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Landscape Ecology Of Large Fires In Southwestern Forests, USA

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LANDSCAPE ECOLOGY OF LARGE FIRES IN SOUTHWESTERN FORESTS, USA

A Dissertation Presented

By

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DEDICATION

For my parents

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ABSTRACT

LANDSCAPE ECOLOGY OF LARGE FIRES IN SOUTHWESTERN FORESTS, USA

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The recent increase in large fires in southwestern forests has prompted concern regarding their ecological consequences. Recognizing the importance of spatial patterns in influencing successional processes, I asked: 1) How do large fires change plant communities?; 2) What are the implications of these changes for ponderosa pine forests?; and 3) What is the relationship of fire severity to gradients of climate, fuels, and topography? To address the first two questions, I studied succession in the woody plant community at two sites that burned in high-severity fire: La Mesa fire in northern New Mexico (1977) and Saddle Mountain in northern Arizona (1960). After large fires, abiotic conditions, associated prefire plant distributions, and spatial patterns of burning interacted to result in particular successional outcomes. Variation in abundance and diversity of species that spread from a refuge of seed sources remaining after the fire followed the model of wave-form succession. I investigated the implications of large fires for ponderosa pine by examining the influence of spatial patterns of burning on regeneration. Tree density corresponded most closely with particular scales of seed dispersal kernel and neighborhood severity metrics. Spatial patterns of burning remained

influential even after consideration of variables describing subsequent burning and the physical and biotic environment. Age structure of young forests indicated that populations spread in a moving front and by long-distance dispersal. To explore the relationship between fire severity and climate, I investigated how the spatial heterogeneity of high-severity patches varied among 20 fires across gradients in fire size and climate. The largest fires generally occurred during cool dry La Niña climates, however, several fires deviated from this trend. Some spatial properties of severity did not correspond to fire size or to changes in climate. Characteristics of fuels and topography altered spatial patterns of severity, but interactions with extreme burning conditions may have disrupted these local influences in both La Niña and El Niño fires. Spatial patterns of fire severity are central to understanding ecological dynamics following large fires in southwestern forests. Moreover, simplistic assumptions regarding the relation of fire severity to fire size and climate should be viewed with caution.

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CHAPTER 1

INHABITANTS OF LANDSCAPE SCARS: SUCCESSION OF WOODY PLANTS AFTER LARGE, SEVERE FOREST FIRES IN ARIZONA AND NEW MEXICO

1.1 Abstract

Understanding consequences of changes in climate and fire regimes for succession in plant communities is critical for conservation planning at broad spatial and temporal scales. I selected two sites that burned in high-severity fire decades ago and studied succession in the woody plant community and its variations across two environmental gradients; elevation and distance from a lower-severity/unburned edge. By overlaying an ordination of data for woody species on the modeled environmental gradient most closely related to variation in communities, I analyzed the interaction of life-history traits of species and landscape heterogeneity at each study site. Species that resprout from surviving roots were widespread across the distance gradient 28 years after the La Mesa fire in New Mexico. Species that reproduce from off-site seed, including *Pinus ponderosa*, were more prevalent where resprouters (e.g., *Quercus*) were less important in defining communities. At Saddle Mountain, Arizona, 45 years post-fire, I observed neighborhood interactions across the elevation gradient, for example, where shade-tolerant conifers (e.g., *Abies concolor*) occurred in understories of *Populus tremuloides*. At both sites, greater cover of woody plants that reproduce from off-site seed at shorter distances from a lower-severity/unburned edge suggested migration of these species following the model of wave-form succession. Contrary to conventional wisdom, these young forest communities, as well as the persistent non-forest

communities known as landscape scars, support high species and community diversity that underlines their importance to broad-scale conservation efforts.

1.2 Introduction

The mosaic of species and communities on forested landscapes is influenced greatly by large fires (Allen et al. 1998, Johnson et al. 1998, Turner and Dale 1998, Morgan et al. 2003). In recent years, characteristics of large fires in parts of the southwestern United States differ from those documented by historical evidence in that effects of fire are more severe over a greater proportion of the area burned (Swetnam and Baisan 1996, Schoennagel et al. 2004). Conservationists have expressed concern regarding the uncertain consequences of recent large fires for biodiversity in general and *Pinus ponderosa* specifically (McCarthy and Yanoff 2003). Conversion of *P. ponderosa* to persistent, nonforested grass or shrub communities has been discussed as an undesirable outcome of severe fire in forests of *P. ponderosa* (Savage and Mast 2005, Strom and Fulé 2007). These nonforest communities, or landscape scars, can remain from decades to centuries because seeds of *P. ponderosa* have relatively short dispersal distances, and establishment of seedlings is sporadic (Allen et al. 2002).

Recent evidence suggests, however, that over long time frames large, severe fires occurred historically in some forests of *P. ponderosa*. There is evidence from *P. ponderosa* forests in the Payette River region of Idaho that infrequent high-severity fires occurred at intervals of about 300 to 450 years (Meyer and Pierce 2003, Pierce et al. 2004). Erosion and sedimentation studies of fire-related debris flows indicate that severe fire events were coincident with extreme, widespread drought during the Medieval Climatic Anomaly (ca. 1050 to 650 cal. yr BP; Pierce et al. 2004). Furthermore, dendrochronological studies in *P. ponderosa* forests of the Colorado Front Range (Brown et al. 1999, Ehle and Baker 2003) and in the Black Hills of South Dakota and Wyoming (Shinneman and Baker 1997) documented a high-severity component of historical fire regimes that was considered part of the natural range of variability. Within the zone of *P. ponderosa* forests in Arizona, New Mexico, and southwestern Colorado, persistent shrublands are thought to be legacies of severe fires in the past (W. Romme, pers. comm.). Thus, over a longer time period, it is possible that *P. ponderosa* forests have persisted in a fire regime that includes fires that are large and severe in nature. In that case, forests of *P. ponderosa* persisted in a fire regime that included fires that were large and severe, and plant communities emerging after high-severity fire represent an important stage in variability of ecosystems related to climate change.

On the other hand, if present and future climates differ in important ways from those experienced in the past (Millar and Woolfenden 1999, Miller 2003), it is possible that changes observed on contemporary landscapes may represent unique communities outside of our current understanding of variability in forest systems. Both models (McKenzie et al., 2004) and empirical data (Westerling et al. 2006) suggest that large, severe fires throughout the Rocky Mountains region are directly related to effects of changing climate. All of this poses a particularly difficult conundrum for those concerned with conservation of natural systems over large areas and time frames. A better understanding of the complexities of vegetational response to large, severe disturbance is needed (Clark 1993, Turner et al. 1998) to evaluate the potential importance of post-fire plant communities to conservation efforts.

The purpose of my research was to better understand plant succession after severe fire events in the southwestern United States, given the possibility that these landscapes occupy an important place in long-term variability of ecosystems. To that end, I selected two sites that burned in high-severity fire decades ago and studied succession of woody plant communities and its variations across two environmental gradients; elevation and distance from potential seed source, or lower-severity/unburned edge. In this way, I examined how successional outcomes varied given different pre-fire communities and in relation to heterogeneity of landscapes created by the fire.

The influence of post-fire spatial heterogeneity on succession after severe fires (often called stand-replacing, or crown fires) has been documented in northern Rocky Mountain coniferous forests (e.g.,Turner et al. 1997, Turner et al. 1998). Crown fires burn with variable intensity (Van Wagner 1983), producing a remarkably heterogeneous mosaic of burn severities, or ecological effects, on the landscape (Christensen et al. 1989). The spatial heterogeneity of burn severity leads to different successional changes, depending on life-history strategies (Turner and Romme 1994, Turner et al. 1997, Frelich 2002). I defined functional life-history groups of species as follows: 1) species that primarily sprout from surviving roots and root collars, 2) species that reproduce primarily by on-site seed that is cached and sometimes require scarification, and 3) species that reproduce exclusively by seed dispersed from off-site via wind or animals. The following expectations were based on studies in forest systems that have been characterized by large, severe fires. First, I expected that rate of establishment of plants that depend on seed dispersal, including *P. ponderosa*, would be influenced by the spatial distribution of surviving individuals (Turner and Romme 1994, Frelich 2002). In contrast, plants that resprout from residual living tissue (e.g., *Quercus* or *Populus tremuloides*) or that reproduce from scarified seed (e.g., *Arctostaphylos*) can be distributed widely across gradients of distance and elevation because they survive regardless of position relative to source of seed (Frelich 2002). Second, neighborhood effects can be positive or negative depending on the species involved (Frelich and Reich 1995, Ponge et al. 1998). I expected to observe regeneration of *Pinus edulis* shaded by other plants (Floyd 1982), and shade-tolerant conifer species, including *Abies concolor*, benefitting from quickly resprouting *P. tremuloides* (Brown and DeByle 1987, Keyser et al. 2005). Conversely, abundant resprouting shrubs (e.g., *Quercus*) might limit resources for off-site seeders, including *P. ponderosa*.

1.3 Materials and Methods

1.3.1 Study Areas

I selected two study sites where large fire events resulted in extensive areas of dead trees: the 1960 Saddle Mountain fire on the Kaibab Plateau in northern Arizona and the La Mesa fire of 1977 on the Pajarito Plateau in northern New Mexico. The fires occurred across an elevational gradient that encompassed major community types, including *P. edulis*-*Juniperus* woodland, *P. ponderosa*, and mixed-conifer (*P. ponderosa*-*Pseudotsuga menziesii*-*A. concolor*-*P. tremuloides*) forest. The study sites represented diverse conditions in the geographic range of *P. ponderosa*; thus, providing highly variable landscapes in which I expected to observe a diversity of successional outcomes following high-severity fire.

Both sites were located on regional plateaus with markedly different geologic histories. Ash-flow tuffs, erupted from the Jemez Mountains, define the Pajarito Plateau; its alternating broad mesas and steep canyons drain eastward to White Rock Canyon of the Rio Grande (Reneau and McDonald 1996). In contrast, the Kaibab Plateau was formed from sedimentary rock layers deposited with shifts in sea level (Hopkins 1990). The topography creates dramatic relief; steep scarp slopes, or combs, are adjacent to narrow stream bottoms, with sheer walls on the south forming the Nankoweap Rim.

Climate patterns were similar in both areas, with fluctuations at a decadal scale influenced by the El Niño Southern Oscillation (Swetnam and Betancourt 1998). Annually, frequent, strong thunderstorms occur during July through early September (Woodmencey 2001). Storms in winter (December-March) also bring moisture, but in lesser amounts than received during the summer monsoon. Snow accumulates in winter at elevations >1,500 m; below-freezing, overnight lows occur throughout winter and are possible in any season (Woodmencey 2001).

Land use and management at the two sites have included many influences. These areas are traditional and current homelands to many Native American peoples. The Saddle Mountain burn is entirely within the Saddle Mountain Wilderness on the Kaibab National Forest, except for a small area in Grand Canyon National Park. La Mesa falls under several jurisdictions including Bandelier National Monument and the Dome Wilderness, the Santa Fe National Forest, and the Los Alamos National Laboratory, a United States Department of Energy facility. Because both fires burned in areas with active post-fire management programs, salvage logging, seeding of non-native grasses and planting of seedlings of *P. ponderosa* occurred in some places (C. Allen and D.

Steffensen, pers. comm.). Subsequent wildland and prescribed fires have burned in portions of both study sites (National Park Service, unpubl. data; United States Forest Service, unpubl. data).

1.3.2 Data Collection and Analysis

For La Mesa, I obtained aerial photos taken in 1973, 1975, 1977, 1981, and 1983 that covered portions or all of the burn. Photos varied in scale from 1:600 to 1: 24,000. Photos obtained of the Saddle Mountain burn were taken in 1957 and 1963 at a scale of 1:15,840. Using the pre-fire and post-fire aerial photos, I mapped areas that had changed from forest to non-forest corresponding to fire perimeters available from the United States Forest Service and the National Park Service. I did not distinguish mortality of trees that was a direct result of crown fire from mortality caused by surface-fire, or trees that initially survived the fire but later succumbed to damage or disease. Therefore, areas where all trees were killed were labeled as high-severity, and areas of surviving trees were labeled as lower-severity/unburned because they could have experienced low, moderate, or mixed effects of fire, or could represent unburned islands within the perimeter. The minimum mapping unit for areas of surviving trees within high-severity patches was two live trees. I used ArcInfo version 9.0 (Environmental Systems Research Institute, Redlands, California) for spatial analyses.

I sampled 68 plots at La Mesa and 79 plots at Saddle Mountain between 16 May and 30 June 2005. Locations were chosen at random within high-severity patches at greatest distances from lower-severity/unburned edge. I distributed the sample plots throughout burns to the greatest extent possible (Figures 1.1 and 1.2). However, access was limited in some places by Los Alamos National Laboratory, and I also avoided locations where tree planting was documented (e.g., on the Mesa del Rito at the La Mesa burn). Plots were circular with 25-m radius (0.2 ha).

I conducted point-intercept surveys at each plot along two 50-m transects positioned North-South and East-West. At each 1-m mark, I recorded all woody species present above the meter-mark on the transect tape, i.e., that would be intercepted by a vertical pin extending up from the ground. Cover for each species was derived by summing its frequency for a given sample plot. In the case of species that tend to hybridize (*Quercus*), or if similarities led to difficulty in identification to the species level (*Arctostaphylos* [Arsp1], *Artemisia* [Arsp2], *Gutierrezia*, *Rubus*, *Sambucus*, and *Symphoricarpos*), data were presented at the genus level (Table 1.1). I also recorded additional woody species present outside of the line transects but within the plot.

I verified origin of forest opening (i.e., the high-severity patch) by presence of downed wood, stumps, or snags. Also, I field-checked maps for accurate representation of surviving trees, and modified maps in a few cases upon my return from the field. Photos were taken from center of plots in the four cardinal directions.

To determine how species form communities, and describe relationships among functional groups and the environment, I first conducted a plant-community ordination using non-metric multidimensional scaling. I deleted uncommon species (i.e., occurring at <5% of plots) to emphasize major compositional patterns in the dataset. Data were square-root transformed and Wisconsin double-standardization was used to equalize emphasis among sample units and among species. To derive the species matrix of dissimilarities, I used the Bray-Curtis algorithm (Bray and Curtis 1957). I chose a three-dimensional model based on goodness of fit, evaluated with a stress statistic that reflected the linear or non-linear correlation between original dissimilarities and ordination distances (Clarke, 1993; stress = 13.2 and 11.6, for La Mesa and Saddle Mountain, respectively). The final configuration was rotated so that the variance of points was maximized on the first dimension. I determined that the rotation allowed minimal loss of information when multi-dimensional solutions are displayed in two-dimensional plots.

Then, I chose a single environmental-variable model that explained the greatest amount of deviance in ordination for each site using generalized additive models. The models are driven by characteristics of the data, rather than parametric classes so that generalized additive models can take any smooth shape (Yee and Mitchell 1991, Oksanen and Minchin 2002). The regression surface is the sum of the smooth functions for each variable. Selection of smoothing parameters was accomplished through minimizing a generalized cross-validation score that incorporated multiple penalties because the model attempts to accommodate every variation in the data (Wood 2000).

The environmental variable chosen was different at the two sites. At La Mesa, the generalized additive model with distance as the dependent variable explained a greater proportion of variation in the data (adjusted $r^2 = 0.42$), compared to elevation (adjusted $r^2 = 0.25$). Therefore, I superimposed the ordination on the distance gradient. At Saddle Mountain, the generalized additive model with elevation as the dependent variable explained a greater proportion of deviance (adjusted $r^2 = 0.85$) compared to the distance model (adjusted $r^2 = 0.19$), and so I superimposed the ordination on the elevation gradient. I used the R statistical package (R Development Core Team, http://www.R-project.org) for all statistical analyses, the R-vegan library functions for ordination using non-metric multidimensional scaling (J. Oksanen, http://cc.oulu.fi/~jarioksa), and the R-mgcv library for generalized additive models (S. N. Wood, http://www.maths.bath.ac.uk/~sw283/simon/mgcv.html).

Defining functional groups in relation to reproductive strategies is challenging because most plants demonstrate more than one strategy depending on conditions at a specific time and place. For my analysis, I used several references that described life-history characteristics (Epple 1995, Foxx and Hoard 1995, Ecological Restoration Institute 2004, U.S. Forest Service 2007), chose the most-likely strategy based on available information, and assigned a functional group accordingly (Table 1.1). I enhanced interpretation of the arrangement of species, functional groups, and communities in ordination space using two strategies. First, I displayed a four-letter abbreviation of each species centered at the location of its peak cover (i.e., weighted-average scores); nearby locations had less cover and farther distances in the ordination space contain low levels or no cover of the species. This enabled an overview of distributions of species along the modeled environmental gradients in the ordination space (Figures 1.3 and 1.5). Second, I used gray circles scaled in size relative to the total cover of species in each functional group to symbolize each sample site. In this way, I examined the distribution of functional groups as they varied in cover across the environmental gradient and in terms of the role of each group in defining similarities among sample sites (Figures 1.4 and 1.6).

1.4 Results

I identified 52 species of native trees and shrubs in sample plots at the study areas (Table 1.1). Several species were abundant in terms of both cover and frequency of occurrence across sample plots at both study sites (e.g., *Quercus*, *Robinia neomexicanus*).

Others were observed frequently only at La Mesa (e.g., *P. ponderosa, Artemisia* [Arsp2], *Rosa woodsii*) or Saddle Mountain (*A. concolor, Arctostaphylos* [Arsp1], *Berberis [Mahonia] repens*, *P. tremuloides*, *Symphoricarpos rotundifolius*). Species observed infrequently with low mean total cover at either study site included *Ceanothus greggii*, *Garrya flavescens*, *Holodiscus dumosus*, *Prunus virginiana*, and *Pinus flexilis*.

La Mesa--For La Mesa, one species of tree and 11 species of shrubs were represented in the ordination diagram (Figure 1.3). Minimum distance from lower-severity/unburned edge shown on the gradient corresponds to optimal locations for *Berberis fendleri*, *P. ponderosa*, *Fallugia paradoxa*, *R. woodsii*, and *R. neomexicanus*. Distribution of these species extended across the entire gradient of distance; *R. neomexicanus*, for example, was fairly ubiquitous, occurring at locations up to ca. 225 m. *Pinus ponderosa* was recorded at a maximum distance of ca. 222 m. *Ribes viscosissimum*, *Quercus*, and *C. fendleri* were at peak cover levels at intermediate distances. *Quercus* was present across the range of distances from 10 to ca. 300 m. *Juniperus monosperma*, *Cercocarpus montanus*, *Artemisia* (Arsp2), and *Gutierrezia* were located optimally at the highest modeled distances of any species. Distribution of these species was fairly dispersed, compared to that of species with greatest cover at the shortest distances.

Species that reproduce primarily by resprouting played an important role in defining ecologically similar locations at La Mesa (Figure 1.4). Greatest variation in cover for resprouters occurred at shorter distances from center of sample plot to edge of lower-severity/unburned, and sample plots with greater cover of resprouters clustered in one area of the ordination space. Sample sites located at the edge of the distance gradient, at both small and large distances, tended to have relatively sparse cover of resprouters.

Robinia neomexicanus, *Quercus*, *F. paradoxa*, and *R. woodsii* were major contributors to cover of this functional group. *Populus tremuloides* occurred at one sample plot at La Mesa.

The off-site seeders at La Mesa made a marked contribution to similarities in sample sites at locations where resprouters tended to be less prevalent (Figure 1.4). In ordination space, distribution of sample sites with maximum cover of off-site seeders was separate from the cluster of sites containing the greatest cover of resprouters. In addition, sites with more abundant cover of off-site seeders were located in two distinct areas of ordination space; one at the low end of the distance gradient and the other at intermediate distances. At the smaller distances, *P. ponderosa* was the greatest contributor to cover of off-site seeders; *Artemisia* and *Gutierrezia* had greater cover at intermediate distances in this group. Off-site seeders exhibited a general decreasing trend across the range of increasing distances (Figure 1.4, scatter plot).

Cover was relatively low across the range of distances for on-site seeders at La Mesa. Location of the sample with abundant cover of *C. fendleri* (largest gray-shaded area in Figure 1.4, on-site seeders plot) was exceptional for this functional group. Otherwise, *B. fendleri*, *P. virginiana*, *Rhus trilobata*, and *Ribes* were present at low total-cover values with no apparent interpretation for similarities in locations of samples.

Saddle Mountain--At Saddle Mountain, optimal locations for 6 species of trees and 17 species of shrubs were distributed across an elevational gradient (Figure 1.5). Composition of communities varied with greatest cover of *Cowania mexicana*, *Artemisia tridentata*, *Chrysothamnus nauseousus*, and *P. edulis* occurring at lowest elevations. Communities in which *Quercus*, *Purshia tridentata*, and *C. montanus* had relatively abundant cover were nearby at the lower end of the elevation gradient. Some species exhibited a broader distribution than others; for example, *C. nauseousus* occurred at elevations from 2,021 to 2,382 m, *Quercus* was observed from 2,021 to 2,680 m, and *P. tridentata* was only at locations from 2,317 to 2,372 m. Optima for *Artemisia* (Arsp2), *Amelanchier utahensis*, and *Arctostaphylos* (Arsp1) were located on the next contour, moving up along the gradient. These three species were at much higher elevations; I recorded *Arctostaphylos* (Arsp1), for example, at sample plots that ranged from 2,021 to 2,680 m, and *A. utahensis* occurred from 2,117 to 2,658 m.

