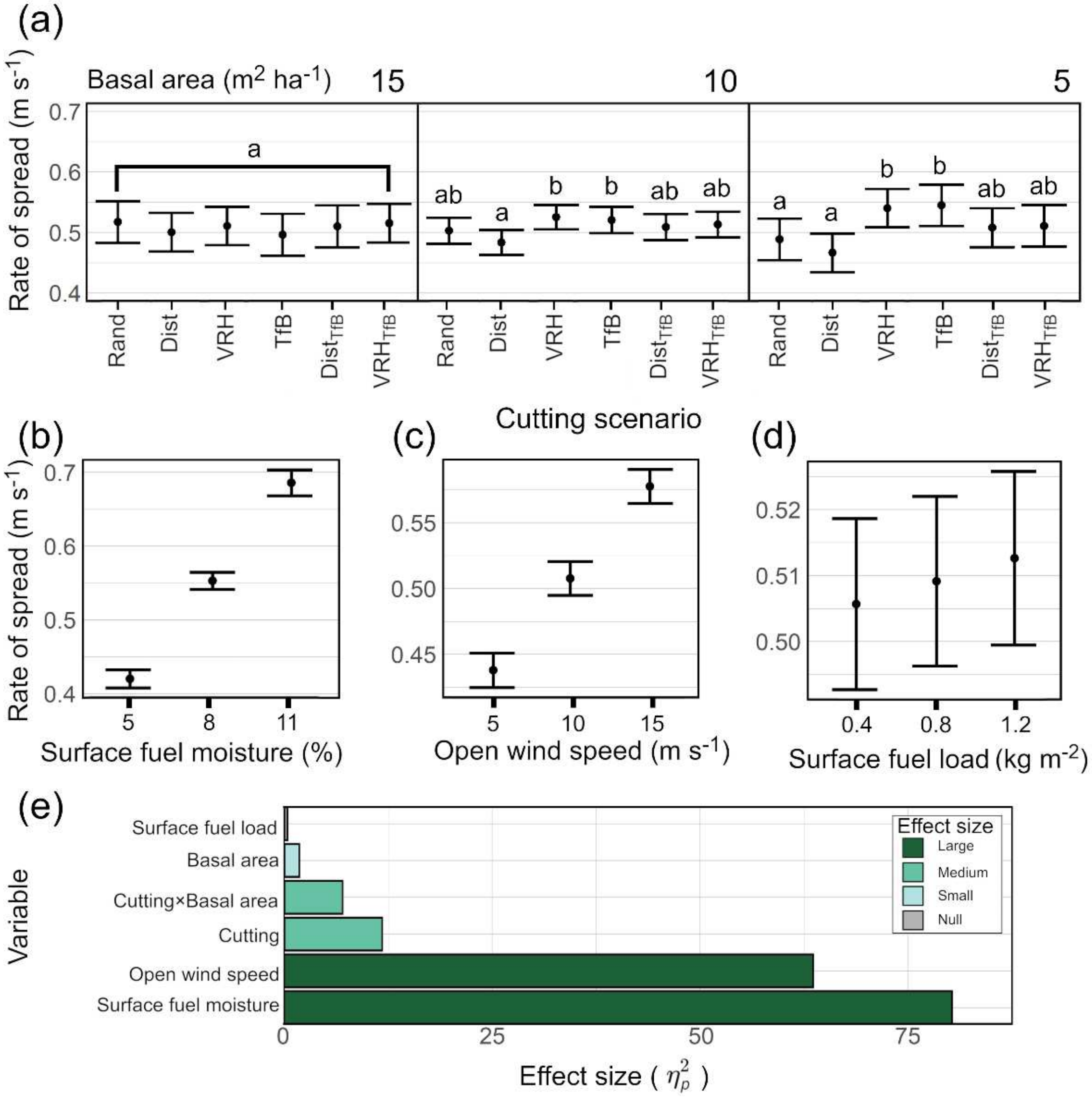

Figure 5.5 Cutting impacts on rate of spread

Marginal effects of (a) cutting scenario × basal area, (b) surface fuel moisture, (c) open wind speed, and (d) surface fuel load following mixed effects modelling on rate of spread, and (d) effect size of variables. Letters indicate significant differences between cuttings using pairwise comparison procedures.

Among the other independent variables, surface fuel moisture most explained ROS (Analysis of deviance, $\chi^2(df = 1) = 759.9$, $p < .001$; Figure 5.5e), with ROS ranging from 0.42 to 0.69 m s^{-1} as fuel moisture decreased from 11% to 5% (Figure 5.5b). Meanwhile, ROS ranged from 0.44 to 0.58 as open wind speed increased from 5 to 15 m s^{-1} (Analysis of deviance, $\chi^2(df = 1) = 323.1$, p

$< .001$; Figure 5.5c). Surface fuel load was the only variable which did not explain variability in ROS (Analysis of deviance, $\chi^2(df = 1) = 0.8$, $p = .381$; Figure 5.5d).

The percent canopy consumption (CC) averaged 73% before cuttings and significant dropped to between 43% and 54% across cuttings (Dunnett's test, all *p*-values < 0.001). CC did vary between cutting scenarios (Analysis of deviance, $\chi^2(df = 5) = 65.6$, $p < .001$) and explained the most variance alone of any variable (Figure 5.6a, e). In general, I found that the cuttings with only or partial thinning from below had lower CC than those cuttings without any thinning from below; of the latter scenarios, variable retention harvests were the highest at any level of basal area. While CC diminished with lower residual basal areas (Analysis of deviance, $\chi^2(df = 1) = 34.5$, $p < .001$), I identified an interaction with cutting scenarios. Specifically, the spread in CC between cutting scenarios was greater with less residual basal area (Analysis of deviance, $\chi^2(df = 5) = 23.3$, $p < .001$). In general, I found that, as residual basal area diminished, CC dropped dramatically among the cuttings with a thinning from below component, dropped marginally after variable retention harvest cuttings, and dropped by a moderate amount among the random and distance-based cuttings.

