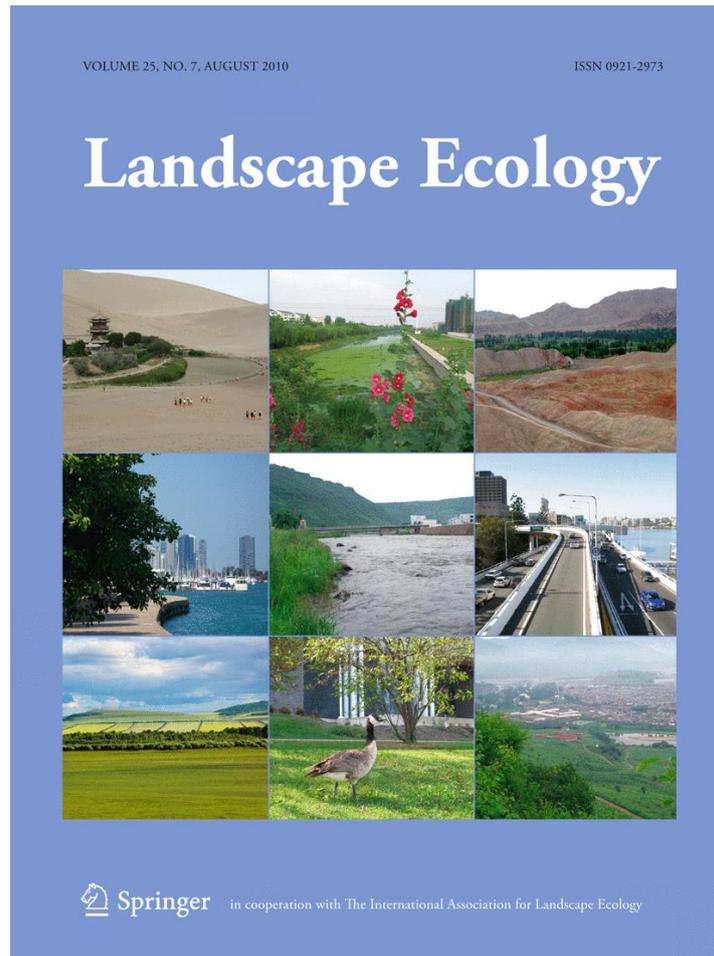


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Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (*Pinus ponderosa*) in New Mexico and Arizona, USA

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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, we 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. We 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, with the exception of a few cases in which

simpler models were equally well-supported by the data. Analysis of tree ages revealed slow progress in early post-fire years. Our observations suggest that populations spread in a moving front, as well as by remotely dispersed individuals. Based on our results, recent large fires cannot be summarily dismissed as catastrophic. We conclude that management should focus on the value and natural recovery of post-fire landscapes. Further, process centered restoration efforts could utilize our findings in formulating reference dynamics under a changing fire regime.

Keywords Spatial heterogeneity · Burn severity · Spatial scale · Forest recovery · Generalized linear models · Seed dispersal kernel · Forest age structure · Ecological restoration

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

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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. Our 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.

Our primary objective was to identify at what scale spatial patterns of severity influence ponderosa pine regeneration at La Mesa and Saddle Mountain. Therefore, we 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). We quantified the importance of spatial patterns in models that included several groups of variables: (1) subsequent burning, either prescribed or wildland fire events which can influence seedling survival (Moore et al. 2004); (2) physical environment (topographic variation including elevation) which creates a template of basic resources for germination and growth (Baird et al. 1999; Bonnet et al. 2005); and (3) the biotic environment, because it reflects neighborhood interactions that alter resource availability (Frelich 2002).

Lastly, our 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, our 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. We discuss the relevance of our 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 (Pierce et al. 2004; Westerling et al. 2006).

Methods

Study areas

Fires at our 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 twentieth 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 2000s (NCDC 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.). 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.

Quantifying burn spatial patterns

For both locations, we mapped high severity using aerial photography obtained within 4 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 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. We 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).