Symphoricarpos rotundifolius reached its peak at a group of sample locations at middle elevations, set apart from optima of other species. Its distribution overlapped with lower-elevation and higher-elevation species ranging from 2,111 to 2,707 m. Species of shrubs with optimal locations above the 2,500-m contour included some common plants such as *C. fendleri* and *R. neomexicanus*, as well as some less-frequently observed species; *Pachystima (Paxistima) myrsinites*, *Rubus*, *Sambucus*, and *B. repens*. Maximum cover of *P. ponderosa* was located at the next position as the gradient ascended; its range of occurrence was 2,261 to 2,713 m. Locations with maximum cover of *R. viscosissimum*, *P. tremuloides*, *A. concolor*, *Picea engelmannii*, and *P. menziesii*, were clustered at the upper end of the elevation gradient. Observations of these species were confined to sample plots within a fairly narrow range of elevation, with *P. tremuloides* and *A. concolor* observed above 2,459 m, *P. menziesii* and *R. viscosissimum* observed only above ca. 2,550 m and *P. engelmannii* ≥2,673 m.

Variation in plant communities at Saddle Mountain was influenced by total cover of resprouting species, which reached their greatest values at higher-elevation sites, and also were influencial at several mid-elevation sites (Figure 1.6). Cover of *P. tremuloides* was a major contributor to ecological similarity in sample sites at high elevations. Across the gradient of elevation, *Quercus* and *R. neomexicanus* contributed to total cover in this functional group. At Saddle Mountain, abundant cover of resprouters and off-site seeders coincided, in contrast to patterns at La Mesa.

Off-site seeders were limited in cover across the gradient of elevation except for one cluster of sample sites at the higher end of the gradient (Figure 1.6). The species with greatest maximum cover among the off-site seeders was *A. concolor*. *Pinus ponderosa*, *P. engelmannii*, and *P. menziesii* also contributed to cover of off-site seeders at higher-elevation sites. Cover of off-site seeders decreased with increasing distance to lower-severity/unburned edge at Saddle Mountain; greatest variation in cover was observed at the shortest distances whereas moderate-to-large cover was never observed at farther distances to lower-severity/unburned edge (Figure 1.6, scatter plot). Maximum cover of off-site seeders occurred at sample plots where on-site seeders were less prevalent.

Distribution of on-site seeders also contributed to defining similarities of sites, with greater cover occurring at sites all along one side of the gradient in elevation (Figure 1.6). Moderate and low levels of on-site seeders were scattered at sites in other areas. *Arctostaphylos* exhibited the largest maximum cover among on-site seeders. Other influential species in the on-site seeder group were *S. rotundifolius*, *C. fendleri*, *P. myrsinites*, *Rubus*, and *R. viscosissimum*.

1.5 Discussion

Community composition of woody species within high-severity patches at La Mesa and Saddle Mountain was a function of spatial heterogeneity created by the fire, with its particular configurations of seed sources and neighborhood conditions. For example, variation in abundance and diversity of species that spread from a refuge of seed sources remaining after the fire (i.e., off-site seeders) influenced the spatial dynamic of community composition across the landscape. My finding of greater cover of off-site seeders at shorter distances from lower-severity/unburned edge suggests gradual migration of these species following the model of wave-form succession (Frelich 2002; Figure 1.7). Interacting environmental conditions that allow establishment of seedlings (e.g., for *P. ponderosa*; Bonnet et al. 2005) likely influence the temporal and directional dynamic of migration into high-severity patches by off-site seeders.

In addition, woody communities at my study areas resulted from legacies of spatial pattern in the pre-disturbed landscape including distribution of species that survive within the disturbance perimeter. This successional dynamic was evident in distribution of species that survive and resprout within a high-severity patch, such as *Quercus* or *P. tremuloides*, which corresponds with their distribution before the fire, and depends on environmental conditions in the pre-fire landscape. As expected, resprouting species were widespread across the full range of distances and elevations (Figures 1.4 and 1.6). Abundant cover of resprouting species generally did not coincide with greater cover of off-site seeders at La Mesa, suggesting potential neighborhood effects between resprouters that establish quickly and off-site seeders that move into openings through time. Although *Quercus* can initially limit regeneration of trees after fire, succession to pine and other conifers has been documented (Moir and Ludwig 1979, Moir et al. 1997). Differing distributions of on-site and off-site seeders at Saddle Mountain could represent a similar process in which abundant cover of *Arctostaphylos* precedes movement of conifers into openings over long time frames (Skau et al. 1970).

I observed possible neighborhood effects from shading at some places. Some seedlings of *P. edulis* were observed growing in the shade of *Juniperus*, although *Juniperus* and *P. edulis* were uncommon at both study areas. *Pinus edulis*-*Juniperus* woodlands are relatively slow to return to a mature state, and based on historical evidence, disturbance regimes are characterized by infrequent stand-replacing fires in some places (Floyd et al. 2004). Regeneration by *Abies concolor* was common in understories with *P. tremuloides* at Saddle Mountain; this observation is consistent with predicted neighborhood effects. Dense regeneration of *P. ponderosa* has been documented in small stands of *P. tremuloides* after fire (Keyser et al. 2005). I observed some regeneration of *P. ponderosa* in larger forest openings of *P. tremuloides*, but optimal locations for *P. ponderosa* at Saddle Mountain were farther away from locations with greatest cover of *P. tremuloides* than of *A. concolor* (Figure 1.5). At farthest distances from lower-severity/unburned edge, no species at La Mesa reached maximum cover (Figure 1.3) and cover was low for all functional groups (Figure 1.4). Significance of this observation is uncertain because of the limited number of sample locations at the greatest distances.

Differences due to spatial and temporal location were important in interpreting the relationship of successional outcomes to environment. Important biogeographical differences in study sites may have resulted in stronger association with one environmental gradient rather than another. It is possible that the broad mesas on the Pajarito Plateau provided a better environment in which to observe effects of distance from lower-severity/unburned edge in structuring plant communities after the La Mesa fire. In contrast, the greater topographic relief and dissimilarity of species associated with lower and higher elevations at Saddle Mountain resulted in a better correspondence of plant communities with changes in elevation.

Certain underlying environmental gradients can become more influential through time. Soon after the Yellowstone fires of 1988, patterns of burn severity strongly affected vegetational response, but the importance of other abiotic factors has increased through time (Turner et al. 2003). Topography, therefore, could have more influence on communities at Saddle Mountain, 45 years post-fire, while the influence of spatial heterogeneity resulting from the fire still persists at La Mesa, only 28 years post-fire. The environmental gradients I examined undoubtedly interact with multi-scale temporal and spatial variables, including regional pools of species, precipitation, and heterogeneity of resources (Keeley et al. 2005). Further investigation is needed to understand the role of these factors and their interactions in structuring plant communities at La Mesa and Saddle Mountain.

Understanding landscape change after severe fire events is of vital importance, given predictions of a warming climate accompanied by an increase in frequency, size, and duration of fires. Explicit consideration of spatial patterns of burning in relation to life-history characteristics is key to understanding complex successional outcomes after severe disturbance. In large fires, broad gradients affect spatial patterns of burning, and vegetation patterns are influenced in turn (Turner and Romme 1994). If these factors are not considered, important variability in species and communities is likely to be missed. Detailed information about species can benefit conservation assessments (Brooks et al.

2004), especially when variability in ecosystems is likely changing with climate. Individual species and the communities they compose play ecological and cultural roles on contemporary landscapes (sensu Nabhan 1997, Center for Sustainable Environments 2002). Areas burned in severe fire at Saddle Mountain and La Mesa included communities that might diversify function of landscapes through creation of early successional habitats for wildlife (Romme and Knight 1982). In addition, woody species at the study sites have a wide range of traditional and current uses; basketry and other building material, important food sources, a plethora of medicinal remedies, and ceremonial uses (Dunmire and Tierney 1995, 1997, U.S. Forest Service 2007). Contrary to conventional wisdom, these young forest communities, as well as the persistent non-forest communities known as landscape scars support high species and community diversity that underlines their importance to broad-scale conservation efforts.

Table 1.1 Cover (mean and *SD*) and frequency (%) of woody species observed at the study sites. Functional group designations are as follows: 1 = Resprouters; 2 = On-site seeders; 3 = Off-site seeders. Species that did not contribute to cover are designated with an asterisk.

		La Mesa (n = 68)		Saddle Mountain (n = 79)		Functional
Scientific Name (Common Name)	Abbrev.	Cover Mean (*SD*)	Freq. %	Cover Mean (*SD*)	Freq. %	Group
Abies concolor (white fir)	Abco	0.01 (0.12)	0.01	2.92 (8.55)	0.29	3
Acer glabrum (Rocky Mountain maple)	Acgl			0.19 (1.12)	0.04	1
Acer grandidentatum (big tooth maple)	Acgr			0.13 (0.81)	0.03	1
Amelanchier utahensis (Utah serviceberry)	Amut	0.03 (0.24)	0.01	1.44 (4.50)	0.18	1
Arctostaphylos pringlei (Pringlei manzanita) *Arctostaphylos pungens* (pointleaf manzanita)	Arsp1			14.99 (21.87)	0.49	2
Artemisia carruthii (wormwood) *Artemisia dranunculus* (false tarragon) *Artemisia frigida* (fringed sage) *Artemisia ludoviciana* (wormwood)	Arsp2	2.19 (3.44)	0.46	0.27 (1.00)	0.09	3
Artemisia tridentata (big sagebrush)	Artr			0.53 (2.15)	0.11	3
Berberis fendleri (Colorado barberry)	Befe	0.09 (0.41)	0.06			2
Berberis (Mahonia) repens (creeping barberry)	Bere			1.19 (2.39)	0.37	1
Ceanothus fendleri (Fendler ceanothus)	Cefe	1.90 (6.54)	0.18	0.82 (3.32)	0.14	2

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Table 1.1, continued

Ceanothus greggii (Gregg ceanothus)	Cegr			0.01 (0.11)	0.01	2
Cercocarpus montanus (true mountain mahogany)	Cemo	0.22 (0.77)	0.10	0.85 (3.71)	0.08	1
Chrysothamnus nauseousus (golden rabbit brush)	Chna			0.39 (1.22)	0.18	3
Cowania mexicana (cliff-rose)	Come			0.54 (1.65)	0.11	3
Ephedra trifurea (longleaf ephedra or Mormon tea)	Eptr			0.03 (0.16)	0.03	1
Fallugia paradoxa (Apache-plume)	Fapa	0.66 (3.75)	0.07			1
Garrya flavescens (ashy silktassel)	Gafl			0.08 (0.68)	0.01	1
Gutierrezia sarothrae (snakeweed)	Gusp	0.75 (3.14)	0.10	0.01 (0.11)	0.01	3
Holodiscus dumosus (rock-spirea)	Hodu			0.03 (0.23)	0.01	3
Juniperus communis (common juniper)	Juco			0.06 (0.33)	0.04	3
Juniperus deppeana (alligator juniper)	Jude	0.01 (0.12)	0.01			1
Juniperus monosperma (one-seed juniper)	Jumo	0.06 (0.24)	0.06			3
Juniperus osteosperma (Utah juniper)	Juos			0.03 (0.16)	0.03	3
Juniperus scopulorum (Rocky Mountain juniper)	Jusc	0.07 (0.43)	0.03			3
Pachystima (Paxistima) myrsinites (mountain lover)	Pamy			1.57 (4.68)	0.22	2
Physocarpus monogynus (mountain ninebark)	Phmo			0.14 (0.78)	0.04	1

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Table 1.1, continued

Picea engelmannii (Engelmann spruce)	Pien			0.22 (1.00)	0.06	3
Pinus edulis (piñon pine)	Pied			0.06 (0.29)	0.05	3
Pinus flexilis (limber pine)	Pifl	0.01 (0.12)	0.01			3
Pinus ponderosa (ponderosa pine)	Pipo	5.34 (9.96)	0.54	1.30 (3.98)	0.24	3
Populus tremuloides (quaking aspen)	Potr	0.10 (0.85)	0.01	20.90 (28.21)	0.47	1
Pseudotsuga menziesii (Douglas-fir)	Psme	0.03 (0.24)	0.01	0.20 (0.72)	0.10	3
Ptelea trifoliata (narrowleaf hoptree)	Pttr			0.11 (0.60)	0.04	2
Prunus virginiana (chokecherry)	Prvi	0.01 (0.12)	0.01			2
Purshia tridentata (antelopebrush)	Putr			0.05 (0.22)	0.05	2
Quercus gambelii (Gambel oak) *Quercus turbinella* (shrub live oak)* *Quercus undulata* (wavyleaf oak)	Qusp	12.00 (13.89)	0.78	8.38 (14.53)	0.46	1
Rhus trilobata (skunk bush)	Rhtr	0.06 (0.34)	0.03	0.01 (0.11)	0.01	2
Ribes cereum (wax currant) *Ribes inerme* (gooseberry)	Risp	0.38 (2.27)	0.06			2
Ribes viscosissimum (sticky currant)	Rivi			0.43 (2.61)	0.05	2
Robinia neomexicanus (New Mexico locust)	Rone	10.54 (11.01)	0.79	16.18 (17.78)	0.76	1

Continued on next page

Table 1.1, continued

Rosa woodsii (wild rose)	Rowo	1.07 (2.56)	0.29	0.20 (1.09)	0.04	1
Rubus parviflorus (raspberry or thimbleberry) *Rubus neomexicanus* (thimbleberry)	Rusp			1.11 (4.18)	0.13	2
Sambucus racemosa (elderberry)	Sasp			0.51 (1.50)	0.16	2
Symphoricarpos rotundifolius (snowberry)	Sysp			2.92 (7.28)	0.33	2

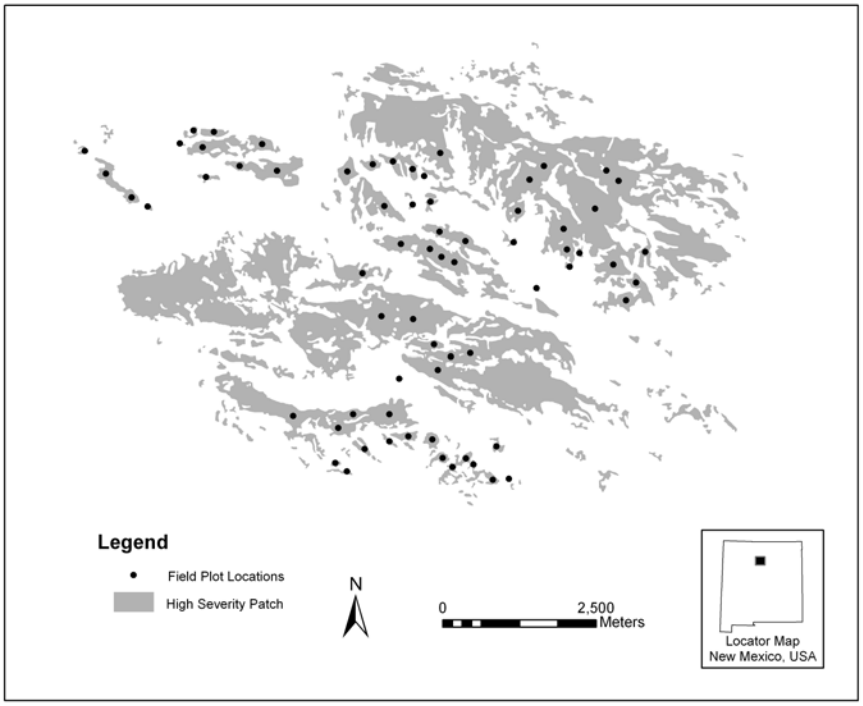

Figure 1.1: Locations of 68 field plots at the La Mesa burn, New Mexico. High-severity patches, mapped from aerial photos, are shown in gray, with black dots representing the center of the 25-m radius field plots. The ponderosa pine-mixed conifer zone is at the northwest, with a general decrease in elevation and associated change in forest types toward the southeast. Forest Service lands are on the western side, and Los Alamos National Laboratory properties occur at the northern edge of the burn. The central and eastern portions of the burn are located in Bandelier National Monument and the Dome Wilderness.

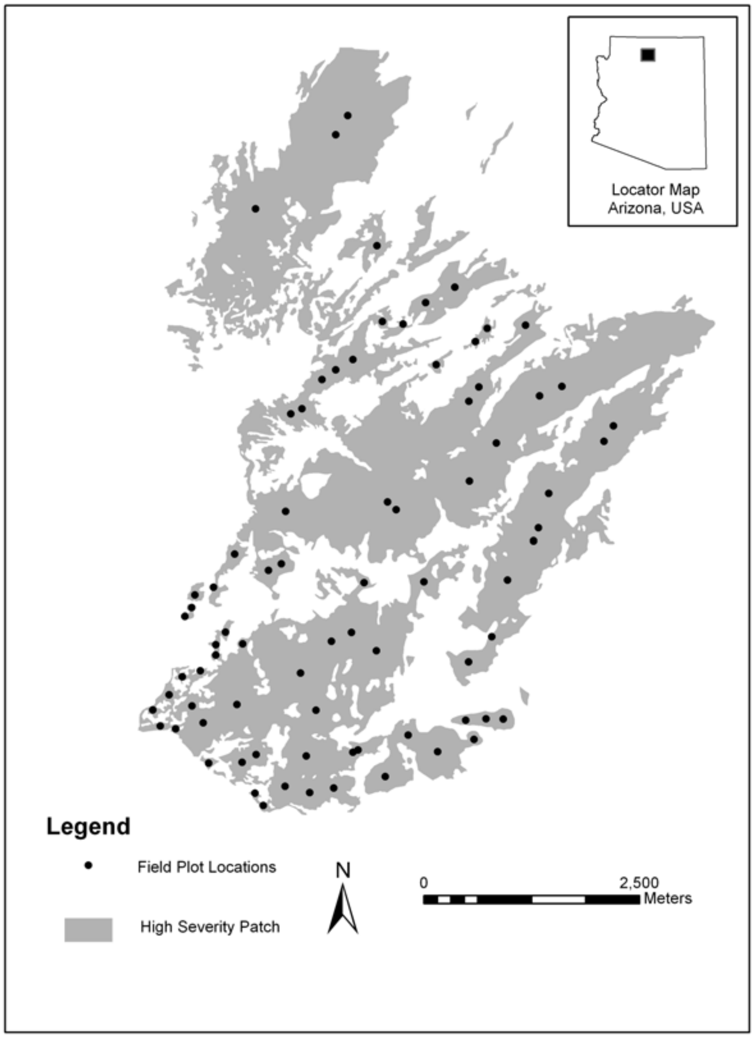

Figure 1.2: Locations of 79 field plots at the Saddle Mountain burn, Arizona. High-severity patches, mapped from aerial photos, are shown in gray, with black dots representing the center of the 25-m radius field plots. Elevation decreases from the southwest aspen-mixed conifer zone along the boundary of Grand Canyon National Park to the northeast (piñon-juniper woodland zone). Most of the burn is within the Saddle Mountain Wilderness, Kaibab National Forest.

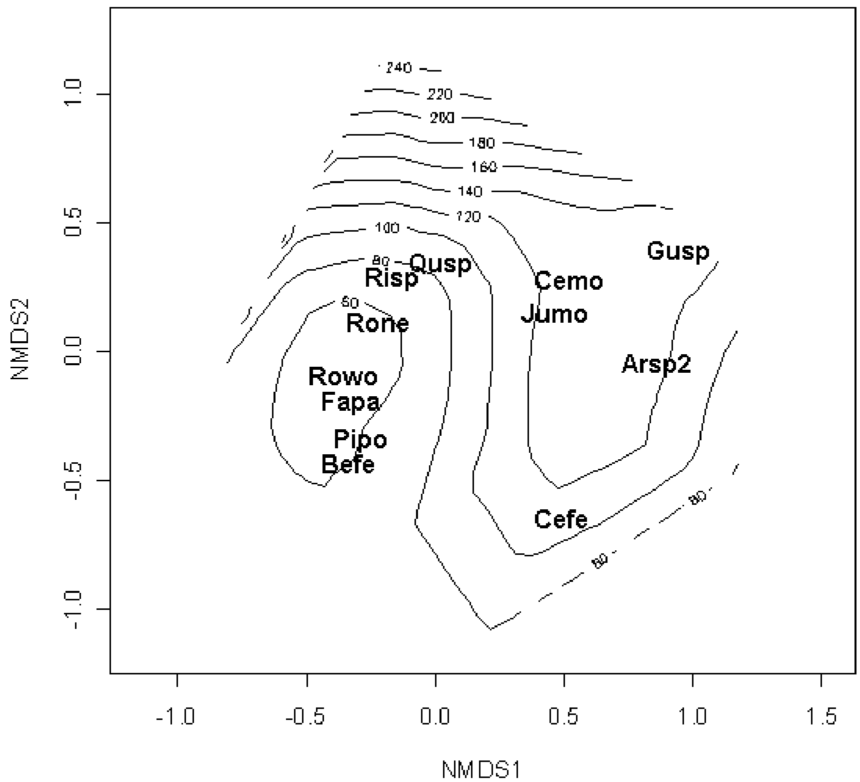

Figure 1.3: The La Mesa species NMDS ordination results, displayed on a modeled surface of distance to low-unburned edge (m). The location of the species 4-letter code (see Table 1.1) represents the optimum, or peak of response in the ordination space along the distance gradient. Locations at the lower end of the distance gradient were optimal for *R. woodsii*, *R. neomexicanus*, and *P. ponderosa*, among others. Higher distances along the gradient corresponded with peak abundance for species including *Quercus*, *J. monosperma* and *C. montanus*.