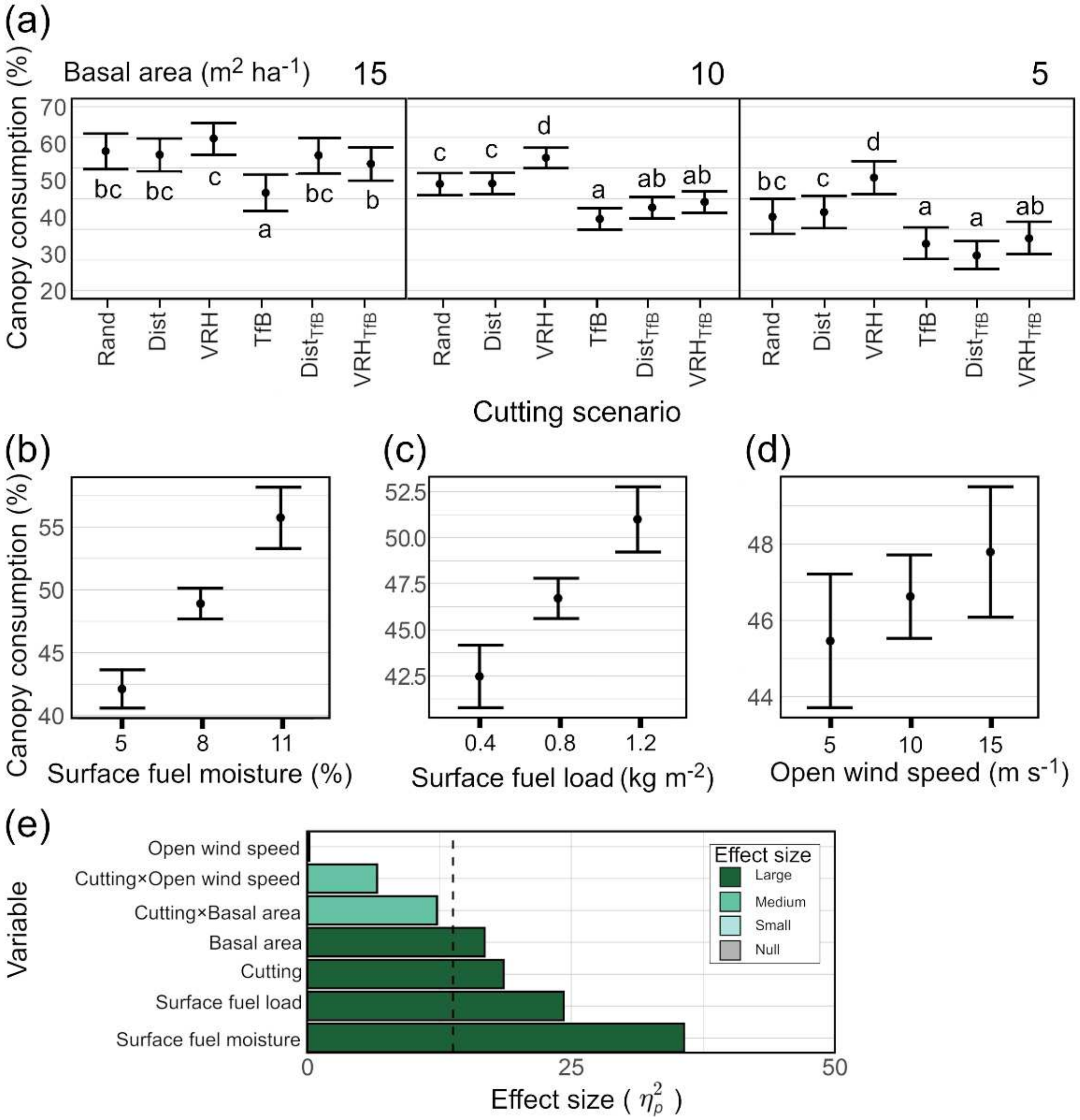

Figure 5.6 Cutting impacts on canopy consumption

Marginal effects of (a) cutting scenario × basal area, (b) surface fuel moisture, (c) surface fuel load, and d) open wind speed following mixed effects modelling on canopy consumption, and (d) effect size of variables. Letters indicate significant differences between cuttings using pairwise comparison procedures.

Surface fuel moisture was the second most important variable (Analysis of deviance, $\chi^2(df = 1) = 95.7$, $p < .001$) as CC rose from 42% at 11% surface fuel moisture to 56% at 5% surface fuel moisture (Figure 5.6b). As surface fuel loads increased from 0.4 to 1.2 kg m^{-2}, CC averaged 42% to 51% (Analysis of deviance, $\chi^2(df = 1) = 56.4$, $p < .001$; Figure 5.6c). Last, open wind speed was a significant predictor of CC (Analysis of deviance, $\chi^2(df = 1) = 4.0$, $p = .045$; Figure 5.6d), but had only a small effect size (Figure 5.6e).

5.4 Discussion

This work shows that all cutting methods reduced fire behavior and severity, as measured by rate of spread and canopy consumption, respectively. Further, the specifications used during fuel treatments influenced the degree of fire hazard reduction. The differences in fire behavior and severity emerged as more basal area was removed. This occurred because, as tree removal intensified, the forest structure increasingly diverged between methods.

Notably, cuttings with thinning from below and the variable retention harvests significantly increased the size of openings. Variable retention harvests often create openings purposefully (Reynolds et al. 2013b; Underhill et al. 2014; Addington et al. 2018), while removal of small trees can inadvertently create openings because regeneration of shade-intolerant species can cluster in openings between groups of mature trees (Sánchez et al. 2009; Larson and Churchill 2012; Ziegler et al. 2021). The creation of openings also can lead to higher midflame wind speed, as has been measured *in situ* following variable-retention thinning in Sierran mixed conifer forests (Bigelow and North 2012). While wind flow following distance-based cuttings can be streamlined and laminar because the dispersed canopy imposes drag on the wind uniformly (Figure 5.7a), the creation of openings, however, allows wind to be entrained (Figure 5.7b). This can lead to locally higher wind speeds, adding to broadscale increases in wind speed commensurate with thinning throughout the canopy.