We derived three metrics to quantify spatial patterns of burning (Table 1, Fig. 1). First, the burn severity maps were used to calculate Euclidean distance (m) from each point (i.e., 10-m grid cell) within a high-severity patch to the nearest edge of lower severity. We defined the second metric, neighborhood severity, as the percent of the landscape that burned with high severity at different spatial scales (Fig. 1). We calculated neighborhood severity in circular windows of variable size centered at each grid cell; the window radius (100, 150, 200, 250, 300, 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 (Fig. 1). In order to reflect abundance of seed sources as it varied across the study site, we used a map of ponderosa pine cover to weight the kernel. Cover was mapped at La Mesa using post-fire (1981/1983) aerial photography by

Table 1 Variables included in model tests

	Description
Spatial variables	
Distance to edge of lower severity (m)	Euclidean distance from each point (i.e., 10-m grid cell) in high-severity patch to lower-severity edge
Seed dispersal kernel ^a scales (<i>h</i>): 50, 60, 70, 80, 90, 100, 150, 200, 300, 400	Kernel surface weighted by cover of ponderosa pine at the edge of high severity patches. Multiple scales (<i>h</i>)
Neighborhood severity (%) scales: 100, 150, 200, 250, 300, 400 m	Percent of the landscape around the sample point that is high severity (i.e., total tree mortality). Multiple scales defined by radius of moving window in meters
Physical variables	
Elevation (m)	Digital elevation model (http://nationalmap.gov/)
Topographic wetness index (TWI) ^b	Ratio of the slope to the specific catchment area (contributing area) based on digital elevation model
Radiation or heat load (MJ cm ⁻² year ⁻¹)	Potential annual direct incident radiation and heat load. Best derivation selected using AIC for each site, either aspect rotations folded about the north–south line such that NE = NW (radiation; La Mesa) or aspect folded about the NE-SW line (heat load; Saddle Mountain)
Topographic position	Classified relative to the local (plot context) condition: summit or mesa top, flat side-slope, shoulder, toe, or bottom
Disturbance variable	
Disturbance	Number of times an area burned subsequent to the La Mesa or Saddle Mountain fires. Based on records from the U.S. Forest Service and National Park Service
Biotic variables	
Ground cover (%)	Grass, forb, soil, rock, or organic: recorded along 2 50-m transects at 1-m intervals
Community characteristics: Total cover of resprouters (La Mesa); total cover of aspen (Saddle Mountain)	Cover of species which were predicted to interact with ponderosa pine regeneration: recorded along two 50-m transects at 1-m intervals
Ponderosa pine response variables	
Number of individuals ha ⁻¹ : regression response	In a variable-width belt along either side of the line transects: count of all ponderosa pine trees (seedlings, saplings, and adults). Age estimate based on whorl counts (see text for details)
Age estimate (years): graphical analysis	

All possible combinations of variables were compared in zero-inflated negative binomial models using Δ AIC

^a Programs written by B. W. Compton, University of Massachusetts, in APL + Win (version 6.0, APLNow, Brielle, New Jersey)

^b TauDem: Copyright (C) 2004 David Tarboton, Utah State University (<http://hydrology.neng.usu.edu/taudem/>)

Allen (1989); values ranged from 0 to 95%. A comparable map for Saddle Mountain, which we developed from aerial photography, was scaled categorically: 1 (<25% cover), 2 (25–60% cover), 3 (>60% cover). We used a Gaussian kernel but varied the smoothing parameter ($h = 50, 60, 70, 80, 90, 100, 150, 200, 300, 400$; Silverman 1986) to examine regeneration response across a range of different spatial scales (i.e., potential seed dispersal distance functions).

Physical environment and disturbance predictor variables

We measured the physical environment of the study areas using both digital map and field data (Table 1). We used digital elevation maps to model topographic wetness (TWI) and to calculate models of potential annual direct incident radiation and heat load (McCune and Keon 2002). In addition, we used digital fire history maps available from local land managers to