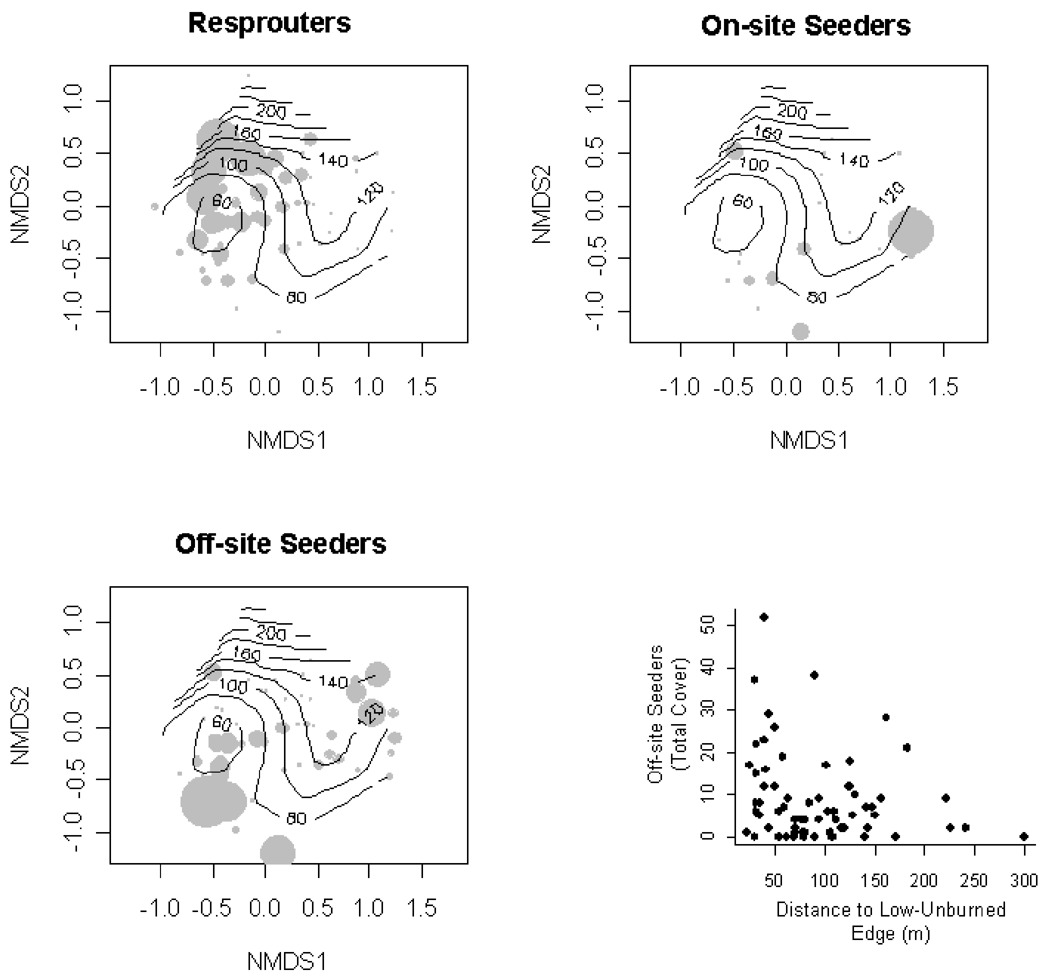

Figure 1.4: The distance gradient (m) at La Mesa, modeled with GAM, and sample site symbols (gray shaded circles) scaled relative to total cover of species in a functional group. Off-site seeders define ecologically similar locations at low and intermediate distances, and these sites tend to be separate from sites where resprouters predominate. On-site seeders were abundant in only one location. The scatter plot shows a decreasing trend in total cover for off-site seeders in relation to distance from plot center to low-unburned edge.

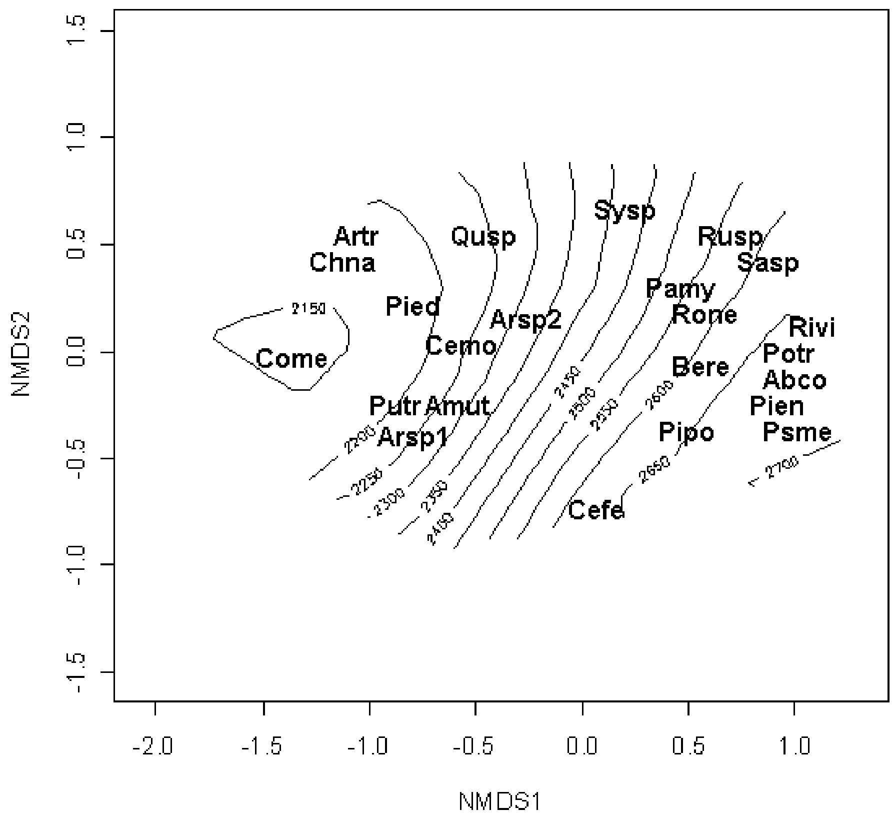

Figure 1.5: The Saddle Mountain species NMDS ordination results, displayed on a modeled elevation surface (m). The location of the species abbreviation (see Table 1.1) represents the optimum, or peak of response in the ordination space. *Cowania mexicana* and *P. edulis* are among species reaching their highest abundance at lower elevations. Species with peak locations at higher elevations included *S. racemosa, B. (Mahonia) repens*, *P. tremuloides* and *P. menziesii*.

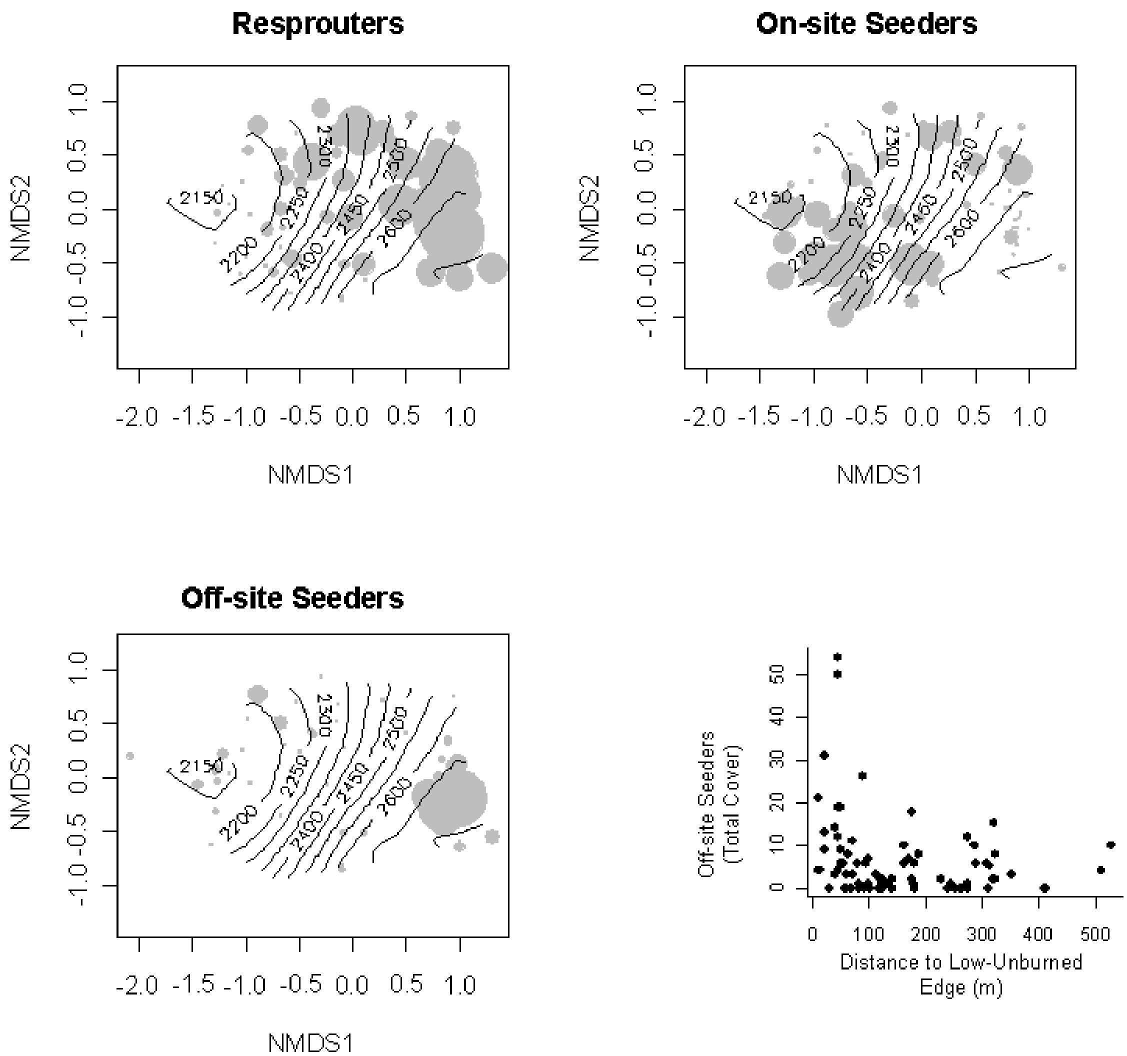

Figure 1.6: For Saddle Mountain, the elevation surface (m) modeled with GAM, and sample site symbols (gray shaded circles) scaled relative to cover of species in a functional group. Highest total cover of resprouting species occurred at higher elevations sites. Off-site seeders were fairly low in abundance across the gradient of elevation except for one cluster of sample sites at the higher end of the gradient. Plots with higher cover of off-site seeders had lower cover of on-site seeders. The scatter plot illustrates a general decrease in cover of off-site seeders with increasing distance to low-unburned edge.

Figure 1.7: Locations at La Mesa (upper photos) and Saddle Mountain (lower photos), where *P. ponderosa* (an off-site seeder) regenerated in openings created by the fire. Adult trees appearing in the background of each photo survived the fire event, and represent refugial *P. ponderosa* seed sources in low-unburned islands within the fire perimeter. Woody plant communities at these locations included *Quercus* and *R. neomexicanus* (La Mesa), *P. tremuloides*, *C. fendleri*, and *Arctostaphylos* (Saddle Mountain). *Arctostaphylos*, a shrub in the on-site seeder group, formed a dense understory in some places (lower right).

CHAPTER 2

EFFECTS OF LANDSCAPE PATTERNS OF FIRE SEVERITY ON REGENERATING PONDEROSA PINE FORESTS (*PINUS PONDEROSA*) IN NEW MEXICO AND ARIZONA, USA

2.1 Abstract

Much of the current effort to restore southwestern ponderosa pine forests to historical conditions is predicated upon assumptions regarding the catastrophic effects of large fires that are now defining a new fire regime. To determine how spatial characteristics influence the process of ponderosa pine regeneration under this new regime, I mapped the spatial patterns of severity at areas that burned in 1960 (Saddle Mountain, AZ) and (La Mesa, NM) 1977 using pre- and post-fire aerial photography, and quantified characteristics of pine regeneration at sample plots in areas where all trees were killed by the fire event. I used generalized linear models to determine the relationship of ponderosa pine stem density to three spatial burn pattern metrics: 1) distance to nearest edge of lower severity; 2) neighborhood severity, measured at varying spatial scales, and 3) scaled seed dispersal kernel surfaces. Pine regeneration corresponded most closely with particular scales of measurement in both seed dispersal kernel and neighborhood severity. Spatial patterns of burning remained important to understanding regeneration even after consideration of subsequent disturbance and other environmental variables. Analysis of tree ages revealed slow progress in early post-fire years. My observations suggest that populations spread in a moving front, as well as by remotely dispersed individuals. Based on my results, recent large fires cannot be

summarily dismissed as catastrophic. I conclude that management should focus on the value and natural recovery of post-fire landscapes. Further, process centered restoration efforts could utilize my findings in formulating reference dynamics under a changing fire regime.

2.2 Introduction

The recent increase in large fires in forests of the southwestern U.S. is considered a harbinger to catastrophic ecological effects (Covington 2000, Covington et al. 2001). For species that rely on legacy seed sources, such as ponderosa pine (*Pinus ponderosa*), spatial patterns of biological legacies are critical to recolonization of severely affected areas (Turner et al. 1997, Romme et al. 1998). Given variability in seed production, germination success, and time to achieve seed bearing age, species with limited dispersal capabilities may not successfully re-establish in large openings before fire recurs (Turner et al. 1994, Frelich and Reich 1995, Romme et al. 1998, Allen et al. 2002). Historically (prior to ~1700), openings created by frequent fire in southwestern ponderosa pine forests were small, often less than 1 ha (Cooper 1960, White 1985), and landscape patterns of burning did not limit the occurrence and persistence of post-fire regeneration (Agee 1998). As a result, ponderosa pine forests exhibited an uneven-age structure over large areas which remained stable through time (Cooper 1960). In contrast, recent fires have left much larger openings, and a significant overall proportion of stand mortality (Westerling et al. 2006). However, the role of landscape patterns created by contemporary fires in longer-term recovery of ponderosa pine forests is unknown.

Seminal work in landscape ecology following the Yellowstone fires of 1988 provides a basic framework for exploring fire size and pattern (Turner et al. 1994) and their relationship to ecological processes, including succession (Turner et al. 1997). Landscape heterogeneity, associated with variable fire severity within burned areas, was a striking characteristic of the 1988 fires (Turner et al. 1994). More recent work has uncovered the persistent effects of landscape patterns on forest communities, as they evolve through time (Turner et al. 2003, Kashian et al. 2004).

Fires affect landscape pattern at many scales: across an entire region, within an area burned in a particular fire event, and within a burned patch (Turner et al. 1994). There is not a single, relevant spatial scale for understanding the effects of landscape pattern, but potentially important spatial scales can be identified for a specific process (Delcourt et al. 1983, Levin 1992). In particular, seed dispersal capabilities may define key spatial scales for regeneration of species such as ponderosa pine because their recovery relies on patchily-distributed biological legacies (Franklin et al. 2000, Allen et al. 2002). Using statistical approaches, it is possible to identify scales at which spatial pattern best describes variation in response of the ecological process of interest (Wiens 1989).

Similarly, ecological processes operate at different temporal scales, and variables including reproductive age and disturbance interval can define an appropriate time frame for studying pattern-process relationships. My previous work at two burns, Saddle Mountain, which occurred on the Kaibab Plateau, Arizona, USA in 1960 and La Mesa, which burned on the Pajarito Plateau, New Mexico, USA in 1977 indicated that diverse communities were present years after these large, severe fire events, including young forests (Haire and McGarigal 2008). In addition, observations at these sites were consistent with a wave-form model of succession (Frelich and Reich 1995), where species that rely on legacy seed sources outside of severely burned areas, such as ponderosa pine, gradually migrate into openings of varying size.

My first objective was to identify at what scale spatial patterns of severity influence ponderosa pine regeneration at La Mesa and Saddle Mountain. Therefore, I examined relationships across a range of spatial scales that encompassed variability in dispersal distances, potential long-distance dispersal, and seed production by young trees coming of cone-producing age (Clark and Ji 1995, Clark et al. 2001). Recognizing that spatial factors can be confounded by other, local variables, my second goal was to determine the relative importance of spatial pattern to pine regeneration after consideration of other, non-spatial factors. For this purpose, I considered several groups of variables: subsequent burning, either prescribed or wildland fire events, which can influence seedling survival (Moore et al. 2004); physical environment (topographic variation including elevation, and soil characteristics) which creates a template of basic resources for germination and growth (Baird et al. 1999, Bonnet et al. 2005, Certini 2005); and the biotic environment, because it reflects neighborhood interactions that alter resource availability (Frelich 2002).

Lastly, my study sites afforded the rare opportunity to observe the longer-term formation of forest structure as it occurred across varying distances from surviving seed sources following severe fire. Therefore, my final objective was to describe the temporal progress of regeneration in post-fire years in a spatial context defined by patterns of severity under the new fire regime. I discuss the relevance of my findings to restoration efforts given the likelihood that expansive fires will continue to play a role in fire regimes of southwestern forests with predicted changes in climate (Westerling et al. 2006).

2.3 Methods

2.3.1 Study Areas

Fires at my two study sites, La Mesa and Saddle Mountain, encompassed a broad gradient in elevation that includes several major community types: piñon-juniper (*P. edulis-Juniperus* spp.) woodland, ponderosa pine forest, and mixed conifer forest that varied in composition of ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and aspen (*Populus tremuloides*). La Mesa, thought to be human-caused, burned across the Pajarito Plateau of northern New Mexico (35°48′N, 106°20′W) in 1977; Saddle Mountain, a lightning-caused fire, occurred on the Kaibab Plateau in northern Arizona (36°20′N, 111°59′W) in 1960. Both sites were located on regional plateaus, but geologic histories were markedly different. Ash-flow tuffs, erupted from the Jemez Mountains, define the Pajarito Plateau; its alternating broad mesas and steep canyons drain eastward to White Rock Canyon of the Rio Grande (Reneau and McDonald 1996). In contrast, the Kaibab Plateau was formed from sedimentary rock layers deposited with shifts in sea level (Hopkins 1990). The topography creates dramatic relief; steep scarp slopes, or combs, are adjacent to narrow stream bottoms, with sheer walls on the south forming the Nankoweap Rim.

Climate patterns in the Southwest are influenced by the El Niño Southern Oscillation, in which wetter winter and spring months and dry summers of El Niño alternate with the drier winter and spring months and wetter summers that characterize La

Niña (Swetnam and Betancourt 1998). In years following La Mesa and Saddle Mountain, climate was variable in the 1960s and 1970s, but the wettest period in the region in the 20th century occurred from 1976 to 1999, with a major El Niño event in 1997/98; subsequently a shift to La Niña led to a severe drought in the early 2000's (National Climatic Data Center 2006).

Because both fires burned in areas with active post-fire management programs, salvage logging, seeding of non-native grasses and planting of seedlings of ponderosa pine occurred in some places (C. Allen and D. Steffensen, pers. comm.). I avoided sampling in areas where tree planting was documented. Subsequent wildland and prescribed fires have burned in portions of both study sites (National Park Service, unpubl. data; United States Forest Service, unpubl. data). Influences on land use and management at the two sites have included their status as traditional and current homelands to many Native American peoples. Currently, the Saddle Mountain burn is entirely within the Saddle Mountain Wilderness on the Kaibab National Forest, except for a small area in Grand Canyon National Park. La Mesa falls under several jurisdictions including Bandelier National Monument and the Dome Wilderness, the Santa Fe National Forest, and the Los Alamos National Laboratory, a United States Department of Energy facility.

2.3.2 Quantifying Burn Spatial Patterns

For both locations, I mapped high severity using aerial photography obtained within four years before and after the fire event. Areas where all trees were killed were labeled as high severity, and areas of surviving trees were labeled as lower-severity, because they could have experienced either low, moderate or mixed fire effects or could represent unburned islands within the fire perimeter. The minimum mapping unit for areas of surviving trees within high-severity patches was two live trees in close proximity to each other. I field-checked the maps for accurate representation of surviving trees, and modified the maps in a few cases. The origin of the forest opening (i.e., the high-severity patch) was corroborated in the field by presence of downed wood, stumps, or snags. Total area, composition, and patch size statistics for high and lower-severity were calculated using Fragstats (McGarigal et al. 2002).