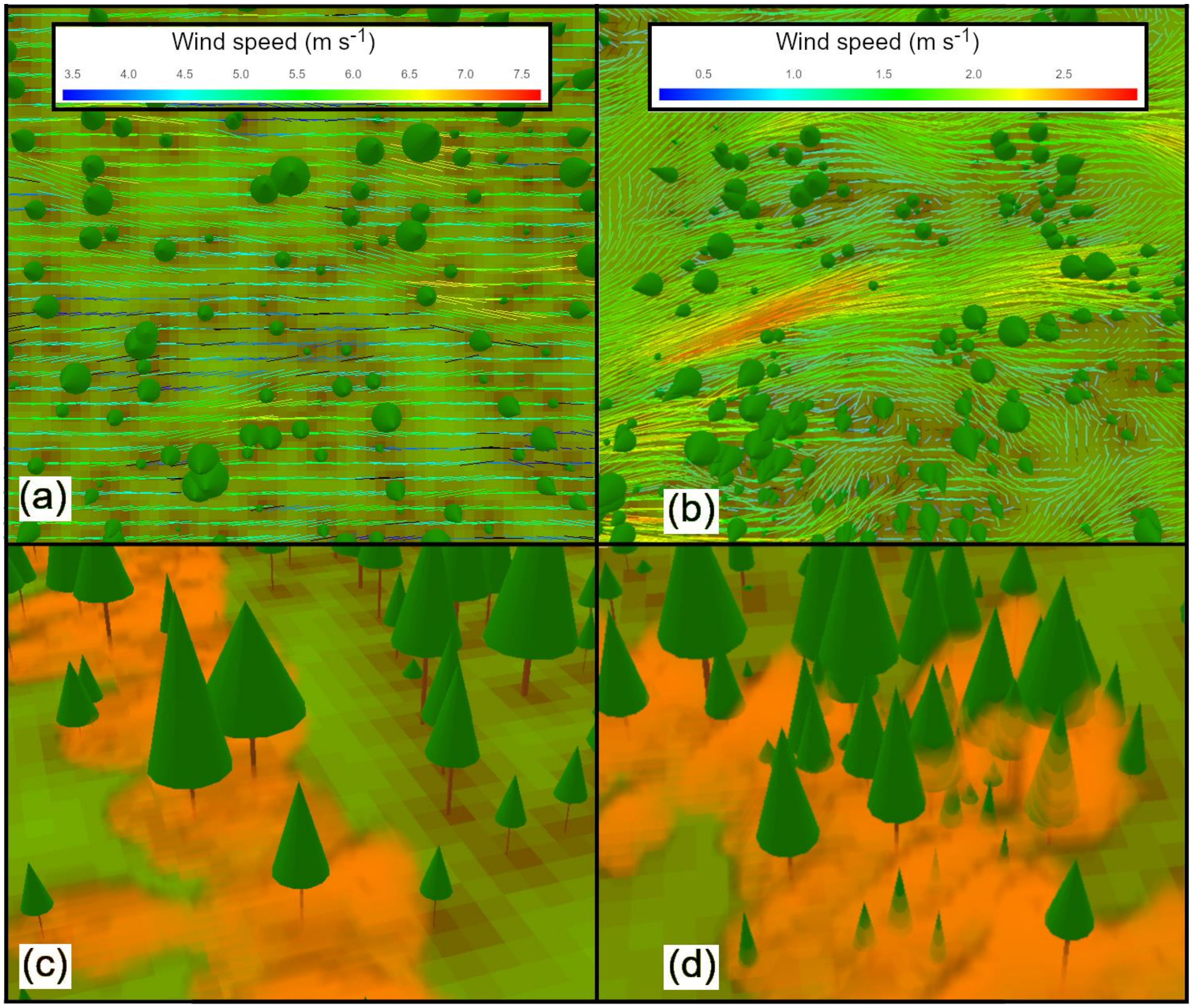

Figure 5.7 Wind and fire behavior varies based on tree arrangement

Demonstration of regimes of pre-fire (a) laminar flow with distance-based cuttings and (b) entrainment of wind following variable retention harvest, with wind vectors at 2 m above ground level flowing from left to right. During fire spread, (c) fire passed under large trees after distance-based cutting, while (d) groups torched after variable retention harvest.

It is sometimes cautioned that increases in wind speeds throughout the canopy and near the forest floor may impair fire behavior reductions (Reinhardt et al. 2008) by increasing surface fire rate of spread and intensities, increasing the potential for surface-crown fire transition. As I observed however, decreases in canopy bulk density, and, in the case of cutting scenarios with thinning from below, the lifting of the canopy base height reduces canopy fuel load and continuity. These results confirming the building consensus that, controlling for surface fuel, reductions in crown fire hazard outweigh increases in surface fire hazard, as identified by modelling studies (Graham et al. 1999; Parsons et al. 2018) and empirical observations of burned treatments (Raymond and Peterson 2005; Crotteau et al. 2016).

However, the variable-retention harvest scenarios were the least effective at reducing burn severity as these cuttings left relatively dense patches with vertical continuous crown fuel. This indicates that variable retention harvests seeking to maximize structural variation, may face trade-offs between the creation of structural heterogeneity and hazard reduction. The relatively higher canopy consumption confirmed the supposition that the retention of tree groups risks the potential for group torching and localized patches of mortality (Larson and Churchill 2012; Stephens et al. 2021). Whereas distance-based cuttings reduced the potential for tree-to-tree crown fire spread (Contreras et al. 2012), group fire initiation and torching was enabled within tree groups of diverse sizes (Figure 5.7c,d). Because crown fire initiation and spread is still possible in these groups, previous fire modelling by others suggests these cuttings should not reduce (Graham et al. 1999), or may even exacerbate (Stephens 1998), fire hazard. However, even though variable retention cuttings did not increase tree spacing or the vertical continuity of crown fuel, I observed fire hazard reductions. This is likely driven by the presence of openings which have been suggested to act as a significant barrier to crown fire spread between tree groups (Churchill et al. 2013b).

These results also suggest there are ways to increase the complementarity of restoration treatments with fire hazard reduction objectives, including increasing cutting intensity and the management of small trees. First, restoration treatments often leave forest stocking on the upper end of historical ranges (Stephens et al. 2015; Lydersen et al. 2019). Restoration treatments in the ponderosa pine forests modelled in this study have been retaining a basal area of 10 to 20 m^2 ha^{-1} (Underhill et al. 2014; Briggs et al. 2017; Ziegler et al. 2017a). In contrast, these forests had historically had an average basal area of 6.3 and density of 97 trees ha^{-1} (Battaglia et al. 2018). Second, these results suggest removal of small trees brings all cutting methods in line with one another, regardless of horizontal tree arrangements. There is a perceived tension between retention of ‘ladder fuels’ and the benefits of retaining multiple size classes (Briggs et al. 2017). Multiple crown strata within tree groups benefits wildlife of concern (Youtz et al. 2008; Reynolds et al. 2013b) and retention of small trees bolsters resilience to disturbances which target large trees (Churchill et al. 2013b; Baker and Williams 2015). On the other hand, case study has found high severities following restoration treatments which retained groups with high vertical diversity for wildlife purposes (Johnson and Kennedy 2019). In many contemporary forests, small trees are overly abundant since their historical fire regimes have been interrupted (Battaglia et al. 2018; Stephens et al. 2018b). In these instances, there is opportunity to retain some tree groups without ladder fuel (Churchill et al. 2013b), especially around old, larger trees of ecological or cultural significance (Lindenmayer and Laurance 2017; Flanary and Keane 2020). In other forests, decades of fire cessation has led to a scarcity in small trees of shade-intolerant, fire resistant species (Knapp et al. 2017); here it may be appropriate to preserve clusters of smaller, regenerating tree groups separate from mature trees (Addington et al. 2018). Bringing silvicultural prescriptions of restoration treatments in line with the range of historical variability, with further reductions in tree density, including judicious removal of small trees, may further gains in hazard reduction.