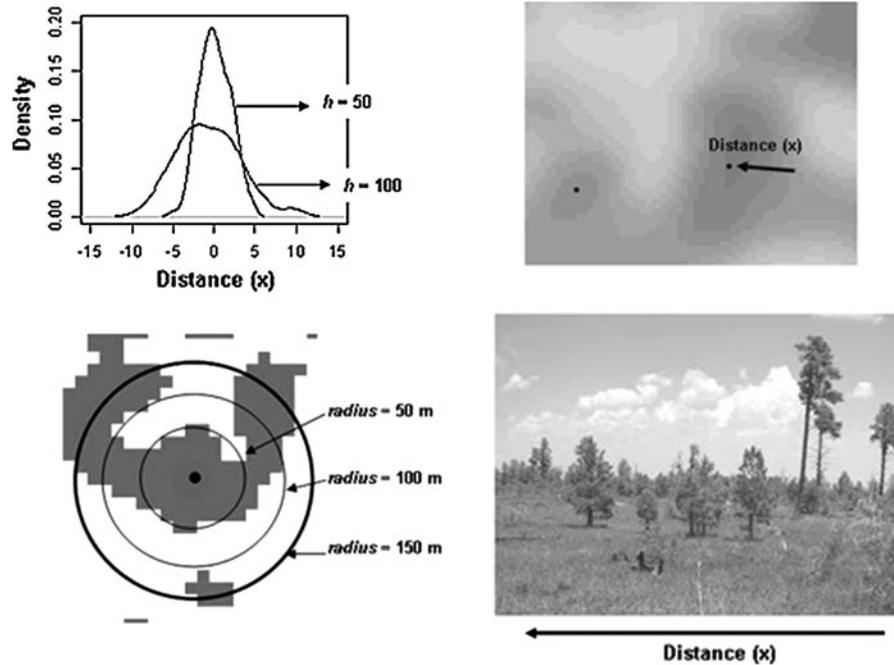


Fig. 1 Illustrations of spatial pattern metrics. *Lower right* Young trees growing at varying distance (x) from legacy seed trees (see background of the right side of the photo). *Lower left* Neighborhood severity, measured around a sample plot location (black dot) in windows that vary in scale; *Upper 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

determine the number of times areas subsequently burned. All data were mapped at 10 m resolution. At each 50-m diameter field plot (see below), we classified topographic position relative to local condition as summit, side-slope, shoulder, toe, or bottom.

Field sample locations were randomly chosen from the set of maximum (Euclidean) distances along a center “line” within each high-severity patch. Locations where tree planting was documented were avoided. We surpassed our goal of $n = 50$ sample plots (based on the general rule of thumb: at least 10 samples per variable for building regression models with a maximum of 5 predictor variables) with a final total of 68 plots at La Mesa and 79 plots at Saddle Mountain (Fig. 2). Field work was completed between 16 May and 30 June 2005.

Biotic environment and regeneration response variables

At each field plot, we 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. Aspen was abundant in the range of ponderosa pine at Saddle Mountain, while several species that tend to quickly resprout after fire were common at La Mesa (e.g. *Quercus* spp., *Robinia neomexicana*; Haire and McGarigal 2008). Because these species could affect resources for shade-intolerant pines, we included total cover of aspen and total cover of resprouters as variables in the analysis.

To determine tree density, we counted all individual ponderosa pine trees in a belt along either side of the 50-m 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 a representative sample in locations where trees were dense. Ponderosa pine trees were aged by counting branch whorls on each tree trunk; whorl-counting has been employed for similar purpose in previous studies; for example, Shatford et al. (2007) aged coniferous trees in regenerating forests of the Pacific Northwest using whorl counts. Whorl-counting was quick and