I derived three metrics to quantify spatial patterns of burning. First, the burn severity maps were used to calculate Euclidian distance (m) from each point (i.e., 10-m grid cell) within a high-severity patch to the nearest edge of lower-severity. I defined the second metric, neighborhood severity, as the percent of the landscape that burned with high severity at different spatial scales (Figure 2.1). I calculated neighborhood severity in circular windows of variable size centered at each grid cell; the window radius (100, 150, 200, 250, 300, 350, and 400-m) defined a particular spatial scale of analysis.

The third spatial pattern metric extended the concept of a dispersal kernel, which describes the scatter of offspring about the parent plant in the form of a probability density function (Clark et al. 2003), to a landscape dispersal kernel (Figure 2.1). For my purpose, I developed a landscape dispersal kernel using a distance-decay function in the shape of a Gaussian distribution with a variable bandwidth (Silverman 1986). In order to reflect abundance of seed sources as it varied across the study site, I weighted the kernel with the cover values for ponderosa pine in areas surrounding the high-severity patches. In this way, the kernel surface within high-severity patches took a higher value in locations nearer to greater cover of ponderosa pine. By varying the bandwidth of the Gaussian distribution (*h* = 50, 60, 70, 80, 90, 100, 150, 200, 300, 400) the kernel shape changed, defining a range of spatial scales (i.e., potential seed dispersal distance functions). For the kernel weights, a ponderosa pine cover map developed using post-fire (1981/83) aerial photography (Allen 1989) was available for La Mesa; values ranged from 0-95%. A comparable map for Saddle Mountain, which I developed from aerial photography (taken in 1963), was scaled categorically: 1 (< 25% cover), 2 (25-60% cover), 3 (> 60% cover).

2.3.3 Physical Environment and Disturbance Predictor Variables

I measured the physical environment of the study areas using both digital map and field data. I used digital elevation maps to model topographic wetness with TauDem (http://hydrology.neng.usu.edu/taudem/), and to calculate three alternate models of potential annual direct incident radiation and heat load (Incident Radiation/ Radiant Heat Load [MJ cm^{-2} yr^{-1}]; McCune & Keon 2002). In addition, I used digital fire history maps available from local land managers to determine the number of times areas within the study areas subsequently burned. All data were mapped at 10 m resolution.

In the field, I sampled 68 plots at La Mesa and 79 plots at Saddle Mountain between 16 May and 30 June 2005. Locations were chosen at highest distances from edge within high-severity patches (Figure 2.2). I distributed the sample plots throughout the burns to the greatest extent possible, with the goal of avoiding locations where tree planting was documented. At each plot, I classified topographic position relative to local condition as summit, side-slope, shoulder, toe, or bottom. Soils were characterized on-site using categories of stoniness, degree of development, and texture based on properties when wet.

2.3.4 Biotic Environment and Regeneration Response Variables

At each field plot, I recorded ground cover (grass, forb, rock, soil, or organic material) and cover of all woody species using point-intercept at 1-m intervals along two 50-m line transects positioned North-South and East-West. To determine tree density, I counted all individual ponderosa pine trees in a belt along either side of the transects. Width of the belt varied from 2 to 10 m with the goal of including some trees in more open locations, or to obtain an efficient sample in locations where trees were dense. Ponderosa pine trees were aged by counting branch whorls on each tree trunk; adult trees were cored selectively La Mesa, n = 25; Saddle Mountain, n = 12) to determine confidence in age estimates based on whorl counts.

2.3.5 Statistical Analysis

I derived separate generalized linear models (GLMs) for each spatial pattern metric: distance from lower-severity edge, dispersal kernel and neighborhood severity at all of their measured spatial scales. The model takes the form:

$$[\text{number of individuals ha}^{-1}{}_i] = \beta_0 + \beta_1(\text{spatial pattern metric}_i) + \varepsilon \qquad [1]$$

where number of ponderosa pine individuals ha^{-1} was calculated from number of trees recorded within the belt transect. To determine the scale at which spatial pattern was most relevant to regeneration, I evaluated changes in the magnitude of response (slope coefficient: β_1) across scales, as well as model fit (% deviance explained). The scale of the predictor variable (Seed Dispersal Kernel or Neighborhood Severity) with the greatest slope and the best model fit. was selected as the "best" scale. Two Saddle Mountain plots with extreme values for pine abundance were excluded from the analysis.

Then, I developed GLMs for each of three predictor subsets: Disturbance, Physical Environment, and Biotic Environment. For the Physical Environment model, variables with $P > 0.05$ were removed one at a time. An *F*-test was conducted at each step to determine if the reduced model represented improvement over the model with additional terms, and to reassess significance of terms. For the Biotic Environment model, I tested each of the ground cover variables separately. Previous analysis of woody plant communities at the study areas indicated interactions between resprouters (i.e., species that reproduce primarily from surviving roots and root collars) and species that reproduce from off-site seeds such as ponderosa pine (Haire and McGarigal 2008), so I predicted that they would also play a role in pine regeneration. To test this prediction, I modeled the response of pine regeneration to cover of species that could affect resources for shade-intolerant pines: aspen, an abundant resprouter within the range of ponderosa pine at Saddle Mountain, and cover of all resprouters at La Mesa.

The best spatial pattern predictor (based on the scale analysis described above) was added to the Disturbance, Physical Environment, and Biotic Environment models and an *F*-test was used to determine the importance of spatial pattern after consideration of other variables in the model. Finally, I applied an *F*-test to judge whether including a spatial pattern variable improved a Full Model that incorporated all variables in the Disturbance, Physical Environment, and Biotic Environment models. I chose the Poisson family, which is applicable to count data, but used quasi-likelihood (*i.e.*, variance proportional to the mean) to account for over-dispersion.

I used age estimates of ponderosa pine trees, based on whorl counts, to analyze regeneration through time and across distance to edge of lower severity. To determine confidence in the whorl count estimates, I compared them with age estimates from tree ring counts using multi-response permutation procedures (Mielke and Berry 2001), and found no significant difference (La Mesa, $n = 25$, $\delta = 4.41$, $P = 0.73$; Saddle Mountain, $n = 12$, $\delta = 5.45$, $P = 0.21$). Using the tree age data, I constructed a data set containing the cumulative number of trees ha^{-1} observed at each plot in each year after the fires. Tree density was plotted at several post-fire intervals across the range of distance to edge of lower severity, which enabled a graphical analysis of regeneration through time and space. All statistical analyses were conducted using R (www.R-project.org), and for spatial analyses I used ArcInfo version 9.0 (Environmental Systems Research Institute, Redlands, California).

2.4 Results

La Mesa and Saddle Mountain were similar in terms of fire size, but differed in composition and configuration of burn severity (Table 2.1). A large proportion of each burned landscape was high severity, but the high-severity patches varied widely in size. The La Mesa fire resulted in a more patchy landscape in comparison to Saddle Mountain. Saddle Mountain was approximately 70% as large as La Mesa; however, it contained only one quarter as many high severity patches and a little more than half the number of lower-severity patches. The more homogeneous patterns that followed the Saddle

Mountain fire were also apparent in the size of the largest high-severity patch size. Both study landscapes had a large background matrix that burned at lower severity or did not burn at all, with many, small patches.

Distance to edge of lower severity was a highly significant predictor of pine stem density at both La Mesa and Saddle Mountain ($P < 0.002$). The distance variable explained a high proportion of deviance in the data as well (27.1 and 34.0% for La Mesa and Saddle Mountain, respectively). At both locations, seed dispersal kernel and neighborhood severity were strongly related to ponderosa pine regeneration, but the magnitude of effect and model goodness-of-fit varied across scales (Figure 2.3). At La Mesa, seed dispersal kernel gradually increased in positive effect across scales of measurement, becoming strongest when the smoothing parameter, $h = 150$ m (12.0 % deviance explained). Regeneration at Saddle Mountain was most influenced by seed dispersal kernel when $h = 50$ m; this scale also produced the best model fit (44.3 % deviance explained).

The negative relationship between regeneration and neighborhood severity was strongest at the 300-m scale at La Mesa (32.1 % deviance explained). At Saddle Mountain, neighborhood severity affected regeneration most significantly when measured in a window of 200-m radius (41.1 % deviance explained). Larger scales of measurement produced slopes of greater magnitude in some cases, but measures of goodness of fit declined, indicating that the measured predictors did not explain ponderosa pine regeneration as well at these scales. Spatial pattern variables were highly significant predictors of regeneration at both sites ($P < 0.001$ in most cases).

Models incorporating predictor subsets had strong explanatory power in general (Table 2.2). Disturbance (number of subsequent burns) was an important variable at La Mesa, with greater tree density at locations with 0 subsequent burns. The Disturbance Model explained 23.4 percent deviance. The influence of subsequent burning was not apparent in the Disturbance Model for Saddle Mountain, although 33 locations had experienced one reburn.

In Physical Environment Models, the importance of broad-scale, as well as local factors was apparent (Table 2.2). Pine regeneration increased with elevation at both sites. At local scales, soil characteristics were influential at both sites, in combination with other physical environment predictors (Table 2.2). Silt loam soil texture was positively associated with pine regeneration at La Mesa, compared to the loam/sandy loam class. At Saddle Mountain, models indicated that regeneration was greater in highly variable and shallow rocky soils than in well developed soils, however, most sampled locations had shallow rocky soils (n = 56). A substantial amount of variation in pine density was attributable to physical environment, represented by elevation, heat load, and soil characteristics in GLMs (Table 2.2).

Biotic environment variables, particularly ground cover, figured prominently in explaining variation in pine regeneration (Table 2.2). Each study site had one highly significant ground cover variable with positive influence on regeneration: organic ground cover at La Mesa, and forb ground cover at Saddle Mountain. Soil cover (La Mesa) and rock cover (Saddle Mountain) were also important predictors, but with negative influence. The Biotic Environment models, containing only the ground cover variable with the lowest *P*-value at each site, were very informative nonetheless (dev. expl. =

48.1% at La Mesa and 23.0% at Saddle Mountain). Contrary to my predictions, neither resprouter nor aspen cover influenced regeneration, based on GLMs.

When the variables from the Disturbance, Physical and Biotic Models were used to develop Full Models, deviance explained increased to 59.7 percent at Saddle Mountain, and 66.4 percent at La Mesa (Table 2.2). But, the relative importance of the variables changed when models were added together. In the Full Model for La Mesa, only heat load, soil, and organic ground cover remained significant. At Saddle Mountain, only elevation, heat load, and forb ground cover retained significance.

Model comparisons demonstrated the strong influence of spatial pattern when added to Disturbance, Physical, Biotic, and Full Models (Table 2.2). Deviance explained always improved with inclusion of a spatial pattern variable, and *F*-test statistics led to rejection of reduced models (i.e., removing spatial pattern from the model). Full Models that included a spatial pattern variable, selected at the best scale (Figure 2.3) explained 74.2 percent deviance for pine regeneration at La Mesa, and 65.6 percent deviance at Saddle Mountain.

Density of trees differed between the two sites, with cumulative total number of trees at lowest distances much greater at La Mesa (~8,000 trees ha^{-1} at La Mesa; ~2,000 trees ha^{-1} at Saddle Mountain; Figure 2.4). However, some general trends were consistent at the two sites. First, at distances less than 100 m from potential seed sources, cumulative totals indicated that very little regeneration occurred in early post-fire years (year 1 to 8 at La Mesa, and year 1 to 15 at Saddle Mountain), but approximately 5 to 15 years after the first recorded regeneration at each site, more productive years occurred. Relatively large increases in tree density, shown in wide intervals between lines at lower distances, indicate that a majority of trees that survived to 2005 germinated during this intermediate time frame (ca 1985-1995 at La Mesa, and ca 1975-1985 at Saddle Mountain). In more recent years, less growth was initiated at locations closer to edge.

Cumulative number of trees steadily declined across the range of distance to edge of lower-severity, but some regeneration was recorded at distances from lower-severity edge greater than 200 m (Figure 2.4). At La Mesa, regeneration occurred at three high distance locations (222, 228, and 304 m), and the first record of seedlings at these plots varied between year 11 and 18 post-fire (ca 1988 to 1995). Out of 23 high-distance plots at Saddle Mountain, there were five locations (306, 310 [n=2], 322, and 410 m) with regeneration. Earliest initiation of growth occurred about year 17 (ca 1977), at 310 m from lower-severity edge. Density was low at all distances greater than 200 m (~11 to 26 individuals ha^{-1}).

2.5 Discussion

Large fire events which now define a new fire regime in southwestern forests can encompass greater heterogeneity in spatial patterns than was common under a fire regime characterized by frequent, low-severity fires. At La Mesa and Saddle Mountain, high-severity patches ranged widely in size and shape, resulting in configurations of openings and seed sources that were probably similar to those of historical fires in some places, as well as situations that were unlikely historically (Agee 1998). The strong and persistent role of spatial patterning on ponderosa pine regeneration at my study sites suggests that an understanding of landscape heterogeneity will be critical to setting realistic and ecologically appropriate long-term restoration goals (Dellasala et al. 2004) under this new regime.

The three metrics of severity I used to quantify spatial pattern were all good predictors of pine response, but each provided a different slant on landscape heterogeneity. Distance from lower-severity edge assumed homogeneity within high-severity patches, but had the benefit of providing a simple description of spatial pattern that incorporates both patch size and shape. Neighborhood severity reflected complexity in burn patterns because it is influenced by patchiness and edge effects. Both distance and neighborhood severity have the benefit of being very easy to calculate using a map of burn severity, thus facilitating testing of relationships at other sites. On the other hand, neither of these metrics addressed the influence of variations in species composition of legacy forests.

The landscape seed dispersal kernel incorporated variation in seed sources across broad elevational gradients and complex spatial patterns in burn severity which are often encompassed by large fires. The statistical importance of the kernel variable in models of ponderosa pine regeneration supports the theory that seed dispersal orders recolonization of disturbed sites, and is a primary scaling factor for succession after severe fire (Paine et al. 1998). The kernel was the best spatial predictor for regeneration at Saddle Mountain, possibly because the distribution of seed sources was more localized and therefore more identifiable in model relationships.

The extension of the traditional dispersal kernel to landscapes in which legacy seed sources are critical resources could provide a valuable enhancement to the classic models (e.g., Clark 1998). In a study of spatial patterns of post-fire ponderosa pine regeneration in South Dakota, USA, modeled seed availability was used to correct for variable seed inputs when determining the importance of environmental conditions (Bonnet et al. 2005). Analogous surfaces could be constructed for other species that are limited by seed dispersal ability such as white fir and Douglas-fir. For example, Shatford, Hibbs, and Puettmann (2007) described seedling density and distribution for several species across a gradient of forest types following fires in California and Oregon, USA. Interpretation of their results in relation to models of seed dispersal would enable a better understanding of regenerating and legacy forest dynamics.

Spatial patterns of burning remained important to understanding regeneration response in final models even after consideration of subsequent disturbance, and physical and biotic environment variables. At the same time, subsequent burning held significance to regeneration at La Mesa, as did indirect gradients in elevation and radiant heat load, and local soil characteristics at both sites. My predictions regarding resource competition between ponderosa pine, an off-site seeder, and resprouters that come back quickly after fire were refuted, based on Biotic Environment models. This finding calls into question the notion that resprouters "capture" a site in areas of fire-induced tree mortality (Allen et al. 2002, Savage and Mast 2005). However, models that incorporate spatial and temporal dynamics are necessary to resolve these disparate findings about species interactions, especially in cases where species are expanding their range and distribution (Guisan et al. 2002).

Regeneration at both sites proceeded slowly and unevenly across the range of distance from lower-severity edge, and across post-fire time intervals. Other research has documented high numbers of seedlings in early post-fire periods (Bonnet et al. 2005), but according to my estimates, either few seedlings originated or few survived until approximately 5 to 10 years post-fire at either site. Years 5 to 15 were associated with high rates of establishment, followed by much lower rates in subsequent time intervals. These observations could be related to decreased resource availability with infilling of trees, and climate may have played a part as well (Savage et al. 1996).

General trends in post-fire climate did not point to clear association with progress of forest recovery. The periods of substantial regeneration at Saddle Mountain corresponded to the beginning of the generally wet years in the Southwest (ca 1976), however regeneration slowed considerably before the drought of 2000 to 2004. Early post-fire years at La Mesa were also generally wet, but regeneration progress lagged nonetheless. It is possible that soil and other environmental conditions were too harsh for seedlings to establish immediately after these fire events. Changes in soils, for example, were dramatic in high-severity areas of the Cerro Grande fire that burned in New Mexico in 2000 (Kokaly et al. 2007). My observations concur with the general theory that the rate of recovery of community composition slows with increasing distance from seed sources when disturbance intensity is high (Turner et al. 1998).

In addition to relatively slow migration of trees in a moving front, ponderosa pine populated areas at farther distances from the lower-severity edge through long distance dispersal. As migrating trees and long-distance dispersers reach cone-bearing age, the result is a staggered arrangement of seed sources located apart from the original legacy trees (Clark and Ji 1995). Long-distance dispersal is an important mechanism for faster population spread where distances from legacy trees are great (Clark et al. 2001). The Gaussian model I employed approaches zero rapidly with distance, predicting spread of individuals from the frontier of the population (Clark et al. 1999). Theoretically, my data would be better fit with a fat-tailed kernel model that accommodates regeneration from long-distance dispersal.

2.5.1 Implications for Restoration and Post-fire Management

Recent large fires cannot be summarily dismissed as catastrophic (Beschta et al. 2004), in particular, when viewed over a longer term and at spatial scales of importance to regenerating ponderosa pine forests. My findings indicated that significant reforestation had occurred at La Mesa and Saddle Mountain in some places. If the population front at La Mesa continued to progress at the rate I observed, trees could inhabit distances over 200 m from edge of lower severity in approximately 15 years from the date of my observations, and could progress to the farthest occurring distances by 50 years post-fire. These estimates do not include the increased speed of reforestation that results from long-distance dispersers.

Those concerned with restoration of areas burned in recent large fires should focus on the importance of naturally recovering post-fire landscapes (Turner et al. 2003) and post-fire management that enhances the capacity for natural recovery (Beschta et al. 2004). Areas disturbed by fire contain a wealth of valuable legacies, including large old trees of fire-resistant species, and large snags and logs that contribute to habitat refugia, movement of organisms and materials, and renewal of soils. Early successional habitats resulting from fire are valued for their diverse communities (Dellasala et al. 2004, Haire and McGarigal 2008) but are rare in many regions (Lindenmayer and Franklin 2002; DellaSala et al. 2004). Indeed, open habitats found in spatial heterogeneous post-fire landscapes make valuable contributions to biodiversity that cannot be replicated by rapid, uniform reforestation or extensive timber salvage (Lindenmayer and Franklin 2002).

As large fires define a contemporary fire regime in southwestern forests, the restoration paradigm will likewise require adjustments in its assumptions and key concepts (Choi 2007). Traditionally, ecological reference conditions for restoration are solely defined by composition and structure, but a definition that links key ecosystem processes (e.g., fire) to dynamic reference conditions has been proposed (Falk 2006). In process centered restoration, the range of variation in fire regimes could potentially incorporate variability in spatial patterns and ecological response that may accompany non-equilibrial systems, including large fires (Wallington et al. 2005). My findings regarding the spatial and temporal scales of reestablishment of ponderosa pine forests after large fires contribute to the on-going formulation of reference dynamics under a changing fire regime.

Table 2.1 Characteristics of the study areas calculated within fire perimeters.

Landscape Characteristics	La Mesa	Saddle Mountain
Total Area Burned (ha)	5745	4060
High Severity (%)	34	48
High-Severity Patches (*n*)	190	45
High-Severity Patch Size (ha) mean, range	10, (0.08- 634)	43 (0.11- 947)
Lower-Severity-Patches (*n*)	150	96
Lower-Severity-Patch Size (ha) mean, range	25, (0.01-3673)	22 (0.01-2047)

Table 2.2 Combined models include the best predictors of ponderosa pine density from Disturbance, Physical, and Biotic variable subsets. Small *P*-values for the *F*-test indicate the model was improved by including the best spatial pattern variable at the scale selected from Figure 2.3.

Combined Model	Predictor Variables	% Dev. Expl. (without spatial)	% Dev. Expl. (include spatial)	*F*-test Comparison (*P*-value)
Disturbance				
La Mesa	Number of Subsequent Burns[1] [− Neighborhood Severity (300-m radius scale)]	23.4	45.8	< 0.001
Saddle Mountain	None	na	na	na
Physical				
La Mesa	Elevation + Heat Load + Soil Texture [− Neighborhood Severity (300-m radius scale)]	41.6	61.9	< 0.001
Saddle Mountain	Elevation + Heat Load + Soil Development + Soil Stoniness [+ Seed Dispersal Kernel (scale: *h* = 50)]	52.0	65.0	< 0.001
Biotic				
La Mesa	Organic Ground Cover [− Neighborhood Severity (300-m radius scale)]	48.1	61.3	< 0.001
Saddle Mountain	Forb Ground Cover [+ Seed Dispersal Kernel (scale: *h* = 50)]	23.0	45.7	< 0.001

Continued on next page

Table 2.2, continued

Combined Model	**Predictor Variables**	**% Dev. Expl. (without spatial)**	**% Dev. Expl. (include spatial)**	***F*-test Comparison (*P*-value)**
Full				
La Mesa	Number of Subsequent Burns + Elevation + Heat Load + Soil Texture + Organic Ground Cover [− Neighborhood Severity (300-m radius scale)]	66.4	74.2	< 0.001
Saddle Mountain	Elevation + Heat Load + Soil Development + Soil Stoniness + Forb Ground Cover [+ Seed Dispersal Kernel (scale: *h* = 50)]]	59.7	65.6	0.009

[1] Locations without any subsequent burns had greater pine density than places that burned again once or twice.