5.4.1 Considerations

The design of cutting methods and experimental control of surface fuel loads were established to concentrate on differences between horizontal and vertical arrangements of crown fuel, under a range of typical burning conditions. The applicability of simulation results may be altered in context of real-world management of forests and fire hazard. First, specific cutting methods, in practice, usually are associated with different levels of residual forest stocking, dictated by desired objectives and convention (Johnson et al. 2019). For example, Ritter et al. (in press)'s modeling efforts found no difference in potential fire severity between fuel reduction treatments designed to support uniform timber production (basal area = 12.4 m^2 ha^{-1}) and restoration treatments designed to provide heterogeneous wildlife habitat (basal area = 6.3 m^2 ha^{-1}). As the results demonstrate, these differences in forest stocking between different silvicultural methods—as typically implemented—are likely to impactful as the arrangement of tree crowns. Fire behavior and effects studies contrasting different silvicultural methods designed to meet differing co-objectives need to take into consideration how forest stocking and fuel loads may differ.

Second, I modelled surface fuel assuming a transition to herbaceous vegetation in open areas. While this relationship naturally occurs in the ponderosa pine forests simulated here (Matonis and Binkley 2018), shrubs can rapidly colonize openings in other dry forests (Lydersen et al. 2013) which may lessen fire hazard reduction in treatments designed to increase opening sizes (Crotteau et al. 2016). Moreover, the model of surface fuel transition post cutting ignored the addition of activity surface fuel. Treatment of surface fuel is key to reduce the potential for crown fire initiation (Agee and Skinner 2005). As demonstrated by these results, the level of surface fuel load is a larger determinant on fire severity than any manipulation of the canopy fuel. Prescribed fire and management of unplanned ignitions under benign burning conditions, are a cost effective secondary treatment to, not only reduce surface fuel, but to further reductions in forest stocking, increasing resistance to undesirable fire effects (Stephens and Moghaddas 2005; Fulé et al. 2012). Previous studies have affirmed these managed fires are especially effective when coupled with restoration treatments because their variable fire effects strengthen fuel heterogeneity (Knapp et al. 2017; Huffman et al. 2018). However, the reintroduction of fire is often delayed or never completed (Addington et al. 2018; Stephens et al. 2021). Given that surface fuel loads are elevated in many contemporary forests with interrupted fire regimes (Collins et al. 2016) and that failure to address activity fuel can negate any gains made by reducing canopy fuel loads (Stephens 1998; Fulé et al. 2001; Raymond and Peterson 2005), reintroducing fire is as critical as cuttings are for restoration (Fulé et al. 2002; Addington et al. 2018).

Last, I simulated fires under burning conditions spanning 5% to 11% surface fuel moisture and winds of 5 to 15 m s^{-1}. Extending durations of fire seasons and changes in climate patterns are increasing the number of days where extreme fire weather and dry fuels align co-occur (Khorshidi et al. 2020). The simulated conditions here span the range of typical fire weather (Nagy et al. 2018), including average fire weather during extreme fire spread events (DeCastro et al. 2022), but topography and fire-driven weather can align to produce extreme conditions at stand scales. As many have found failure of treatments under such situations (Reinhardt et al. 2008), I do not expect these findings of fuel reduction effectiveness to hold under all burning conditions.

5.5 Conclusions

The simulations here provide evidence that cuttings spanning a range of forest structural arrangements can all be effective at reducing fire behavior under moderate to high burning conditions. I did find tradeoffs, whereby treatments that maximized structural variability by retaining tree groups were less effective at reducing fire severity. However, managers can compensate for these tradeoffs through reductions in surface fuel, and where appropriate, targeted removal of small trees and more aggressive tree removal overall.

In the context of the landscape planning of treatments, the ecological and social priorities should inform the placement of treatments with different designs (Hessburg et al. 2013; Stephens et al. 2021). The study here supports the use of uniforming fuel reduction within the wildland-urban interface (WUI) where protection of life and property is paramount (Stephens et al. 2021). Prior modeling from Stevens et al. (Stevens et al. 2016) demonstrated that strategic allocations of fuel treatments in the WUI can have an outsized effect on landscape fire behavior; in combination with restoration treatments in the wildland, this mix of treatment designs can be more effective than random placements of conventional fuel treatments alone. This permits greater flexibility to plan a mixture of treatments in such a way that reflects differences in biophysical settings and values at risk across landscapes in order to simultaneously meet multiple resource management objectives (Hessburg et al. 2015; Stevens et al. 2016; Stephens et al. 2021).

CHAPTER 6 – CONCLUSIONS

In this dissertation I explored: 1) causes of tree spatial patterns in dry fire-frequent forests; 2) the consequences of tree spatial patterns on potential fire behavior and effects; and 3) how alternate silvicultural strategies targeted at manipulation of tree spatial patterns can influence fire behavior and effects. They key findings are reviewed briefly here and in depth below. The aggregated patterns of trees commonly observed in dry forests of the western US can form in the absence of fire (Chapter 2). Most mature overstory trees are arranged in tree groups, leaving open spaces which are available for tree regeneration to establish with minimal competition from the overstory. In turn, tree regeneration forms the next generation of tree groups. This pattern of clustered tree regeneration forming tree groups also occurs without the driving competition of overstory trees (Chapter 3). After stand-replacing fires, topographic variation creates spatially heterogeneous niche availability. In addition, co-facilitation among tree regeneration promotes the organization of tree regeneration into tree groups. When fires return, clusters of regeneration and dense tree groups are most at risk of tree mortality. Subsequently, the trend towards aggregation occurring during fire-free periods is reversed momentarily (Chapter 4). After fire, tree spatial patterns resume trending towards aggregated distributions of tree groups. This is especially true for species such as *Pinus ponderosa* which benefit from exposed mineral soil patches where fire-killed trees were previously present (Malone et al. 2018). Because individual tree damage is greatest among small trees and dense tree groups, the silvicultural prescriptions that most maximize fire severity are conventional fuels treatments (Chapter 5). Separating overstory tree crowns reduces crown fire spread and thinning from below reduces crown fire initiation. By reducing canopy and surface fuel loads, restoration-based treatments that maintain heterogeneous tree patterns can reduce potential fire severity while meeting other ecological objectives. But conventional and homogenizing treatments remain a key tool for reducing fire behavior in areas like the wildland-urban interface where protection of lives and property are paramount.

6.1 Key Findings

6.1.1 Heterogeneity is Endogenous in Dry, Western Forests

The first key finding from this research is that dry forests self-organize into heterogeneous patterns in the absence of fire. Regenerating trees did not uniformly establish across available growing spaces. This is likely because the trees themselves modify the local environment, giving rise to new niches (Stoll and Prati 2001; Suzuki et al. 2008). In the *Pinus ponderosa* forest studied in Chapter 2, the patterns I identified suggest large trees were modulating the conditions experienced by regeneration. Seedlings preferred establishing, and had greater survivorship, in openings likely due to competitive inhibition by mature trees in the overstory. As a result, these new cohorts formed their own distinct tree groups, mimicking the clumping pattern of the mature, overstory trees.

Further, these spatial patterns of tree regeneration covaried with climate. This finding has two major applications. First, competitive pressures from the overstory lessened under periods with harsher climate. As climate was warmer and drier, patterns of regeneration indicted lowered repulsion from the overstory and lower mortality rates near the overstory. These patterns are a manifestation of the stress-gradient hypothesis which states that the net of facilitative and competitive interactions varies inversely across abiotic stress gradients (Bertness and Callaway 1994).

Second, as climate influences the competitive and facilitate interactions between trees, the variation in tree spatial arrangement across landscapes could be partially explained by climate (Fajardo et al. 2006; Clyatt et al. 2016). For example, the link between climate and overstory—regeneration interactions offers a potential resolution to disagreements over the proto-typical structure of tree groups in *Pinus ponderosa* forests. In study on tree groups in a *Pinus ponderosa* forest, Cooper (1960) originally stated that these forests are composed of single-aged tree groups which experience cycles of whole group replacement by fire. White (1985) explicitly disagreed with Cooper (1960). Observing separate forests, White (1985) concluded that tree groups in most *Pinus ponderosa* forests were multi-aged. White (1985) suggested multi-aged tree groups formed because regeneration in tree groups replaced selective fire-caused tree death. Chapter 2 demonstrated that tree—tree interactions responding to a stress gradient over decades can yield both single-aged and multi-aged tree groups barring any fire.

6.1.2 The Abiotic Environment Amplifies Heterogeneous Forest Structure

Chapter 3 demonstrated that local growing conditions also mediate niche availability and influence tree—tree interactions. These further shape tree patterning beyond the impact of "global" (i.e., site-wide) resource scarcities imposed by climate. In Chapter 3, I studied the spatial organization of tree regeneration following historically uncharacteristic high severity fires in ponderosa pine forests. Here, unlike Chapter 2, no overstory trees were present to influence the growing conditions of establishing tree recruits. While all stand-replacing disturbances leave behind a legacy of remnant material to a degree (Bače et al. 2015), high-severity fires create quasi-'blank slates'. This study provided evidence to support ecological theory proposed previously by Donato et al. (2012): sparse reforestation would exhibit rapid heterogeneous forest development because no forest canopy remains to moderate growing conditions at a stand scale.

This was later observed by Bače et al., (2015) following a bark beetle outbreak in Norway spruce (*Picea abies* (L.) Karst) forests in the Czech Republic, but to date had not been extended to dry western US forests.

Here I found that stand recovery—albeit low in stand density relative to that desired by forest stocking guidelines—exhibited aggregation of seedlings, akin to the tree groups observed in historical ponderosa pine forests with intact fire regimes (Larson and Churchill 2012). In this chapter, where facilitation or competition from the overstory was not a possible factor, two likely candidate causes of tree spatial patterning. First, topography provided niches, at scales up to 20 m, which were either hospitable or inhospitable for the germination and establishment of trees. For example, conifers *ex* ponderosa pine were most abundant on northern aspects where heat loads are lower, and quaking aspen more abundant in swales, mirroring patterns found in other studies (Addington et al. 2018; Francis et al. 2018). In addition to the influence of topography, co-facilitation drove development of tree spatial patterns. Here I found the interspecific attraction of ponderosa pine to other species suggests proximity to other species might lead to enhanced regeneration establishment. This was further evidenced by the presence of a positive correlation between seedling height and local seedling density. This may be because clustered seedlings can shade one another (Keyes et al. 2009). Since the same time of publication of this chapter, the same patterns of co-facilitation among seedlings after fires has been observed in other dry forests (Owen et al. 2017; Malone et al. 2018). If post-fire recovery is more sparse than desired, forest managers may opt to use artificial plantings. These results suggest artificial plantings after fires may have greater establishment success if they cluster seedlings together. In summary, these chapter's findings affirm that heterogeneous forest structures can arise through trees' self-organization.

6.1.3 Fires Reduce Heterogeneity of Forest Structure

In Chapter 4, I found that fires—as a spatial process of retaining surviving trees and removing fire-killed trees—function as a uniforming agent. This impact on tree spatial patterns was inverse to findings from Chapters 2 and 3 which identified that biotic interactions and topographic variation led to aggregations of distinct tree groups. Not only did fires reduce the size class diversity of trees and the relative abundance of species with less fire-resistant physical forms, but fires also reduced the aggregation of surviving trees relative to fire-killed trees. During fire-free periods new groups of small trees form and small trees are recruited into preexisting groups (Chapter 2). It was hypothesized that these local areas characterized by smaller crown base heights can lead to local group torching and localized mortality (Larson and Churchill 2012). To date, most studies on tree spatial patterns following fire relied on comparisons between sites with long-interrupted versus intact fire regimes (e.g., Fry et al., 2014; Schneider et al., 2016) and could not be applied to confirm or disconfirm Larson and Churchill's (2012) hypothesis. One notable exception was a field-based study of fire-killed and surviving tree locations in a Mongolian pine (*Pinus sylvestris* L. var. *mongolica* Litv.) forest with an intact fire regime (Yu et al. 2009). The results in chapter 4 confirm findings from Yu et al. (2009): density-dependent mortality, specifically among groups of small trees, leads to greater uniformity of tree arrangement after fire. This suggests many forest types globally with markedly heterogeneous and relatively open canopies should respond similarly to fires of low and moderate severity.