[2] Silt loam soil texture was positively associated with pine regeneration at La Mesa.

[3] Shallow rocky and well-developed soils had less regeneration than soils that were highly variable at Saddle Mountain.

[4] My intention was to develop a Biotic Environment model by combining the best ground cover variable with either Resprouter Total Cover (La Mesa) or Aspen Total Cover (Saddle Mountain), but only ground cover variables were significant in single-variable tests.

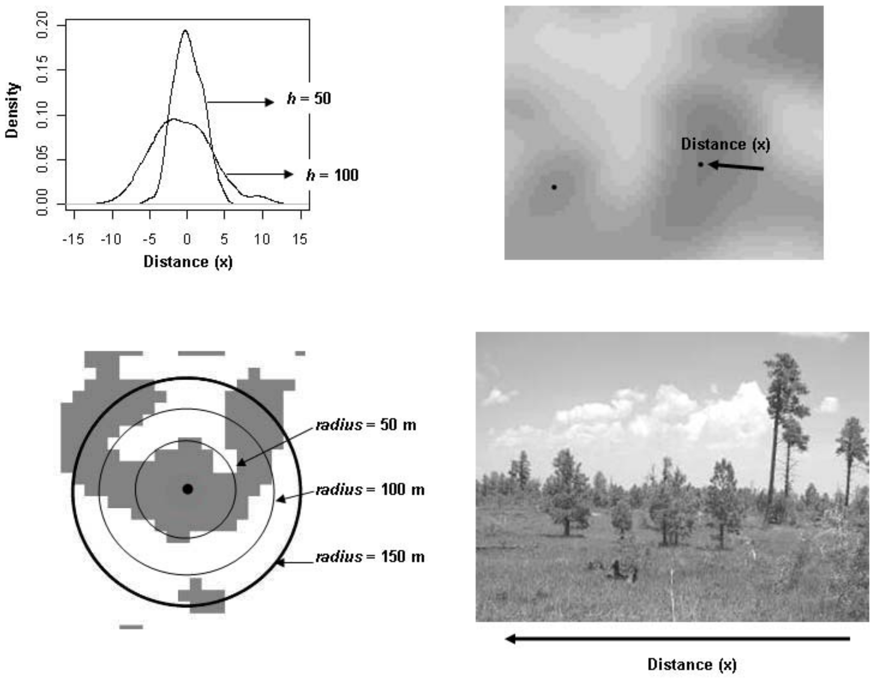

Figure 2.1: Illustrations of spatial pattern metrics. Lower right: Young trees growing at varying distance (*x*) from legacy seed trees (see background of the right side of the photo). Lower left: Neighborhood severity, measured around a sample plot location (black dot) in windows that vary in scale; Upper left: Theoretical distributions of seed dispersal kernels, with scale defined by kernel shape (*h*). Upper right: Seed dispersal kernel applied to the burn severity map, where white to light gray values indicate higher values for seed source abundance and darker shades symbolize decreasing values as seed sources become more distant from sample plots (black dot) within high-severity patches.

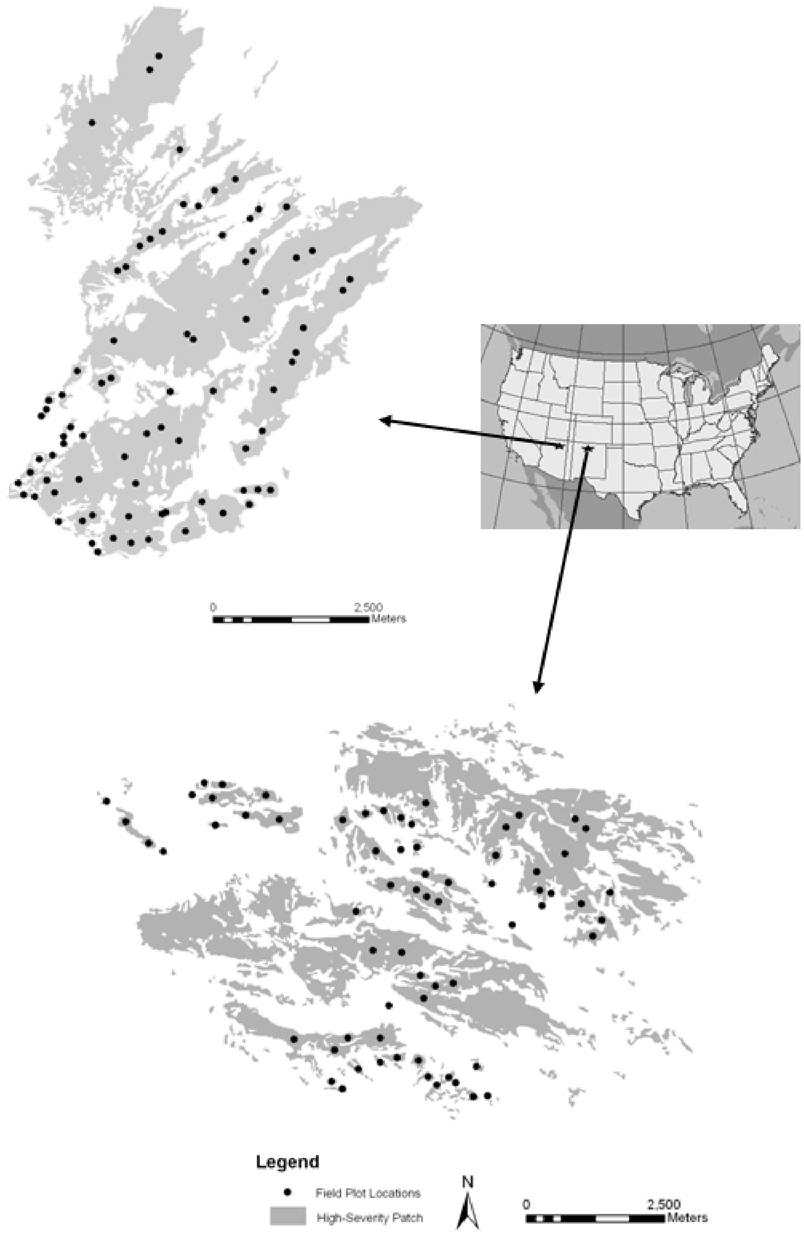

Figure 2.2: Severity maps of Saddle Mountain (Arizona, USA; upper map) and La Mesa (New Mexico, USA; lower map). Gray patches symbolize areas where all trees were killed (high severity) based on pre- and post-fire aerial photography. Field plot locations are shown as black dots.

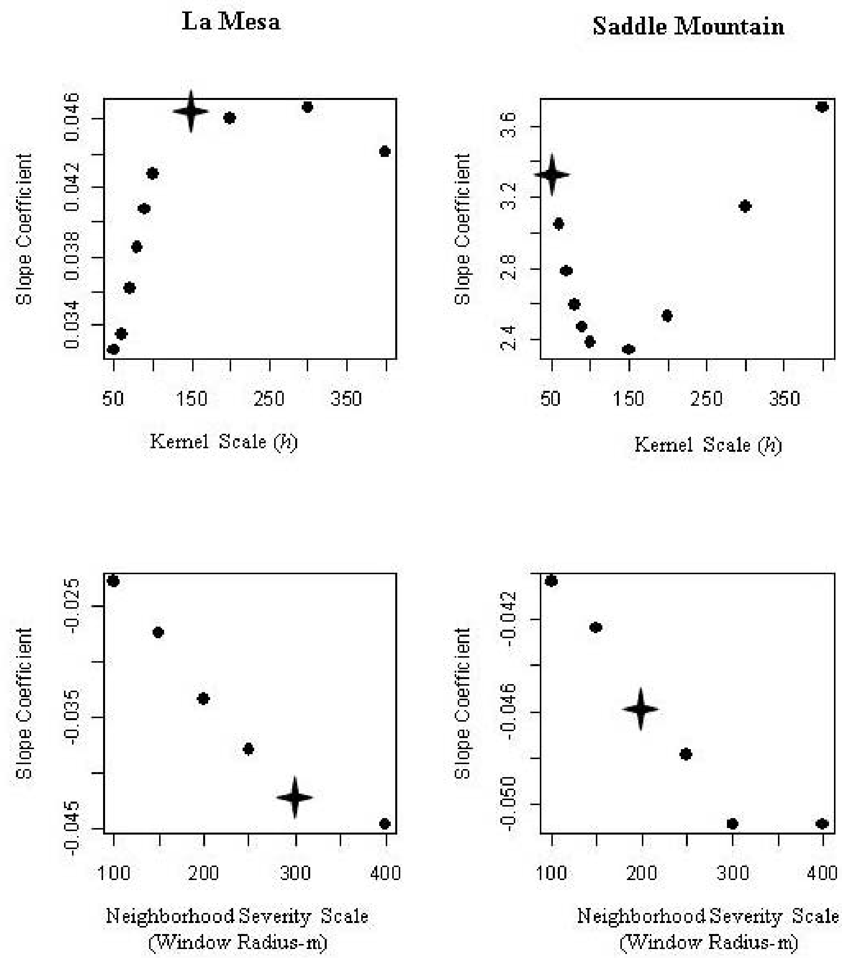

Figure 2.3: Magnitude of effect of spatial pattern variables on regeneration, represented by GLM slope coefficient, plotted across scales of measurement for La Mesa (left) and Saddle Mountain (right). "Best models" (starred) were chosen at the scale with strongest influence on regeneration of ponderosa pine (i.e., greatest slope) that also had the best model fit (i.e., highest % deviance explained).

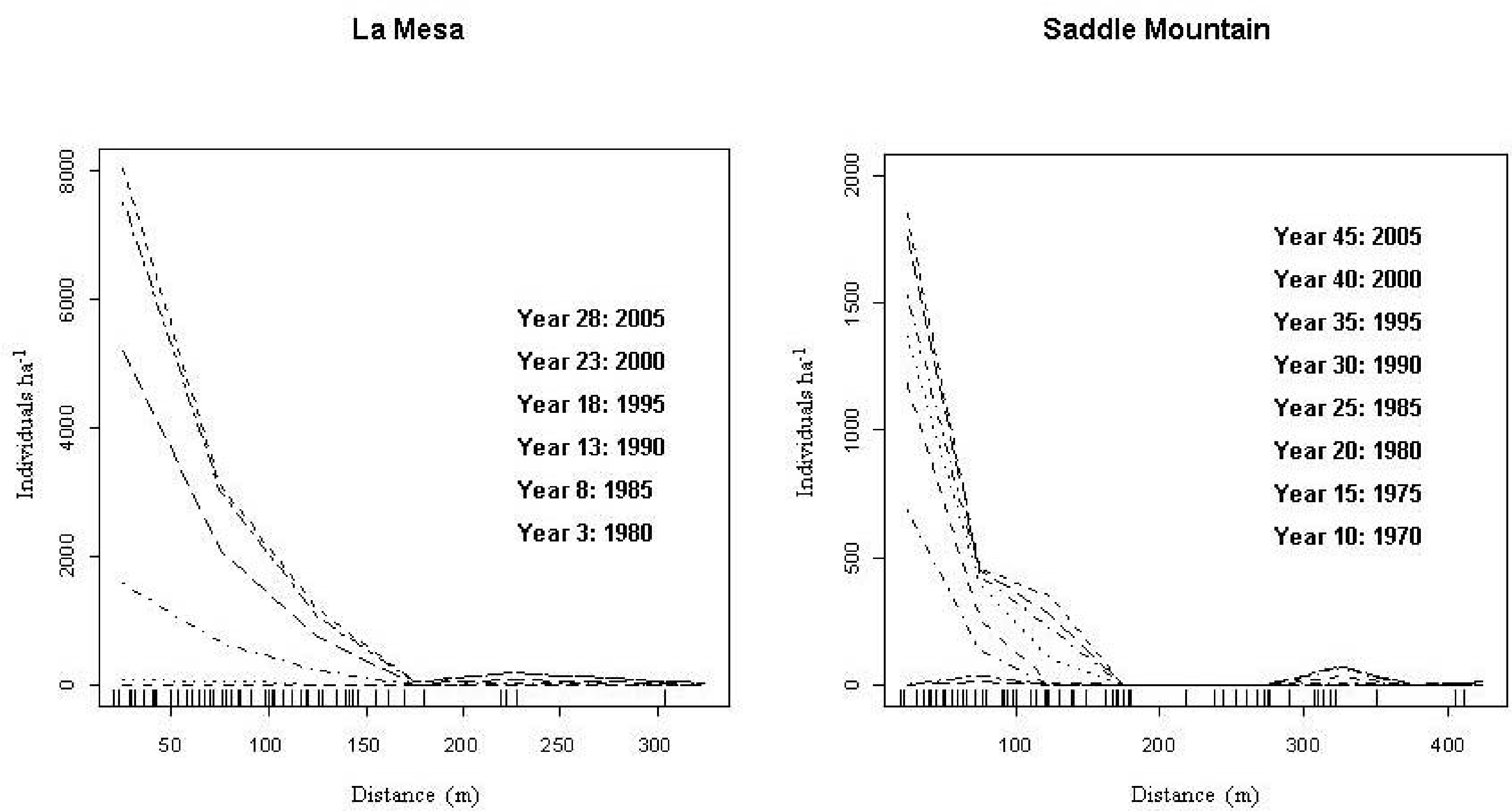

Figure 2.4: Cumulative regeneration (number of individuals ha^{-1}) through time, plotted across the gradient of distance to edge of lower severity at La Mesa (left) and Saddle Mountain (right). Observations were binned within 50-m distance intervals. Vertical lines along the *x*-axis represent locations of field plots. Years listed correspond to the descending sequence of dashed lines.

CHAPTER 3

ANALYSIS OF FIRE SEVERITY ACROSS GRADIENTS OF CLIMATE, FIRE SIZE, TOPOGRAPHY, AND FUELS

3.1 Abstract

Changes in frequency of fires and area burned have been documented with recent changes in climate, but relationships between fire severity and climate have rarely been explored. I investigated how the amount and spatial arrangement of high-severity patches varied 1) among 20 fires that occurred across gradients in fire size and climate and 2) within four fires in relation to landscape characteristics defined by fuel and topographic discontinuities. The climate gradient was based on the Multivariate ENSO Index, which represents the dry, cool conditions prevalent in La Niña at one extreme, and warm, wet conditions in El Niño at the other. Fires in my study were generally larger in La Niña climates, however, several of the fires I examined deviated from this trend. Moreover, some spatial properties of severity did not correspond to fire size or to changes in climate. Consistent with previous studies, characteristics of fuels and topography created breaks that altered spatial patterns of severity, but model fit was poor, indicating high variability in relationships. Contrary to expectations, fuel configurations apparently maintained their influence on severity even in extreme La Niña conditions. High winds and hot burning conditions could conceivably complicate local influences on fire behavior and resulting patterns of severity. My results emphasize the need to view simplistic assumptions about relationships between fire severity, fire size and climate change cautiously.

3.2 Introduction

The frequency of fires and area burned in the western United States have apparently increased in relation to climate (Grissino-Mayer and Swetnam 2000, Schoennagel et al. 2004, Westerling et al. 2006). However, a third attribute of fire regimes, fire severity, has not been explicitly examined with regard to changes in climate. Larger fire size is ostensibly accompanied by increased severity, and some studies conclude that landscapes will become more homogenized, and species diversity will decline as fires increase in size (McKenzie et al. 2004). However, analysis of several large individual disturbance events demonstrated that a range of responses is possible, and disturbance impact does not always increase with extent (Romme et al. 1998). Determining the effects of fires is contingent upon understanding the spatial heterogeneity of fire severity, how spatial patterns change through time, and the traits of species and communities that determine critical thresholds for dramatic shifts in composition and function. For example, the spatial patterns of biological legacies which are directly related to fire severity influence succession of plants that are limited by dispersal abilities (Turner et al. 1998).

Fire severity, as an attribute of landscape structure, has multiple properties that may relate to various ecological processes. For example, the connectivity of fire severity along a flowpath was related to runoff and erosion after the Cerro Grande fire (Moody et al. 2007). Variation in patch size, composition, and edge effects were associated with habitats for different bird species after this same fire (Kotliar et al. 2007). Thus, different descriptors, or metrics are necessary to associate spatial patterns of severity with ecological processes. Determining whether severity increases with fire size or with climate therefore requires a multivariate description of its spatial patterns.

In this study I asked, at the scale of individual fire events, how do multiple attributes of fire severity, including its relative proportions and its spatial configuration, change across gradients of fire size and climate? I expected to confirm that larger fires occur under certain climate conditions. Historically, extensive surface and stand-replacing fires have been associated with severe drought (Grissino-Mayer and Swetnam 2000, Margolis et al. 2007). In recent years, area burned has increased with earlier snowmelts and higher temperatures (Westerling et al. 2006). These climate characteristics vary with large-scale weather patterns including the El Niño Southern Oscillation (Swetnam and Betancourt 1998). However, I anticipated that some spatial properties of severity may not necessarily correspond to fire size or to changes in climate, or may be more sensitive to subtle variability in prefire conditions. Breaks in fuel or topography can exert local control and disruption of fire spread (Turner and Romme 1994, Baker 2003), resulting in spatial patterns of severity that are more patchy.

Following that line of thought, I asked, how do relationships between fire severity and local-scale variation in fuels and topography vary for fires that burned under different climates? I expected that climate conducive to producing larger fires (La Niña) would overshadow control by these local factors, but that clearer relationships would emerge under more moderate climate conditions. This prediction was based on results of fire behavior and fire spread models which indicated greater influence of landscape characteristics when burning conditions were not extreme (i.e., defined by high winds and low fuel moisture; Turner and Romme 1994). I summarized evidence from both the scale of individual fire events and the local, within-fire scale to support or refute my expectations.

The fire events included in my research occurred in the southwestern U.S. where recent fires include large fires that are generally regarded as more severe than those documented historically (but see Whitlock 2004 and Margolis et al. 2007). A major concern is that regeneration of ponderosa pine (*Pinus ponderosa*), will be limited by large openings associated with severe fires (Allen et al. 2002). The timeframe of fire events in the current study encompassed fluctuations in the El Niño Southern Oscillation (ENSO), including a major El Niño event in 1997/1998 (Wolter and Timlin 1998) and widespread drought (early 1950's and 2000's).

3.3 Methods

I selected 20 fires from databases developed and maintained by the Santa Fe National Forest, NM, Bandelier National Monument, NM, Kaibab National Forest, AZ, and Grand Canyon National Park, AZ (Table 3.1). The criteria for inclusion were: 1) size >100 ha, 2) ponderosa pine forest comprised a portion of prefire covertypes, and 3) available aerial photography, satellite images, and field data were sufficient to map fire severity. I identified and mapped four older fires (pre-1980) that fit these criteria, five New Mexico fires that burned in 1996–2000, and 11 Arizona fires that occurred in 1996–2004 (Table 3.1). Without considering limitations imposed by availability of remotely sensed and field data (see below), the sixteen recent fires represented 22.5% of the eligible fires (n = 71) in the Forest Service and Park Service databases. Two of the older fires, La Mesa and Saddle Mountain, were field sites in my previous research on succession of woody plant communities and regeneration of ponderosa pine (Haire and

McGarigal 2008). The recent fires included a range of sizes, from relatively small (e.g., Nicole and Summit were less than 200 ha) up to the largest fire in the aforementioned time periods, Cerro Grande, which was 17,349 ha.

I obtained aerial photography of sufficient quality to distinguish recently burned areas for the four older fires. High severity was defined as areas with complete tree mortality, identified when charred soil or other blackened surfaces, and standing or down dead trees were visible in forest openings. All other areas were classified as lower-severity, and could include low, moderate, or mixed effects, as well as unburned islands within the fire perimeter. Classification was checked using pre-fire photos in conjunction with field studies at La Mesa and Saddle Mountain (Haire and McGarigal 2008); for American Springs and Summit, I reviewed maps with local managers.

All but two of the recent fires had burn severity maps available through the USGS/NPS burn severity mapping project (http://burnseverity.cr.usgs.gov/). For these two fires (Nicole 1996 and Dome 1996), I acquired Landsat images made available by USGS/NPS project managers, and followed the burn severity mapping project methodology (http://frames.nbii.gov/projects/firemon/FIREMON_LandscapeAssessment.pdf). Burn severity was defined as a gradient of change based on a normalized index of Landsat bands 4 and 7, calculated using images collected within one or two years before and after the fire event (Key and Benson 2005). The post-fire index subtracted from the pre-fire index produces the differenced Normalized Burn Ratio (dNBR), which can be used as a continuous measure of severity, or classified to relate to field conditions reflecting severity.