I hypothesize that tree spatial patterns followed a cyclic temporal pattern related to fire frequency. Historically, stocking, species composition, and fuel load in dry western forests varied over the course of fire intervals. In general, tree densities increased, facilitating the potential establishment of shade-tolerant, fire-sensitive species, and surface fuels accumulated as time since fire passed (Biswell 1973). When fires occurred, partial mortality, especially of fire-sensitive species, and consumption in the forest floor abruptly reversed this trend (Pearson 1950). Analogously, the degree of tree aggregation and sizes of tree groups likely increased with time since fire. The results from this study indicate that the first-order effect when fires occurred was to shift forest structure to a more homogeneous state. This is because fires selectively removed small trees, which tended to aggregate in denser and larger tree groups. The second-order effect on tree spatial patterns was to create opportunities for recovering heterogeneity. Over fire-free periods, trees reestablish in newly created openings and remnant tree groups (Chapter 2; Larson and Churchill, 2012; Sánchez et al., 2009), reestablishing the spatial heterogeneity of forest structure (Figure 6.1).

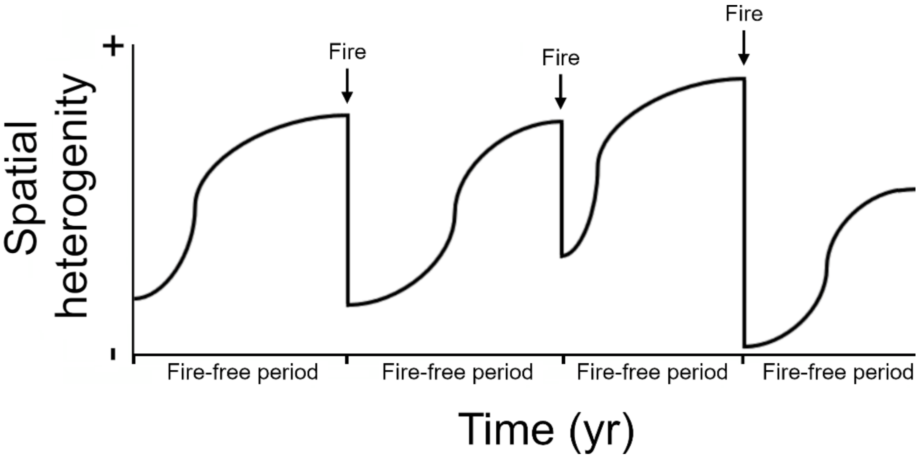

Figure 6.1. Cycles of spatial heterogeneity in frequent-fire forests.

Spatial heterogeneity of forest structure may be cyclical over time in frequent-fire forests. Heterogeneity is initially diminished following fire-caused mortality; after a period of time, aggregated tree regeneration restores spatial heterogeneity up to the arrival of each subsequent fire.

Even in contemporary, over-stocked forests, this cycle may be exhibited. In Chapter 4, I found that fires are likely to promote greater uniformity (i.e., less spatial aggregation and smaller tree groups) in contemporary forests following severe fires just as in historical forests. The key difference here between historical and contemporary periods is that reforestation may be prolonged where fires are uncharacteristically severe and few proximate seed sources persist (Chapter 3; Stevens-Rumann and Morgan 2019). I hypothesize this would lengthen the periodicity of the spatial heterogeneity cycle (Figure 6.1); lower rates of tree regeneration would produce a longer period to reestablish heterogeneity forest structure. In circumstances where climate change is not expected to diminish the capacity to support reforestation, managers may opt to artificially replant trees, expediting the creation of heterogeneity. This provides an opportunity for managers to plant seedlings in tree groups and near favorable microtopography to synthetically create the spatial heterogeneity which would have rebounded following a less severe fire.

6.1.4 Restoration of Heterogeneous Forest Structures Does Not Maximize Fire Hazard Reduction

It is argued that ecological restoration should mimic the heterogeneous structure of historical forests of the western US (Larson and Churchill 2012; Reynolds et al. 2013b; Addington et al. 2018), given that these forests' tree spatial patterns almost universally display a tendency to form heterogeneous tree patterns during fire-free periods (Chapter 2) and following fire (Chapter 3). Restored forest structures provide desirable ecosystem functions such as wildlife habitat (Youtz et al. 2008) and understory diversity (Matonis and Binkley 2018) and increase forest health (Kolb et al. 1994). Restored forest structures are also presumably effective at reducing fire hazard relative to untreated, undisturbed contemporary forests (Reinhardt et al. 2008; Larson and Churchill 2012). Historical forests, by their long-term persistence under regimes of fire, insects, and other disturbances, are considered resilient *ipso facto*; therefore, recreating the traits of forest structure prevalent historically, including structural heterogeneity, is assumed to be an effective means at reducing undesirable fire behavior and effects (Stephens et al. 2021). However, assessments of fire behavior in heterogeneous forests had been limited at the onset of this dissertation (Larson and Churchill 2012; Lutz et al. 2018). Recently, Koontz et al., (2020) found lower fire severities in heterogeneous forests with lower stocking than in denser, more homogeneous forests, but it is unclear whether differences in fire effects are more attributable to differences in forest arrangement or canopy fuel load.

In Chapter 5, I found that silvicultural cuttings aimed at enhancing forest structure heterogeneity did reduce fire behavior, as compared to before any treatment. However, spatially explicit implementation of fire hazard principles did prove to be the most efficacious; Fire severity was maximally reduced when thinning from below and leaving separated residual trees. Rate of spread however marginally increased concomitant with higher wind speeds. This unintended trade-off may influence difficulty of suppression but did not significantly affect fire severity outcomes (Reinhardt et al. 2008). This was because the increase in canopy base heights decreased the likelihood for crown fire initiation.

There are multiple considerations when comparing fire behavior outcomes between different potential silvicultural prescriptions. First, the effects of the level of residual basal area and surface fuel load are on par with the effect of the prescription. Surface fuels typically increase after treatment of the canopy as crown material is deposited on the forest floor (i.e., activity fuels), and can partially negate reductions in crown fire potential (Fulé et al. 2012). By following up with prescribed fire or judicious management of natural ignitions, fire managers can use fire to lower surface fuel loads and further gains in fire hazard reduction (Stephens et al. 2021). Second, it is important to recognize that ‘fire-proofing’ or optimizing strictly for fire hazard reduction may not be desirable to meet other silvicultural or ecological objectives (Reinhardt et al. 2008; Stephens et al. 2021). Forest treatments commonly balance multiple objectives whose maximization of a single outcome may come at the expense of meeting—and possibly precluding—other objectives (Franklin et al. 2007; Puettmann 2009). Managers and stakeholders may find it reasonable to have minor opportunity cost as restoration treatments still realize significant gains in hazard reduction compared to the prior untreated state. Third, I found that thinning from below largely nullified any difference in canopy consumption when paired with variable retention cuttings versus distance-based retention. The treatment of small trees varies between restoration treatment implementations and can include a prioritization of removing small trees near larger overstory trees (Reynolds et al. 2013b), to removal of clusters of small trees (Larson et al. 2012), to maintaining a mix of both singly-sized and variably-sized tree groups (Youtz et al. 2008). Likely, treatments that retain small trees—except those ‘ladder’ fuels near larger trees—would reduce fire transition from the surface to the canopy, obviating the effect of overstory tree arrangement on crown fire spread.

Churchill et al., (2013b), state ‘There is no single, optimal stand-level approach to maximizing resilience and adaptive capacity for all future conditions… Thus, it is sensible to vary patterns and structure types between stands…”. By deploying multiple silvicultural strategies across a landscape, bet-hedging is one strategy to deal with uncertainty in outcomes. Individual treatments may be adapted to site-specific considerations. For example, where prioritization of hazard reduction is greatest, such as the wildland-urban interface, conventional fuels treatments may be ideal; conversely, ecological restoration treatments may be more appropriate in the wildlands where ecological objectives have a higher weight (Addington et al. 2018; Stephens et al. 2021). Bet-hedging minimizes tail-risk, the possibility of low probability events with significant losses. In the context of forest management, the retention of stands with trees of varying size and spatial distributions maintains flexibility for adaptation through time as climates shift (Hessburg et al. 2019), disturbances occur (Stephens et al. 2018a), and forest health issues emerge (Long et al. 2018). For example, some small tree retention across stands can hedge against the loss of the overstory (Baker and Williams 2015). Furthermore, by treating only a portion of the landscape at each entry over long durations of time, the whole of the landscape is perpetually in a state of recovery, thus simultaneously retaining the ecological and social services provided by reestablishing, intermediate, and mature stands (Franklin et al. 2007).

6.2 Future Research Opportunities

One of the key barriers to widespread adoption of complexity-oriented silviculture is a lack of information (Puettmann et al. 2015). Unlocking the information embedded in tree spatial patterns (e.g., the underlying processes and interactions driving the self-organization of trees) can aid in the management of heterogeneous tree arrangements for multiple resource objectives, including restoration. At the moment, reference conditions —datasets describing the structure, abundance, and pre settlement arrangement of forest structure of forests—remain one of the key tools to guide the development of restoration silvicultural prescriptions (Churchill et al. 2013b; Franklin et al. 2013). But these reference conditions are limited in geography and represent a snapshot in time, limiting their applicability (Larson and Churchill 2012). Therefore, translating desirable characteristics of tree spatial patterns and forest structural heterogeneity from science to management remain broad, describing generic qualities rather than quantifiable metrics upon which treatments can be evaluated (Reynolds et al. 2013b; Addington et al. 2018). This stands in contrast to the precision of silvicultural guidelines and metrics used to developed prescriptions for other goals such as timber management (Puettmann et al. 2015) or wildlife habitat (e.g., Youtz et al., 2008).

As a further complication, societal demands are continually changing, regional and global changes to the biotic and abiotic environment are ongoing, and legacies of a fire suppression era can limit the usefulness of a return to pre-settlement forest structures (Fulé 2008). Thus, some future forests may be transitioning to ‘no-analog systems’ where the reference conditions describing the historical range of variability may no longer serve as an appropriate template (Puettmann 2011). The goal of a research theme extending this dissertation could strive to overcome the limitations of reference conditions and aid the intentional engineering of forest structure to meet objectives in a no-analog future.

One framework for extending this dissertation research is complex adaptive systems (CAS). As explained by Puettmann (2011), CAS framework focuses on interconnectedness of agents which exhibit bottom-up control endogenously, mediated by exogeneous top-down conditions, and the nonlinear relations and feedback loops between agents and exogeneous conditions. Ecosystem processes (e.g., nutrient fluxes, mortality, and natality rates) are driven by decentralized agents (e.g., trees); it stems from this view that ecosystems can self-organize, i.e., adapt to changing exogeneous conditions. This implies that ecosystem processes are determined by the ‘rules’ which govern agents’ nonlinear interactions. In the context of forests, examples of rules include physiological responses to resource availability, temperature or damage thresholds for necrosis, and light-response curves. Discovery of these rules can inform researchers and managers of how exogenous conditions shape the interactions of agents. These feedbacks can be positive, such as where exogeneous perturbations change to interactions between agents leading to dramatic re-organization. Conversely, negative feedbacks occur where interactions buffer against perturbations. Examples of perturbations include discrete disturbances such as fire, wind, and drought, as well as slow changes such as the rate and magnitude of change in precipitation or temperature, or immigration and emigration of species. Further elaboration of the application of CAS for ecological management is provided by Anand et al. (2010), Puettmann (2011) and Fahey et al. (2018).