I chose to classify the dNBR to match the aerial photo interpretation of older burns, whose dates preceded satellite image availability. To that end, I examined aerial photography taken soon after fires at random points to classify areas of severe burn for Oso, Dome, and Nicole. For all other fires, I used available field data, either collected with FIREMON methodology (Composite Burn Index), or that applied a comparable rating of severity (Kotliar & Haire, unpubl. data), all collected within two years post-burn. I performed a classification tree analysis (De'ath and Fabricius 2000) to determine thresholds of dNBR image values for the field/random point high-severity and lower-severity classes. The dNBR value, as well as its variance and mean in a 3 x 3 grid cell window (30-m resolution) around the random point/field plot center were included as predictors in the classification trees. Minimum sample size for field/random point data was 40, and overall classification accuracy was ≥89% across all fires.

Metrics used to quantify spatial heterogeneity reflected the two elements of landscape structure: composition, or relative amount of what is present, and configuration, or the arrangement of spatial attributes (Turner et al. 2001, McGarigal et al. 2002). The metrics were chosen to represent several variations on spatial configuration, including aggregation at the cell (AI, CLUMPY) and patch (DIVISION) level. Core area (CAI_AM) was included because of its reflection of both patch shape and size (Table 3.2). The spatial pattern metrics were calculated for each of the 20 fires (among-fires scale) and within a moving window (7 x 7-30-m grid cells) for 4 fires: La Mesa 1977, Oso 1998, Pumpkin 2000, and Poplar-Big-Rose 2003 (within-fires scale). These four fires were chosen because of their diverse locations across the MEI gradient (Table 3.1; Figure 3.1). The moving window size fell within the range of important scales for ponderosa pine regeneration at La Mesa and Saddle Mountain (Haire and McGarigal, in review).

At the among-fires scale, I derived several climate indices, using the Multivariate El Niño Southern Oscillation Index (MEI; http://www.cdc.noaa.gov/ClimateIndices/) and examined variation in severity metrics across the index with the best correlation to fire size. In the Southern Rockies, El Niño years are characterized by wetter than average winter and spring, followed by drier than average La Niña years, in a 2 to 6 year cycle. The MEI is a multivariate measure of the El Niño Southern Oscillation signal, where negative values correspond to La Niña and positive values are associated with El Niño periods. The MEI is based on the first principal component of sea-level pressure, surface zonal and meridional wind components, sea surface temperature and cloudiness observed over the Tropical Pacific (Wolter and Timlin 1998). The recorded monthly value (MEI) is an average of the principal component for the preceding two months. I derived climate indices by averaging the MEI at intervals preceding the detection date of each fire (i.e., 6, 12, 18, 24-mo prior, etc.) and by determining the MEI value for the month in which each fire was detected (Table 3.1).

I used Generalized Additive Models (GAMS; Wood 2006) to explore relationships in the data. Analogous to the uncertainty regarding how species are distributed across environmental gradients (Guisan et al. 2002), I wanted to avoid assuming how severity patterns would vary across broad or local gradients, and thus chose a flexible modeling approach. GAMS were advantageous for my purpose because the solutions are data-driven, and can range from simple linear (parametric) fits to highly complex smooths that require greater degrees of freedom for each term. In the mgcv library implementation (www.R-project.org), smoothing parameters are chosen to minimize a generalized cross-validation score, and overly complex models are prevented by a penalty imposed during maximum likelihood estimation (Wood 2006).

First, at the among-fires scale, I determined which of the MEI-derived indices had the best linear correlation to fire size. Then I modeled the relationship between a) fire size and the best (most correlated) climate index, b) severity pattern metrics and fire size, and c) severity pattern metrics and the best climate index. When relationships were extremely variable at this scale, I increased the penalty for complexity in the smoothing parameter, which reduces wiggliness and thereby emphasizes general trends. I noted the position (residual value) on the GAM smooth plots of four fires that were the focus of the second part of my analysis.

Within the four fires, I developed GAMS to quantify changes in severity across gradients of topographic and fuel discontinuity (within-fires scale). Topographic discontinuity was modeled by calculating the variance of elevation values (1-minute National Elevation Dataset: http://ned.usgs.gov) within the moving windows. Fuel discontinuity was modeled by the same method, but using the pre-NBR, which was possible for the three recent burns only (La Mesa predated Landsat availability). I eliminated some outlying values in variance of pre-NBR values at Oso from the analysis, which I identified as rocky areas that were highly reflective on the Landsat image. Both models were calculated using the Texture Analysis function in ERDAS Imagine (Leica Geosystems 2006). At the within-fire scale, I sampled the moving window severity maps and the topographic and fuel maps using random points, with number of points proportional to fire size, so that density of points was approximately 12 to 15 per 100 ha (La Mesa, n = 689; Oso, n = 370; Pumpkin, n = 765; Big-Poplar-Rose, n = 820).

In my initial modeling efforts, I found that GAM results from different random samples of the moving window maps were inconsistent. Fluctuations in response variables often occurred at the high end of the fuel and topographic variability gradients, which exhibited a negative exponential distribution (i.e., a relatively small number of observations were highly influential on model results). Therefore, I evaluated GAMS conducted with multiple samples with replacement (n = 100 bootstrap samples) for each fire, while increasing the penalty for complexity in the smoothing parameter to avoid overly wiggly models (gamma = 1.5; Wood 2006). For example:

$$[\text{PLAND}_i] = f_1(\text{topographic discontinuity}_i) + f_2(\text{fuel discontinuity}_i) + \varepsilon \qquad [1]$$

(where f is a smooth function) was run with 100 bootstrap samples (n = 370) for Oso. From these model runs, I generated a subset of metrics that had at least 60 significant models ($P \leq 0.1$) out of the 100 runs. This subset of metrics was considered "consistently significant" with regard to the explanatory variable (topography or fuel). The statistically significant models varied in complexity: some were linear, others were more or less complex (i.e., used higher degrees of freedom to fit the model). I took the mean of the estimated degrees of freedom (edf) for consistently significant models to evaluate complexity of relationships and summarized the model fit using percent deviance explained.

It was necessary to incorporate an understanding of the severity metrics in my interpretation of changes in severity with increased topographic and fuel discontinuity. Specifically, as landscape characteristics became more discontinuous, I expected that composition (PLAND) would decrease and configuration would be more divided (greater DIVISION), less aggregated (lower AI and CLUMPY), and that core area (CAI_AM) and patch size (AREA_AM) would also decrease. But, with confirmation of these trends, I was also interested in how well topographic and fuel discontinuity related to severity as a multivariate response, and how the complexity of relationships might change under different climate conditions.

3.3 Results

3.3.1 Among-Fires Scale: 20 fires

Fire size was related to the MEI gradient; the greatest linear correlation was with the MEI 18-month mean (Pearson's $r = -0.50$). This relationship was somewhat weaker without Cerro Grande, $r = -0.39$), but generally held for all intervals up to and including 24 months. Intervals farther out from the fire date had little correlation to fire size (Pearson's r ranged from −0.15 to 0.15). The GAM smooth curve exhibited a significant decrease across the 18-mo mean (Figure 3.2; $P = 0.02$, Deviance explained = 41.4%). The confidence interval at the El Niño end was wide, due to the single fire at that end of the climate gradient (Oso 1998). Two relatively large fires occurred midway along the gradient (Dome 1996 and Poplar-Big-Rose 2003). Cerro Grande (2000) influenced the trend at the extreme La Niña end of the scale because of its outstanding size (17,349 ha; Table 3.1).

Four of the spatial pattern metrics varied in relation to fire size, resulting in statistically significant models (Figure 3.2). Composition of high severity (PLAND), area-weighted mean patch size (AREA_AM), and core area index (CAI_AM) generally increased with the total area burned (GAM smooth $P < 0.2$). However, Cerro Grande, the largest fire, had a lower value for PLAND than some of the smaller fires, which resulted in a downward turn in the smooth curve. Another exception to the overall trend was Saddle Mountain, which was composed of 49% high severity: an outstandingly large value for a fire that burned less than 5000 ha. Its area-weighted mean patch size (AREA_AM) was an extreme value on the size gradient as well (Figure 3.3). Cell aggregation (CLUMPY) exhibited high variability in smaller fires, and consistently high values at intermediate and large sizes. Quartz had extremely low cell aggregation compared to the other fires (CLUMPY = −0.63), indicating that its high-severity burned area was strongly disaggregated.

Only two of the severity pattern metrics (AREA_AM and CAI_AM) were significantly related to the MEI gradient (Figure 3.4). These measures of severity tended to be greater at the La Niña end of the climate scale. Oso, however, had relatively high core area index for an El Niño fire. Values of greater magnitude for these metrics midway along the gradient were contrary to the overall trend exemplified by Saddle Mountain (AREA_AM = 1102, CAI_AM = 41, MEI 18-mo mean = 0.00).

3.3.2 Among-Fires Scale: 4 fires

Climate of the four fires differed both in shorter and longer-term characteristics (Figure 3.1 and Table 3.3 Among-fires Scale). Pumpkin occurred during a severe La Niña drought that followed the major El Niño event of 1997/98. The MEI for Pumpkin's date of detection indicated a fluctuation toward warm wet conditions 2 mo prior to ignition. Oso occurred during the major El Niño event of 1997/98; it stood out among the four fires because of its consistently, relatively high positive MEI values across all the timeframes I examined. Poplar-Big-Rose was also an El Niño fire, but the MEI for its date of detection indicated that drier conditions occurred 2 mo prior to burning.

Fire weather included high temperatures and gusty winds during some portion of the burning period for Pumpkin (http://199.134.225.50/nwcc/t2_wa4/previous/2000_fires/pumpkin/pumpkin_home.htm), La Mesa (Foxx 1984), and Oso (National Weather Service http://www.nws.noaa.gov/; Table 3.3 Among-fires Scale). Some extreme fire weather was reported during Poplar-Big-Rose, but it was short in duration and late in the fire season (http://www.nps.gov/archive/grca/media/2003/2oct03.htm). Duration of burning corresponded to fire weather conditions at Pumpkin and La Mesa, where fire size > 5,500 ha was achieved in 2 weeks or less. Oso was contained after only 16 days, but it was much smaller than the other fires (2,462 ha). In contrast, Poplar-Big-Rose burned for over 60 days and its size (6,839 ha) was similar to Pumpkin's (6,383 ha). All of the fires were actively suppressed throughout the duration of burning, except for Poplar-Big-Rose, which was monitored for natural resource objectives. Containment of Pumpkin, Oso, and La Mesa was assisted by rain.

Proportional composition of high severity was similar among the four fires, except for Poplar-Big-Rose, which was much lower at 19% (Among-fires Scale–Fire Severity–PLAND, Table 3.3). La Mesa high-severity was somewhat less aggregated, with smaller patch sizes and core area , independent of composition (Among-fires Scale–

Fire Severity–AREA_AM, CAI_AM, CLUMPY). Pumpkin had the largest core area, independent of composition, of any of the fires (Among-fires Scale–Fire Severity–CAI_AM).

3.3.3 Within-Fires Scale: Pumpkin

Fuel discontinuities influenced multiple aspects of severity at Pumpkin (Within-fires scale, Table 3.3). Proportional composition (PLAND) and three aspects of configuration (AI, DIVISION, AREA_AM) consistently had a significant relationship with fuel discontinuity. The degrees of freedom required to fit the models corresponded with linear to near-linear trends indicating simple, direct relationships (edf 1.02 to 1.50; see also Figure 3.5). Deviance explained by the models ranged from 2.4 to 3.0%. In contrast, variations in topography did not reliably predict severity at Pumpkin (Within-fires scale, Table 3.3); topographic discontinuity models were not consistently significant (out of 100 runs) for any of the severity metrics.

3.3.4 Within-fires scale: La Mesa

Topographic variability was related to four characteristics of severity at La Mesa (Within-fires scale, Table 3.3). Composition (PLAND), as well as patch size (AREA_AM) and cohesiveness of high-severity cells (CLUMPY) and patches (DIVISION) varied significantly across the gradient in topographic discontinuity. These relationships were complex, generally using more degrees of freedom than topographic models for the other three fires (edf 2.62 to 3.85; see also Figure 3.5). The percent deviance explained was 2.9 to 5.5.

3.3.5 Within-fires Scale: Poplar-Big-Rose

Fire severity at Poplar-Big-Rose was consistently related to topographic discontinuity (Within-fires scale, Table 3.3). Variations in topography influenced composition (PLAND), cohesiveness of high-severity patches (DIVISION), and patch size independent of composition (AREA_AM). Model complexity indicated that these were simple, direct relationships and could be fit without smoothing (edf was always 1.00; see also Figure 3.5).

Fuel discontinuities also influenced severity at Poplar-Big-Rose (Within-fires scale, Table 3.3). Severity metrics with consistently significant models were identical to those reported for topographic models: composition (PLAND), cohesiveness of high-severity patches (DIVISION), and patch size independent of composition (AREA_AM). However, the models were very complex, requiring more degrees of freedom than fuel models for other fires (edf 3.64 to 3.99; see also Figure 3.5). Deviance explained by the models ranged from 3.0 to 6.3%.

3.3.6 Within-fires Scale: Oso

At Oso, several fire severity metrics were influenced by topographic discontinuity (Within-fires scale, Table 3.3). Proportional composition (PLAND), patch size independent of composition (AREA_AM), aggregation of high-severity cells (AI), and patch division (DIVISION) all varied consistently with the topographic gradient. Compared to models for other fires, complexity of relationships based on degree of smoothing was moderate (edf 1.99 to 2.96; see also Figure 3.5).

Fire severity corresponded to fuel discontinuity at Oso as well (Within-fires scale, Table 3.3). Fuel discontinuity was consistent in explaining significant variation in composition (PLAND), aggregation of high-severity cells (AI), patch division (DIVISION), and patch size independent of composition (AREA_AM). These relationships were moderate in complexity (edf 2.18 to 2.58). Models for Oso explained 2.8 to 6.1% deviance.

3.4 Discussion

My results emphasize the need to view simplistic assumptions about relationships between fire severity, fire size and climate change cautiously. Larger fires occurred with certain climate conditions, in particular, during the cool dry extremes of La Niña. However, several of the fires I examined deviated from this trend. For example, Poplar-Big-Rose and Oso were exceptionally large, given their El Niño position on the climate gradient (Figure 3.2).

Clearly, there are limitations imposed when one index of climate is employed at a single timeframe. The 18-mo mean could not capture potentially important fluctuations that might influence vegetation growth and desiccation that leads to flammability. For example, the historic El Niño event of 1997/98 likely provided wet conditions conducive to vegetation productivity prior to Pumpkin, but a single MEI value or mean may not capture that important sequence of prefire climate conditions. Likewise, the area that burned in La Mesa experienced an extended drought, but a lag occurred which situated the fire event in an El Niño period, based on its MEI values.

Furthermore, although climate may influence fire size, other factors cause variability in this relationship. Burning conditions, including wind, humidity, and temperature can inhibit or increase fire spread (Flannigan and Wotton 2001). In addition, the effects of La Niña-El Niño cycles can be intensified by teleconnections with broader-scale climate conditions (Flannigan and Wotton 2001, Baker 2003, Kitzberger et al. 2007). Fires can become larger under favorable conditions, but landscape characteristics, as well as fire management may limit area burned.

As expected, some spatial properties of severity did not correspond to fire size or to changes in climate. Specifically, one or more properties of severity did not increase (or decrease in the case of DIVISION) with larger fire size or in La Niña (negative MEI) climates. Aggregation of high-severity cells and patch division did not relate to fire size; likewise, high-severity composition, aggregation and clumpiness of high-severity cells and patch division were not related to the climate gradient. Size of patches logically increased with fire size; larger overall size can accommodate larger patches, which in turn may include more core area (Figure 3.3). Fires were extremely variable with regard to relative composition of high severity, as evidenced by several outlying values. For example, two of the largest fires, Poplar-Big-Rose and Cerro Grande, did not conform to the trend of increasing high-severity composition with fire size (Figure 3.3).

Fire severity is also influenced by several factors that interact with climate. Variability in fire severity can be affected by fire management activities, for example, backfires, which are high intensity fires lit near a flaming edge, and lower-intensity burnouts tend to reduce burn heterogeneity (FUSEE 2006). Overall, firing operations can significantly increase fire size and severity; the extent of Cerro Grande (2000) increased dramatically after a backfire was set by fire fighting crews (FUSEE 2006). In addition, the vertical and horizontal structure of fuels that often differ among forest communities can affect fire behavior and effects (Brown 1985, Wimberly and Reilly 2007). Topographic variations within a burned area also interact with climate to produce heterogeneity in fire severity that may not directly correspond to expectations based on climate.

Within the four fires, characteristics of fuels and topography altered spatial patterns of severity as fuel and topography became more discontinuous (see examples in Figure 3.5). Decrease in severity was defined by lower values for proportional composition, and for metrics describing patch and core area, while patch division increased. However, a relatively low proportion of the deviance in the data was explained by the models. I interpreted the poor model fit, which occurred in spite of the ability of GAMs to accommodate variability, in two ways. First, fuel diversity can only be partially captured by satellite imagery; detailed field data are needed to quantify surface fuels, in particular (Keane 2008). Likewise, several alternative topographic roughness models have been developed (Stambaugh and Guyette 2008). Experimentation with different models at alternative scales is necessary to determine the adequacy of the fuel and topographic discontinuity models employed here. Second, extreme weather occurred at some period during all four of the fires. High winds and hot burning conditions could conceivably override local influences on fire behavior and resulting patterns of severity.

The nature of the relationships between severity and discontinuities in fuel and topography suggest that fire severity responded to local controls in unique ways during the four fire events. Contrary to expectations, fuel configurations apparently maintained their influence on severity even in extreme La Niña conditions at Pumpkin. Previous studies have documented the predominant effects of fuel treatments on fire severity during extreme drought years, but are not entirely comparable with my work due to the non-spatial measurement of severity and lack of inclusion of topographic influence (e.g., Strom and Fulé 2007).

Consistent with my expectations, both fuel and topographic variability had significant influence on severity at La Mesa, Oso, and Poplar-Big-Rose during more moderate climates of El Niño. The extreme fire weather that occurred during some periods of burning probably resulted in more complex relationships (i.e., models fit with greater degrees of freedom) as burning conditions interacted with landscape gradients in topography and fuels. In future research, the influence of weather conditions on severity could be examined directly using weather data linked to spatial patterns of severity at particular places.

3.4.1 Conclusion

Fire severity has become a topic for increased study as wildfires become of greater concern (e.g., Lentile et al. 2007). Understanding the influence of large-scale climate patterns on fire effects is essential to sorting out confusion that surrounds the current wildfire controversy (Johnson 2003). My examination of the relationship between severity and climate among recent fires in two regions of the Southwest points to several key challenges in building understanding of climate-fire dynamics.

First, what is the appropriate scale at which to measure severity? This question is relevant to other characteristics of fire regimes as well, recognizing that the relevant scale of measurement depends on the question of interest (Wiens 1989, Falk et al. 2007). Second, because fire severity is a spatial attribute its characterization requires choices in how to quantify amount and arrangement of patterns, including exploration of alternatives to the patch-mosaic model of landscape structure (McGarigal and Cushman

2005). Last, what is the appropriate index with which to quantify climate conditions? Further clarification of these questions will require assessments conducted across a range of temporal and spatial scales.

Finally, my research has important implications for identification of climate contexts in which fires can produce an acceptable range of ecological effects. At Poplar-Big-Rose, understory effects predominated and fire-resistant species, including ponderosa pine, persisted with low rates of mortality, meeting natural resource objectives of land managers (Fulé and Laughlin 2007). Fires that are allowed to burn naturally could provide important data for sorting out interactions of regional climates, local weather, fuel, and topography in predictive models of fire effects.

Table 3.1 Fires included in the study, the total area burned, date of detection, and MEI calculated for the detection month and several preburn intervals. The table is sorted by the 24-mo mean.

Fire Name	Location[1]	Total Area (ha)	Detection Date (Yr.JulianDate)	MEI Month of Detection	6-mo mean	12-mo mean	18-mo mean	24-mo mean
Pumpkin	KNF AZ	6383.79	2000.146	0.034	-0.79	-0.77	-0.81	-0.66
Viveash	SFNF NM	8811.09	2000.151	0.034	-0.79	-0.77	-0.81	-0.66
Cerro Grande	SFNF NM	17349.39	2000.125	-0.338	-0.97	-0.82	-0.88	-0.58
Outlet 2000	GRCA AZ	4804.74	2000.131	-0.338	-0.97	-0.82	-0.88	-0.58
Vista	GRCA AZ	1487.52	2001.196	0.147	-0.16	-0.30	-0.36	-0.51
Swamp Ridge	GRCA AZ	1295.01	2001.229	0.288	-0.01	-0.26	-0.28	-0.47
Tower	GRCA AZ	1683.00	2001.241	0.288	-0.01	-0.26	-0.28	-0.47
La Mesa	BAND NM	5745.60	1977.167	0.488	0.40	0.55	0.06	-0.39
American Springs	SFNF NM	703.26	1954.157	-1.547	-0.61	-0.16	0.03	0.02
Saddle Mountain	KNF AZ	3931.74	1960.173	-0.261	-0.21	-0.17	0.00	0.09
Summit	KNF AZ	193.86	1966.169	-0.177	0.54	0.96	0.67	0.18
Nicole	SFNF NM	158.58	1996.175	-0.012	-0.37	-0.30	0.02	0.26
Dome	SFNF NM	6648.57	1996.116	-0.485	-0.49	-0.34	0.04	0.30
Poplar-Big-Rose	GRCA AZ	6839.10	2003.190	-0.004	0.56	0.72	0.58	0.42
Walhalla	GRCA AZ	1325.16	2004.259	0.561	0.43	0.39	0.32	0.49
Bright	GRCA AZ	520.20	2004.237	0.61	0.33	0.38	0.34	0.50
Outlet 2004	GRCA AZ	450.27	2004.236	0.61	0.33	0.38	0.34	0.50
Quartz	GRCA AZ	228.96	2004.222	0.457	0.29	0.35	0.35	0.51
Long Jim	GRCA AZ	820.80	2004.126	0.271	0.29	0.26	0.48	0.56
Oso	SFNF NM	2462.67	1998.182	1.144	2.26	2.39	1.75	1.25

[1] Location codes (one of potentially multiple management agencies): KNF = Kaibab National Forest, SFNF = Santa Fe National Forest, GRCA = Grand Canyon National Park, BAND = Bandelier National Monument, AZ = Arizona, NM = New Mexico.