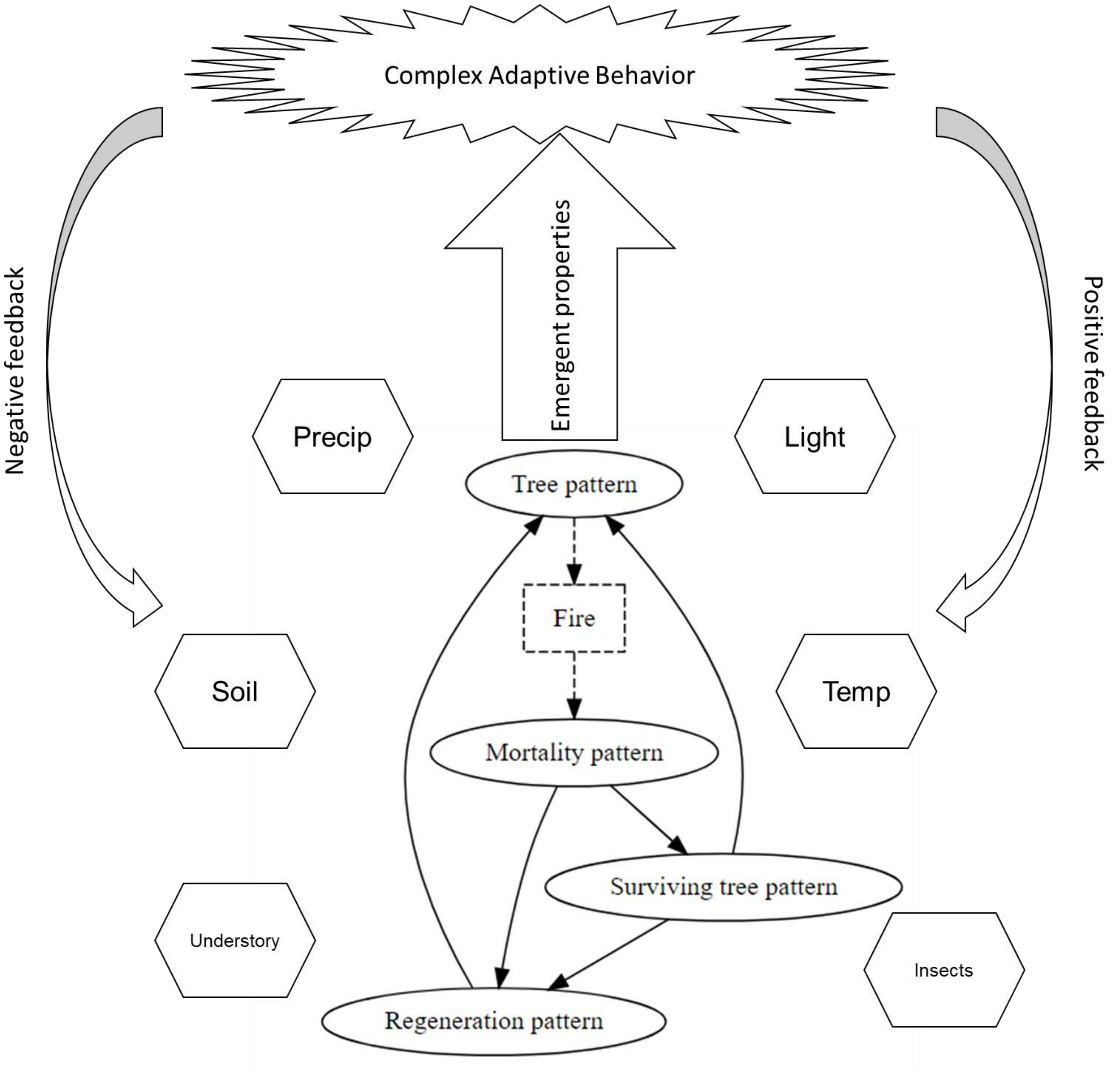

Figure 6.2. Tree spatial dynamics in fire-prone systems as a complex adaptive system

In fire-frequent forests, tree patterns are emergent properties stemming from the self-organization of trees and modified by fires, soil, precipitation, insects, temperature, light, and understory vegetation among other factors. These emergent properties influence complex adaptive behaviors such as growth, mortality, nutrient, and energy flux. Which in turn, feedback to modulate individual trees (Adapted from Puettmann 2011).

The application of a CAS-based framework for forest management is still under development (Puettmann 2011; Fahey et al. 2018). But such a concept may help guide research priorities. In dry forests of the western US, the ecosystems studied in this dissertation, applying a CAS framework (Figure 6.2) can help structure future research. I propose three topics of high priority.

First, fuel treatments are designed and evaluated, generally, by their immediate impact (Tinkham et al. 2016). However, fuel treatments may wait years or decades before experiencing a fire event. In the interim, ecosystems will self-organize in response to the initial perturbation of treatment as well as continual, dynamic exogeneous conditions. Specifically, as concluded by Chapter 2, tree ingrowth patterns will reflect changing climatic conditions. Under harsher conditions associated with shifting regimes of climate in the future, tree ingrowth may be biased towards establishing near existing tree groups. With greater frequency of multi-storied tree groups, fuel treatments may be less effective over time due to increased vertical continuity of canopy fuels(*sensu* Chapter 5). Future investigations can explicate the role of climate change on spatial niches of tree regeneration and the subsequent impact on potential fire behavior and effects.

Second, most analyses of fire-mediated tree spatial patterns in the western US have focused on the effects of wildfires alone. On the other hand, it is known that overlapping disturbances can have synergistic or antagonistic effects, depending on the balance on negative and positive feedbacks (Linn et al. 2013; Hoffman et al. 2015a). Different disturbances will have varying impacts on tree spatial patterns. One example (Case 1) might be the presence of bark beetles followed by wildfire. Bark beetles such as mountain pine beetle homogenize forest structure by removing large trees within denser tree groups (Churchill et al. 2013b). The generation of available surface and crown fuels within tree groups following death of beetle-killed trees might exacerbate fire behavior and mortality within tree groups (Larson and Churchill 2012). This is a potential example of a positive feedback loop, wherein one exogeneous perturbation with a uniforming effect on tree spatial patterns follows another. In contrast (Case 2), a prescribed fire under benign burning conditions could consume small trees within tree groups (Larson and Churchill 2012), making a subsequent wildfire less prone to broadscale mortality within tree groups (Chapter 5). The prescribed fire might create a more uniform pattern of trees after fire, but buffer against potential homogenization of tree patterns after a later wildfire. In Case 1, surviving trees would have greater tree-to-tree distances and experience less resource competition, than Case 2. Consequently, a forest stand in Case 1 might have more growth on a per tree basis than Case 2, all else equal.

Third, a key barrier I found in this dissertation, specifically Chapters 4 and 5, is the linkage between physiological tree responses and physics-based fire models. In Chapter 4, I used canopy consumption as a surrogate for crown volume scorched to estimate tree mortality. This approach underestimates potential tree mortality (Parsons et al. 2018). Learning from this, I used canopy consumption as a generic metric of fire severity in Chapter 5. The development of methods to better link tree death to physical quantities of fire and combustion is still needed to extend the utility of physics-based fire modeling (Hoffman et al. 2018a; Hood et al. 2018). One of the limitations remaining is the ability to computationally resolve the scales of fire behavior occurring over hectares while resolving the scales at which heat flux affects plant tissues (Hood et al. 2018). A second is further clarification of the heat-response curve resulting in necrosis, i.e., the magnitude and duration of heat flux. Approximate methods are being developed for post-processing physics-based model outputs, assigning mortality based on a lower bound particle temperature of 60 °C for 1 s (A. Atchley, pers. comm.). Using this rule, FIRETEC simulations adequately replicate experiments by Van Wagner (1973). Application of this method can improve the use of process-based physical fire models to investigate the interactions of tree spatial patterns and fire effects.

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