Table 3.2 Fragstats spatial pattern metrics chosen to quantify attributes of fire severity, with their abbreviation and interpretation.

Spatial Pattern Metric	Description
PLAND	Percent of the Landscape: Proportional abundance of high-severity patches in the burned landscape; severity composition.
AREA_AM	Area-weighted mean patch size: the proportional area of each high-severity patch, based on total area of all high-severity patches.
AI	Aggregation Index: The number of adjacencies between high-severity cells, divided by the maximum possible number of adjacencies (0–100%). Equals 0 when there are no like adjacencies, and 100 when all cells form a single, compact patch.
CLUMPY	Clumpiness Index: The proportion of adjacencies of high-severity cells, scaled to reflect its deviation from that expected under a spatially random distribution, facilitating comparison of high-severity cell aggregation among landscapes (range −1 to 1).
DIVISION	Division Index: Based on the cumulative patch area distribution, DIVISION is the probability that two randomly chosen cells are not situated in the same high-severity patch (0 to 1). The value approaches 1 as the proportion of the landscape comprised of high severity decreases and as high-severity patches decrease in size.
CAI_AM	Core Area Index (Area-weighted Mean): Percentage of the high-severity patch that is greater than 100-m from an edge of lower severity, summed for all high-severity patches. The index is scaled relative to proportional abundance of high-severity patches to enable comparison among landscapes.

Table 3.3 A summary of the characteristics of the four fires including their climate and severity, and results of the within-fires analysis. Long- and short-term climate was summarized from Table 3.1 and Figure 3.1.

Among-fires scale	**Pumpkin**	**La Mesa**	**Poplar-Big-Rose**	**Oso**
Location	Kaibab National Forest, AZ	Bandelier National Monument, NM	Grand Canyon National Park, AZ	Santa Fe National Forest, NM
Total Area (ha)	6383.79	5745.60	6839.10	2462.67
Year	2000	1977	2003	1998
Pre-fire climate (longer term)	La Niña, greatest negative values for any fire (6 mo to 24 mo).	La Niña in longer timeframes (18 to 24 mo).	El Niño (6 to 24 mo).	Major El Niño event 1997/1998.
Pre-fire climate (shorter term)	Warmer, wetter conditions immediately (2 mo) preceding burn.	Warmer, wetter periods (2 to 12 mo) preceded burn.	Marked shift toward cooler and drier conditions immediately (2 mo) preceding the burn.	Somewhat cooler and drier immediately (2 mo) prior.
Fire Management	Aggressively fought; tactics included back-burning.	Aggressively fought.	Monitored for management objectives; burning was suppressed in some places.	Aggressively fought.

Continued on next page

Table 3.3, continued

Among-fires scale	Pumpkin	La Mesa	Poplar-Big-Rose	Oso
Weather during burning	Extreme winds and high temperatures. Containment aided by rain.	Some high temperatures and gusty winds. Containment aided by rain.	High winds in final days of burning. Significant burning occurred in high wind during one day.	High wind gusts and temperature spikes. Containment aided by rain.
Duration of burning	17 days	8 days	Approx. 60 days	16 days
Fire Severity				
PLAND	26%	34%	19%	29%
CAI_AM	44 ha	20 ha	37 ha	33 ha
AREA_AM	535.56 ha	373.73 ha	587.08 ha	97.54 ha
AI	96.73	91.69	96.76	94.78
DIVISION	0.98	0.98	0.98	0.99
CLUMPY	0.87	0.75	0.84	0.82

Within-fires scale	Pumpkin	La Mesa	Poplar-Big-Rose	Oso
Topographic model characteristics[1]	No relationship	Most complex (edf 2.62 to 3.85)	Simple, direct (edf = 1.00)	Moderately complex (edf 1.99 to 2.96)
Severity metrics related to topographic discontinuity[2]	None	PLAND DIVISION AREA_AM CLUMPY	PLAND DIVISION AREA_AM	PLAND AI DIVISION AREA_AM
Fuel model characteristics[1]	Simple, direct (edf 1.02 to 1.50)	NA	Most complex (edf 3.64 to 3.99)	Moderate in complexity (edf 2.18 to 2.58)

Continued on next page

Table 3.3, Continued

Severity metrics related to fuel discontinuity[2]	PLAND AI DIVISION AREA_AM	NA	PLAND DIVISION AREA_AM	PLAND AI DIVISION AREA_AM

[1]Model complexity was judged by the range of estimated degrees of freedom (edf) for consistently significant terms, with more simple relationships having lower edf. Topographic discontinuity was an inconsistent predictor of severity at Pumpkin (< 60% of the model runs with $P \leq 0.1$). Fuel discontinuity was not modeled for La Mesa (Landsat data unavailable).

[2]Severity metrics with consistently significant models (≥ 60% of the model runs with $P \leq 0.1$) in the 100 runs are listed.

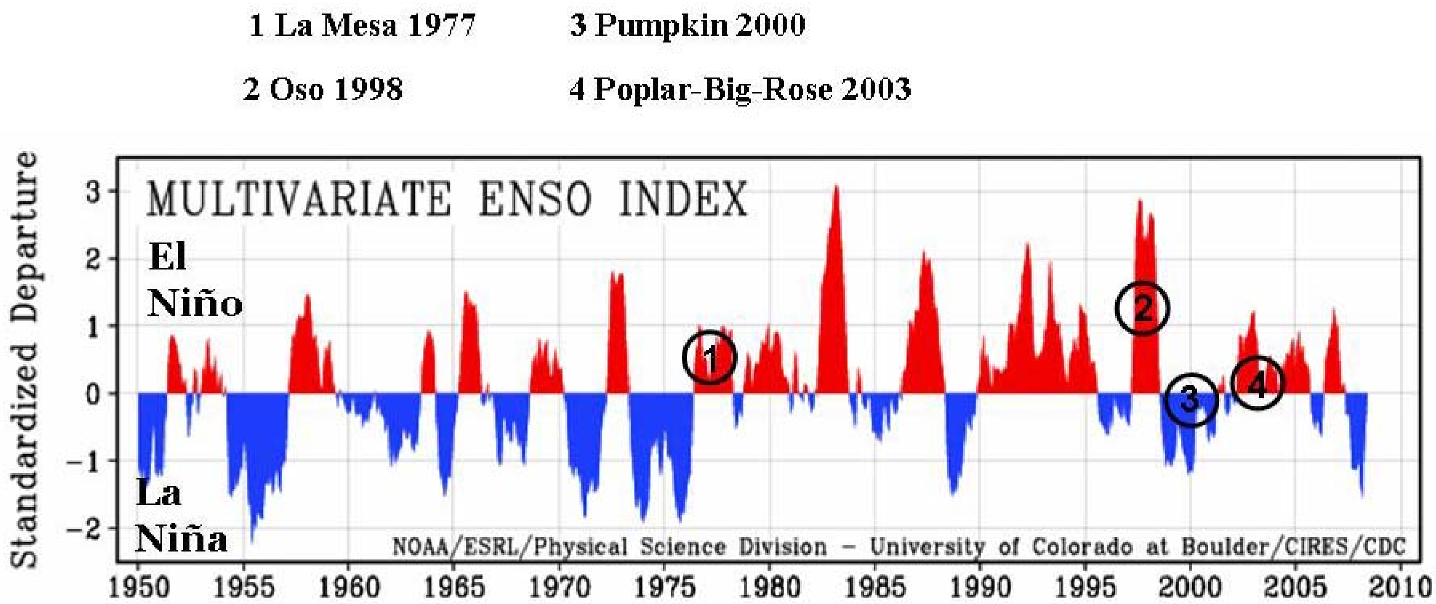

Figure 3.1: The approximate location of the four fires included in the within-fires analysis on the MEI gradient, based on the MEI for the month the fire was detected. La Mesa (1) was preceded by extreme drought in the mid-70's. Oso (2) occurred near the end of the historic 1997/98 El Niño, which preceded the drought period when Pumpkin (3) burned. Poplar-Big-Rose (4) was situated in the more moderate El Niño of 2003-2005.

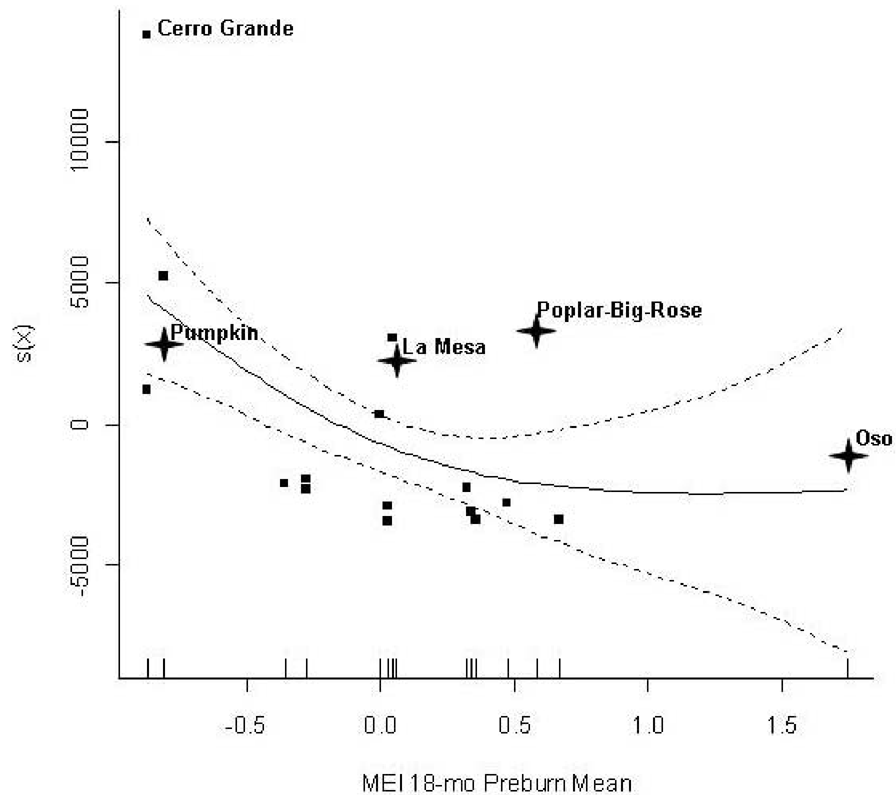

Figure 3.2: Fire size generally decreased across the preburn mean MEI, where negative *x*-axis values correspond to 18-mo preburn time periods that were dominated by La Niña (GAM smooth term *P* = 0.02). Cerro Grande is noted for its exceptional size. Residuals for the four focal fires are starred. Pumpkin and Oso conformed to the negative relationship between fire size and MEI gradient, but La Mesa and Poplar-Big-Rose were larger that most fires with similar climates on the 18-mo gradient. The *y*-axis is scaled by the smooth function of *x*.

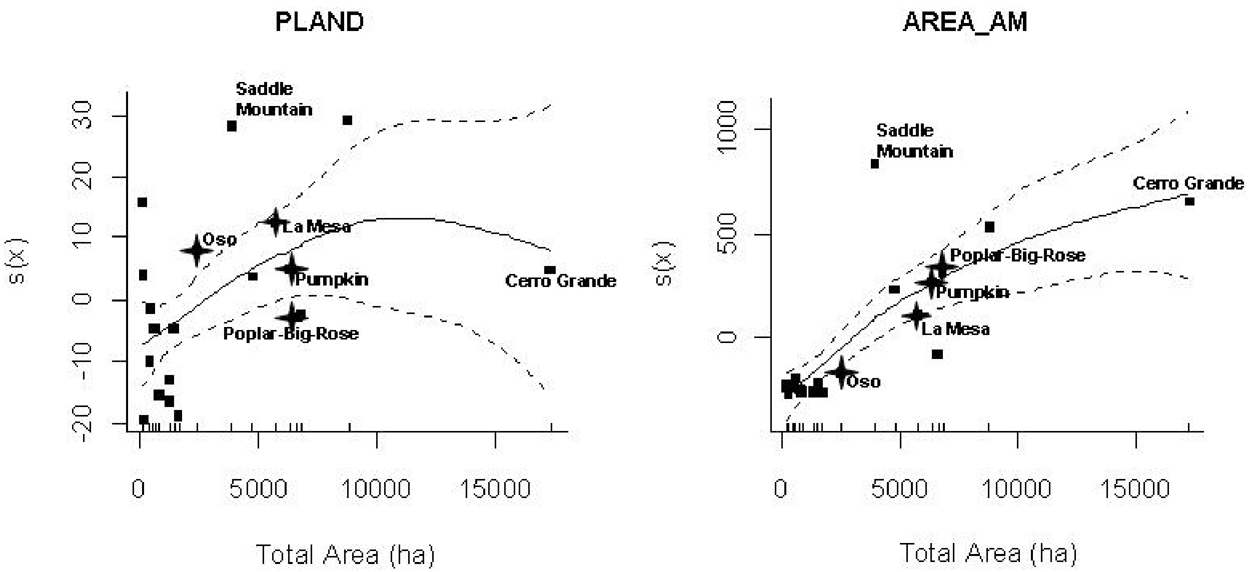

Figure 3.3: Composition of burn severity (PLAND) and three aspects of burn severity configuration (AREA_AM [CLUMPY, and CAI_AM shown on next page]) showed generally positive relationships to fire size (*P* < 0.2). Residuals for the fires examined at within-fires scale are starred. The *y*-axis is scaled by the smooth function of *x*.

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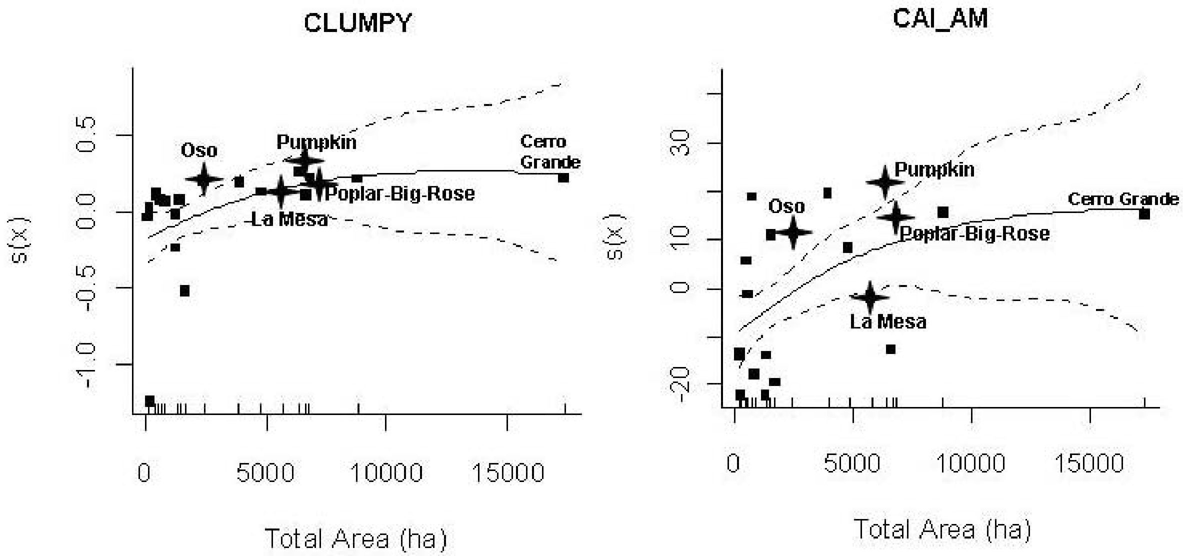

Figure 3.3, continued

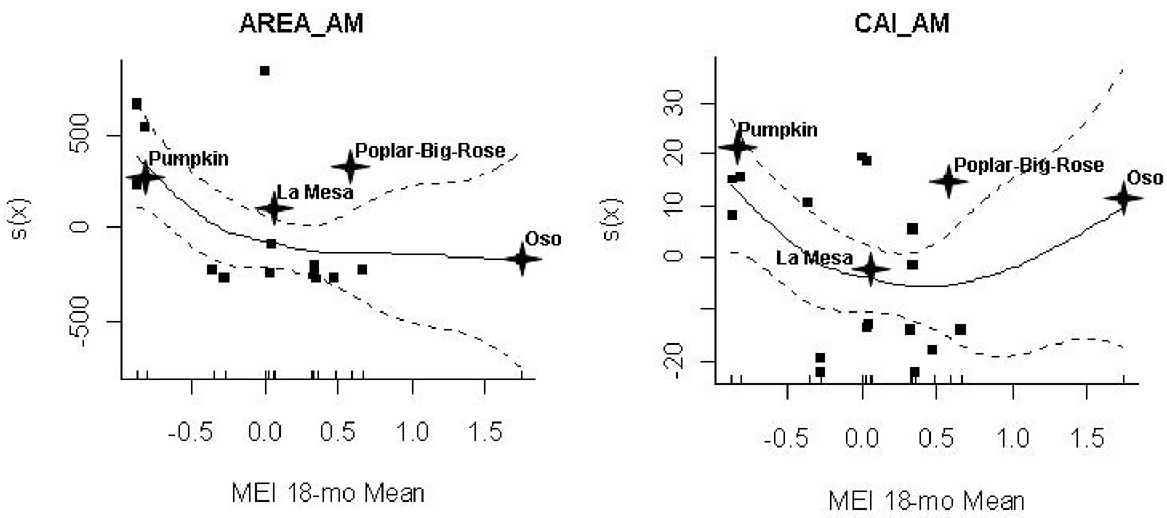

Figure 3.4: Only two metrics were significantly related to variations in the MEI 18-mo mean. Poplar-Big-Rose had high AREA_AM and CAI_AM for a fire with its climate. Oso reversed the trend of the curve with its high CAI_AM value, while Pumpkin, La Mesa, and Oso generally conformed to declining AREA_AM as average 18-mo preburn MEI tended toward El Niño. The smooth function of *x* is plotted on the *y*-axis.

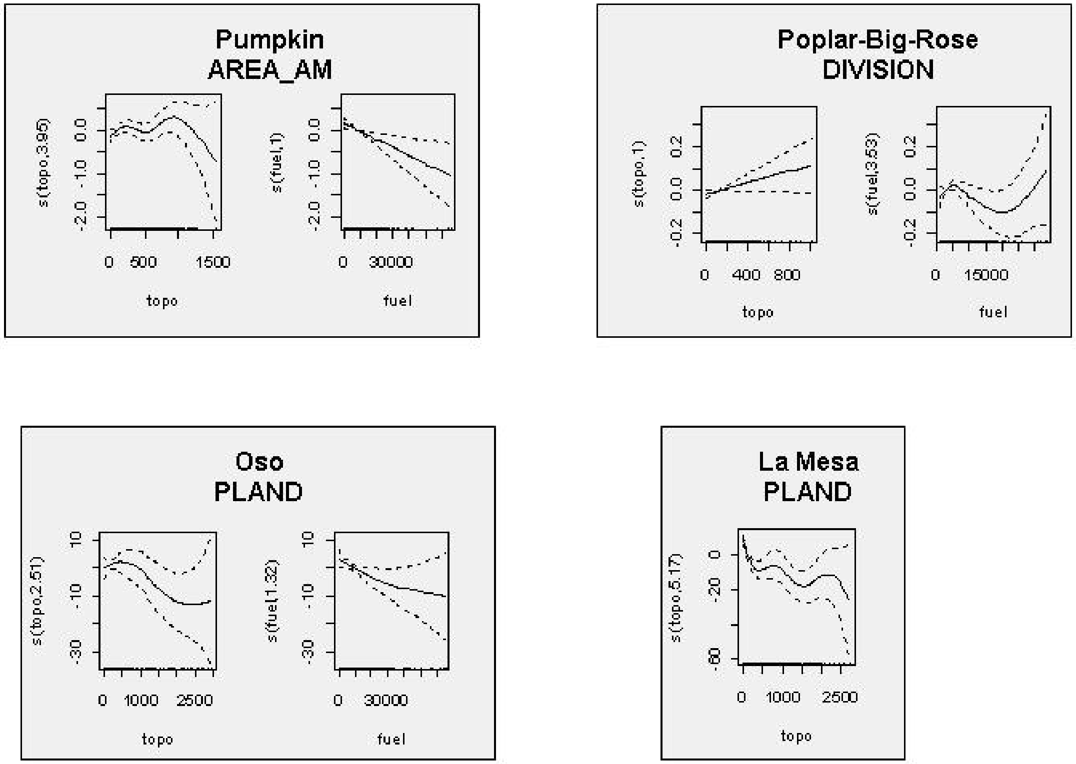

Figure 3.5: Example smooth plots illustrating the variation in model complexity as severity decreased across local gradients at the four fires (e.g., AREA_AM and PLAND decreased while DIVISION increased). The smooth function of *x* is plotted on the *y*-axis. Severity at Pumpkin was consistently predicted by fuel but not topography. La Mesa had no fuel model because its date preceded the availability of Landsat data. A complete list of metrics related to local gradients is located in Table 3.3.

LITERATURE CITED

Agee, J. K. 1998. The landscape ecology of western forest fire regimes. Northwest Science **72**:24-34.

Allen, C. D. 1989. Changes in the landscape of the Jemez Mountains, New Mexico. Ph.D. Dissertation, University of California, Berkeley.

Allen, C. D., J. L. Betancourt, and T. W. Swetnam. 1998. Landscape changes in the southwestern United States: techniques, long-term data sets, and trends. Pages 71-84 *in* T. D. Sisk, editor. Perspectives on the land-use history of North America: a context for understanding our changing environment. United States Geological Survey, Biological Resources Division.

Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. Ecological restoration of Southwestern ponderosa pine ecosystems: A broad perspective. Ecological Applications **12**:1418-1433.

Baird, M., D. Zabowski, and R. L. Everett. 1999. Wildfire effects on carbon and nitrogen in inland coniferous forests. Plant and Soil **209**:233-243.

Baker, W. L. 2003. Fires and climate in forested landscapes of the US Rocky Mountains.*in* T. T. Veblen, W. L. Baker, G. Montenegro, and T. Swetnam, editors. Fire and climatic change in termperate ecosystems of the western Americas. Springer-Verlag, New York.

Beschta, R. L., J. J. Rhoades, J. B. Kauffman, R. Gresswell, G. W. Minshall, J. R. Karr, D. A. Perry, F. R. Hauer, and C. A. Frissell. 2004. Postfire management on forested public lands of the western United States. Conservation Biology **18**:957-967.

Bonnet, V. H., A. W. Schoettle, and W. D. Shepperd. 2005. Postfire environmental conditions influence the spatial pattern of regeneration for Pinus ponderosa. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **35**:37-47.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities in southern Wisconsin. Ecological Monographs **27**:325-349.

Brooks, T., G. A. B. d. Fonseca, and A. S. L. Rodrigues. 2004. Species, data, and conservation planning. Conservation Biology **18**:1682-1688.

Brown, J. K. 1985. The "unnatural fuel buildup" issue.*in* Proceedings-Symposium and Workshop on Wilderness Fire, Missoula, November 15-18, 1983. U.S. Forest Service General Technical Report, INT-182. 434p., Missoula, Montana.

Brown, J. K., and N. V. DeByle. 1987. Fire damage, mortality, and suckering in aspen. Canadian Journal of Forest Research **17**:1100–1109.

Brown, P. M., M. R. Kaufmann, and W. D. Shepperd. 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. Landscape Ecology **14**:513-532.

Center for Sustainable Environments. 2002. Safeguarding the uniqueness of the Colorado Plateau: An ecoregional assessment of biocultural diversity Northern Arizona University, Flagstaff.

Certini, G. 2005. Effects of fire on properties of forest soils: a review. Oecologia **143**:1-10.

Choi, Y. D. 2007. Restoration ecology to the future: A call for a new paradigm. Restoration Ecology **15**:351-353.

Christensen, N. L., J. K. Agee, P. F. Brussard, J. Hughes, D. H. Knight, G. W. Minshall, J. M. Peek, S. J. Pyne, F. J. Swanson, J. W. Thomas, S. Wells, S. E. Williams, and H. A. Wright. 1989. Interpreting the Yellowstone Fires of 1988. Bioscience **39**:678-685.

Clark, J. S. 1993. Paleoecological perspectives on modeling broad-scale responses to global change. Pages 315-332 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer Associates, Sunderland, Massachusetts.

Clark, J. S. 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. American Naturalist **152**:204-224.

Clark, J. S., B. Beckage, P. Camill, B. Cleveland, J. HilleRisLambers, J. Lichter, J. McLachlan, J. Mohan, and P. Wyckoff. 1999. Interpreting recruitment limitation in forests. American Journal of Botany **86**:1-16.

Clark, J. S., and Y. Ji. 1995. Fecundity and Dispersal in Plant-Populations - Implications for Structure and Diversity. American Naturalist **146**:72-111.

Clark, J. S., M. Lewis, and L. Horvath. 2001. Invasion by extremes: Population spread with variation in dispersal and reproduction. American Naturalist **157**:537-554.

Clark, J. S., M. Lewis, J. S. McLachlan, and J. HilleRisLambers. 2003. Estimating population spread: What can we forecast and how well? Ecology **84**:1979-1988.

Cooper, C. F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecological Monographs **30**:130-164.

Covington, W. W. 2000. Prescribed fire is not the issue. Journal of Forestry **98**:48-48.

Covington, W. W., P. Z. Fule, S. C. Hart, and R. P. Weaver. 2001. Modeling ecological restoration effects on ponderosa, pine forest structure. Restoration Ecology **9**:421-431.

De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees:a powerful yet simple technique for the analysis of complex ecological data. Ecology **81**: 3178–3192.

Delcourt, H. R., P. A. Delcourt, and T. Webb. 1983. Dynamic plant ecology: the spectrum of vegetation change in space and time. Quarternary Science Review **1**:153-175.

Dellasala, D. A., J. E. Williams, C. D. Williams, and J. F. Franklin. 2004. Beyond smoke and mirrors: a synthesis of fire policy and science. Conservation Biology **18**:976-986.

Dunmire, W. W., and G. D. Tierney. 1995. Wild plants of the Pueblo Province. Museum of New Mexico Press, Santa Fe.

Dunmire, W. W., and G. D. Tierney. 1997. Wild plants and native peoples of the Four Corners. Museum of New Mexico Press, Santa Fe.

Ecological Restoration Institute. 2004. Plants of northern Arizona forests: A comprehensive guide for the Mogollon Plateau coniferous forest bioregion in Arizona. Northern Arizona University, Flagstaff.

Ehle, D. S., and W. L. Baker. 2003. Disturbance and stand dynamics in ponderosa pine forests in Rocky Mountain National Park, USA. Ecological Monographs **73**:543-566.

Epple, A. O. 1995. A field guide to the plants of Arizona. Globe Pequot Press, Guilford, CT.

Falk, D. A. 2006. Process-centered restoration in a fire-adapted ponderosa pine forest. Journal for Nature Conservation **14**:140-151.

Falk, D. A., C. Miller, D. McKenzie, and A. E. Black. 2007. Cross-scale analysis of fire regimes. Ecosystems **10**:809-823.

Flannigan, M. D., and B. M. Wotton. 2001. Climate, weather, and area burned.*in* E. A. Johnson and K. Miyanishi, editors. Forest fires: Behavior and Ecological Effects. Academic Press.

Floyd, M. E. 1982. The interaction of piñon pine and Gambel oak in plant succession near Dolores, Colorado. Southwestern Naturalist **27**:143-147.

Floyd, M. L., D. D. Hanna, and W. H. Romme. 2004. Historical and recent fire regimes in piñon juniper woodlands on Mesa Verde, Colorado. Forest Ecology and Management **198**:269 289.

Foxx, T. S. 1984. Description of La Mesa Fire. Pages 1-10 *in* T. S. Foxx, editor. La Mesa Fire Symposium, October 6-7, 1981. Los Alamos National Laboratory, LA-9236-NERP, Los Alamos, NM.

Foxx, T. S., and D. Hoard. 1995. Flowering plants of the southwestern woodlands. Otowi Crossing Press, Los Alamos, New Mexico.

Franklin, J. F., D. B. Lindenmayer, J. A. MacMahon, A. McKee, J. Magnusson, D. A. Perry, R. Waide, and D. R. Foster. 2000. Threads of continuity: ecosystem disturbances, biological legacies and ecosystem recovery. Conservation Biology in Practice **1**: 8–16.

Frelich, L. E. 2002. Forest dynamics and disturbance regimes : studies from temperate evergreen-deciduous forests. Cambridge University Press, New York.

Frelich, L. E., and P. B. Reich. 1995. Spatial Patterns and Succession in a Minnesota Southern-Boreal Forest. Ecological Monographs **65**:325-346.

Fulé, P. Z., and D. C. Laughlin. 2007. Wildland fire effects on forest structure over an altitudinal gradient, Grand Canyon National Park, USA. Journal of Applied Ecology **44**:136-146.

FUSEE. 2006. Scorched earth tactics: Backfires and burnouts. Fire Reports, www.fusee.org, May 30, 2006, Eugene, OR.

Grissino-Mayer, H. D., and T. W. Swetnam. 2000. Century-scale climate forcing of fire regimes in the American Southwest. Holocene **10**:213-220.

Guisan, A., T. C. Edwards, Jr., and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling **157**:89-100.

Haire, S. L., and K. McGarigal. 2008. Inhabitants of landscape scars: Succession of woody plants after large, severe forest fires in Arizona and New Mexico. The Southwestern Naturalist **53**:146-161.

Hopkins, R. L. 1990. Kaibab Formation. Pages 225-245 *in* S. S. Beus and M. Morales, editors. Grand Canyon geology. New York and Oxford: Oxford University Press.

Johnson, E. A. 2003. Towards a sounder fire ecology. Frontiers in Ecology and the Environment **1**:271-271.

Johnson, E. A., K. Miyanishi, and J. M. H. Weir. 1998. Wildfires in the western Canadian boreal forest: Landscape patterns and ecosystem management. Journal of Vegetation Science **9**:603-610.

Kashian, D. M., D. B. Tinker, M. G. Turner, and F. L. Scarpace. 2004. Spatial heterogeneity of lodgepole pine sapling densities following the 1988 fires in Yellowstone National Park, Wyoming, USA. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **34**:2263-2276.

Keane, R. E. 2008. Biophysical controls on surface fuel litterfall and decomposition in the northern Rocky Mountains, USA. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **38**:1431-1445.

Keeley, J. E., C. J. Fotheringham, and M. Baer Keeley. 2005. Factors affecting plant diversity during post fire recovery and succession of Mediterranean climate shrublands in California, USA. Diversity Distributions **11**:525 537.

Key, C. H., and N. C. Benson. 2005. Landscape Assessment: Ground measure of severity, the Composite Burn Index, and remote sensing of severity, the Normalized Burn Ratio. In D.C. Lutes, R.E. Keane, J.F. Caratti, C.H. Key, N.C. Benson, S. Sutherland, and L.J. Gangi. 2005. FIREMON: Fire Effects Monitoring and Inventory System. USDA Forest Service, Rocky Mountain Research Station, Ogden, UT. Gen. Tech. Rep. RMRS-GTR-164-CD:LA1-51.

Keyser, T. L., F. W. Smith, and W. D. Shepperd. 2005. Trembling aspen response to a mixed-severity wildfire in the Black Hills, South Dakota, USA. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **35**:2679-2684.

Kitzberger, T., P. M. Brown, E. K. Heyerdahl, T. W. Swetnam, and T. T. Veblen. 2007. Contingent Pacific-Atlantic Ocean influence on multicentury wildfire synchrony over western North America. Proceedings of the National Academy of Sciences of the United States of America **104**:543-548.

Kokaly, R. F., B. W. Rockwell, S. L. Haire, and T. V. V. King. 2007. Characterization of post-fire surface cover, soils, and burn severity at the Cerro Grande fire, New Mexico, using hyperspectral and multispectral remote sensing. Remote Sensing of Environment **106**:305-325.

Kotliar, N. B., P. L. Kennedy, and K. Ferree. 2007. Avifaunal responses to fire in southwestern montane forests along a burn severity gradient. Ecological Applications **17**:491-507.

Leica Geosystems. 2006. ERDAS Imagine 9.1. St Gallen, Switzerland.

Lentile, L. B., P. Morgan, A. T. Hudak, M. J. Bobbitt, S. A. Lewis, A. M. S. Smith, and P. R. Robichaud. 2007. Post-fire burn severity and vegetation response following eight large wildfi res
across the western United States. Fire Ecology **3**:91-108.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943-1983.

Lindenmayer, D. B., and J. F. Franklin. 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington, D.C.

Margolis, E. Q., T. W. Swetnam, and C. D. Allen. 2007. A stand-replacing fire history in upper montane forests of the southern Rocky Mountains. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **37**:2227-2241.

McCarthy, P. M., and S. L. Yanoff. 2003. Biodiversity and altered fire regimes in forests and woodlands of the Rocky Mountain Division: A scientific assessment of threat, need, and opportunity. The Nature Conservancy, unpublished report.

McCune, B., and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science **13**:603-606.

McGarigal, K., and S. Cushman. 2005. The gradient concept of landscape structure. Pages 112-119 *in* J. Wiens and M. Moss, editors. Issues and Perspectives in Landscape Ecology. Cambridge University Press, Cambridge.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps.Available : www.umass.edu/landeco/research/fragstats/fragstats.html. University of Massachusetts, Amherst, MA.

McKenzie, D., Z. Gedalof, D. L. Peterson, and P. Mote. 2004. Climatic change, wildfire, and conservation. Conservation Biology **18**:890-902.

Meyer, G. A., and J. L. Pierce. 2003. Climatic controls on fire-induced sediment pulses in Yellowstone National Park and central Idaho: a long-term perspective. Forest Ecology and Management **178**:89-104.

Mielke, P. W., Jr., and K. J. Berry. 2001. Permutation methods: A distance function approach. Springer-Verlag, New York.

Millar, C. L., and W. B. Woolfenden. 1999. The role of climate change in interpreting historical variability. Ecological Applications **9**:1207-1216.

Miller, C. 2003. Simulation of the effects of climatic change on fire regimes. Pages 69-94 *in* T. T. Veblen, W. L. Baker, G. Montenegro, and T. W. Swetnam, editors. Fire and climatic change in temperate ecosystems of the western Americas. Springer, New York.

Moir, W. H., B. W. Geils, M. A. Benoit, and D. Scurlock. 1997. Ecology of southwestern ponderosa pine forests. Pages 3-27 *in* W. M. Block and D. M. Finch, editors. Songbird ecology in southwestern ponderosa pine forests: a literature review. United States Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Moir, W. H., and J. A. Ludwig. 1979. A classification of spruce fir and mixed habitat types of Arizona and New Mexico. Report RM 207, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Moody, J. A., D. A. Martin, S. L. Haire, and D. A. Kinner. 2007. Linking runoff response to burn severity after a wildfire. Hydrological Processes **on-line: http://www3.interscience.wiley.com/cgi-bin/abstract/116326625/ABSTRACT**.

Moore, M. M., D. W. Huffman, P. Z. Fulé, and W. W. Covington. 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. Forest Science **50**:162-176.

Morgan, P., G. E. Defosse, and N. F. Rodriguez. 2003. Management implications of fire and climate changes in the western Americas Pages 413-440 *in* T. T. Veblen, W. L. Baker, G. Montenegro, and T. Swetnam, editors. Fire and climatic change in temperate ecosystems of the western Americas. Springer, New York.

Nabhan, G. P. 1997. Cultures of habitat: on nature, culture, and story. Counterpoint, Washington, D. C.

National Climatic Data Center. 2006. Southwest Region Moisture Status: http://www.ncdc.noaa.gov/oa/climate/research/2006/jun/st107dv00pcp200606.html.

Oksanen, J., and P. R. Minchin. 2002. Continuum theory revisited: what shape are species responses along ecological gradients? Ecological Modeling **157**:119-129.

Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems **1**:535-545.

Pierce, J. L., G. A. Meyer, and A. J. T. Jull. 2004. Fire-induced erosion and millennialscale climate change in northern ponderosa pine forests. Nature **432**:87-90.

Ponge, J.-F., J. André, O. Zackrisson, N. Bernier, M.-C. Nilsson, and C. Gallet. 1998. The forest regeneration puzzle, biological mechanisms in humus layer and forest vegetation dynamics. Bioscience **48**:523-530.

Reneau, S. L., and E. V. McDonald. 1996. Landscape history and processes on the Pajarito Plateau, Northern New Mexico. Los Alamos National Laboratory Document No. LA UR 96 3035, Los Alamos, New Mexico.

Romme, W. H., E. H. Everham, L. E. Frelich, M. A. Moritz, and R. E. Sparks. 1998. Are large, infrequent disturbances qualitatively different from small, frequent disturbances? Ecosystems **1**:524-534.

Romme, W. H., and D. H. Knight. 1982. Landscape diversity: the concept applied to Yellowstone Park. Bioscience **32**:664-670.

Savage, M., P. M. Brown, and J. Feddema. 1996. The role of climate in a pine forest regeneration pulse in the southwestern United States. Ecoscience **3**:310-318.

Savage, M., and J. N. Mast. 2005. How resilient are southwestern ponderosa pine forests after crown fires? Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **35**:967-977.

Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. Bioscience **54**:661-676.

Shatford, J. P. A., D. E. Hibbs, and K. J. Puettmann. 2007. Conifer regeneration after forest fire in the Klamath-Siskiyous: How much, how soon? Journal of Forestry **April/May**:139-146.

Shinneman, D. J., and W. L. Baker. 1997. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in Ponderosa pine landscapes of the Black Hills. Conservation Biology **11**:1276-1288.

Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, New York.

Skau, C. M., R. O. Meeuwig, and T. W. Townsend. 1970. Ecology of eastside Sierra chaparral: a literature review. University of Nevada, Max C. Fleischmann College of Agriculture, Agricultural Experiment Station, Reno.

Stambaugh, M. C., and R. P. Guyette. 2008. Predicting spatio-temporal variability in fire return intervals using a topographic roughness index. Forest Ecology and Management **254**:463-473.

Strom, B. A., and P. Z. Fulé. 2007. Pre-wildfire fuel treatments affect long-term ponderosa pine forest dynamics. International Journal of Wildland Fire **16**:128-138.

Swetnam, T., and C. H. Baisan. 1996. Historical fire regime patterns in the southwestern United States since 1700. Pages 11-32 *in* C. D. Allen, editor. Fire effects in southwestern forests: Proceedings of the second La Mesa fire symposium. United States Forest Service General Technical Report RM-286, Los Alamos, New Mexico.

Swetnam, T. W., and J. L. Betancourt. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. Journal of Climate **11**:3128-3147.

Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems **1**:511-523.

Turner, M. G., and V. H. Dale. 1998. Comparing large, infrequent disturbances: what have we learned? Ecosystems **1**:493-496.

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. Landscape Ecology in Theory and Practice. Springer-Verlag, New York.

Turner, M. G., W. W. Hargrove, R. H. Gardner, and W. H. Romme. 1994. Effects of Fire on Landscape Heterogeneity in Yellowstone-National-Park, Wyoming. Journal of Vegetation Science **5**:731-742.

Turner, M. G., and W. H. Romme. 1994. Landscape Dynamics in Crown Fire Ecosystems. Landscape Ecology **9**:59-77.

Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs **67**:411-433.

Turner, M. G., W. H. Romme, and D. B. Tinker. 2003. Surprises and lessons from the 1988 Yellowstone fires. Frontiers in Ecology and the Environment **1**:351-358.

U.S. Forest Service. 2007. Fire Effects Information System www.fs.fed.us/database/feis/.

Van Wagner, C. E. 1983. Fire behavior in northern conifer forests and shrublands. Pages 65-80 *in* R. W. Wein and D. A. MacLean, editors. The role of fire in northern circumpolar ecosystems. John Wiley and Sons, New York.

Wallington, T. J., R. J. Hobbs, and S. A. Moore. 2005. Implications of current ecological thinking for biodiversity conservation: A review of the salient issues. Ecology and Society 10:[online] URL:
http://www.ecologyandsociety.org/vol10/iss1/art15/ **10**:16.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. Science **313**:940-943.

White, A. S. 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. Ecology **66**:589-594.

Whitlock, C. 2004. Forests, fires and climate. Nature **432**:28-29.

Wiens, J. A. 1989. Spatial Scaling in Ecology. Functional Ecology **3**:385-397.

Wimberly, M. C., and M. J. Reilly. 2007. Assessment of fire severity and species diversity in the southern Appalachians using Landsat TM and ETM plus imagery. Remote Sensing of Environment **108**:189-197.

Wolter, K., and M. S. Timlin. 1998. Measuring the strength of ENSO events: How does 1997/98 rank? Weather **53**:315-324.

Wood, S. N. 2000. Modeling and smoothing parameter estimation with multiple quadratic penalties. Journal of the Royal Statistical Society B **62 (Part 2)**:413-428.

Wood, S. N. 2006. Generalized Additive Models: An introduction with R. Chapman & Hall, Boca Raton, Florida.

Woodmencey, J. 2001. Weather in the Southwest. Southwest Parks and Monuments Association, Tucson, AZ.

Yee, T. W., and N. D. Mitchell. 1991. Generalized additive models in plant ecology. Journal of Vegetation Science **2**:587-602.