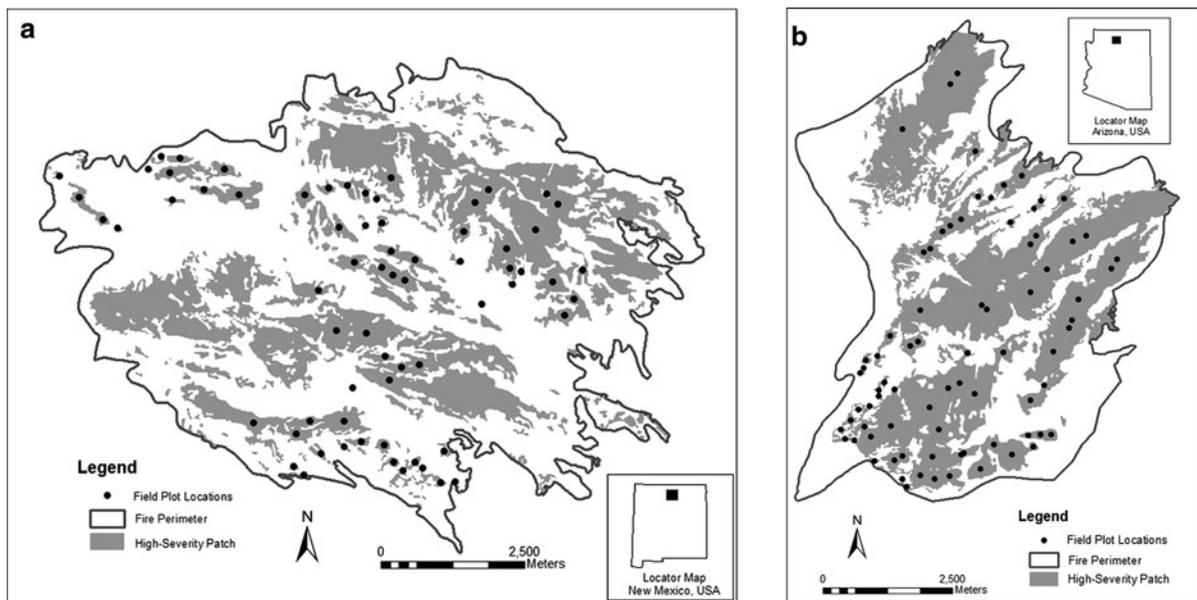


Fig. 2 Severity maps of (a) La Mesa (New Mexico, USA) and (b) Saddle Mountain (Arizona, USA). *Gray patches* symbolize areas where all trees were killed (high severity) based on pre- and post-fire aerial photography. Field plot locations (*black*

dots) were chosen randomly from the set of maximum (Euclidean) distances along a center ridge within each high-severity patch. Fire perimeters, provided by local land managers, represent the spatial extent of burning

efficient, given the open branch structure of ponderosa pine, and the relatively short stature of young trees. Trees were cored selectively (La Mesa, $n = 25$; Saddle Mountain, $n = 12$) to determine confidence in age estimates based on whorl counts.

Statistical analysis

We developed separate regression models for each of three groups of predictor variables: disturbance, physical, biotic. Then, we formulated a combined model containing variables from each of the original three models. In models with multiple predictors, we examined all possible additive combinations of variables to determine the best final model. The response variable was ponderosa pine individuals ha^{-1} calculated from tree counts within the belt transect. Two Saddle Mountain plots with extreme values for pine abundance were excluded from the analysis. Next, we added each of the spatial variables (seed dispersal kernel and neighborhood severity at each scale), in turn, to the disturbance model and to the best physical, biotic, and combined models.

We fit zero-inflated count models to the data (negative binomial with log link) using maximized

likelihood. Zero-inflated models are two-component mixture models that are useful when count data have excess zero counts; the negative binomial adjusts for over dispersion due to extra variation in the count data (Zuur et al. 2009). We chose the zero-inflated models because log-likelihood statistics indicated major improvement in results when compared with Poisson, negative binomial, and zero-inflated Poisson models. In our model results, the sum of fitted densities evaluated at zero using zero-inflated negative binomial models was roughly equal to the observed number of zeros in the data (La Mesa, $n = 18 \pm 0.2$; Saddle Mountain, $n = 51 \pm 0.1$).

Pearson's correlation coefficient (r) and Lin's concordance correlation coefficient (ρ) were calculated to measure goodness of fit between predicted and observed non-zero values for each model. The first statistic indicates linear dependence between variables, and the latter reflects deviation in the linear relationship from a diagonal line (Lin 1989). We employed these statistics to provide a sense of the general correlation and predictive ability of model results, recognizing their limitations in reflecting true agreement in data sets with different degrees of heterogeneity (Atkinson and Nevill 1997).

Model selection was based on minimized Akaike's Information Criterion (AIC). The AIC considers the likelihood of observed data given a particular model (i.e. goodness of fit), but also includes an objective 'penalty' that increases with the number of parameters used (i.e. complexity; Ginzburg and Jensen 2004). We used commonly accepted rules of thumb for judging model improvement: models with $\Delta\text{AIC} \leq 2$ have substantial support (evidence), $4 \leq \Delta\text{AIC} \leq 7$ indicates considerably less support, and models with $\Delta\text{AIC} > 10$ have essentially no support (Burnham and Anderson 2004). To examine the relative contribution of spatial variables, and assess scales of importance, we plotted ΔAIC for each of the original models, with and without an added spatial variable.

Finally, we 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, we 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, we 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 (R Development Core Team 2009) including the implementation of zero-inflated negative binomial models in the `pscl` package. For spatial analyses we used ArcInfo version 9.0 (Environmental Systems Research Institute, Redlands, California).

Results

La Mesa and Saddle Mountain were similar in terms of fire size, but differed in composition and configuration of burn severity (Table 2). 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. Both study landscapes had a large background matrix that burned at lower severity or did not burn at all, with many, small patches.

Analysis of ΔAIC for all additive combinations of physical and biotic variables resulted in fairly simple models at both sites (Tables 3, 4). Saddle Mountain especially stood out in this regard; best-supported physical and biotic models contained a single predictor, with two-parameter models in close competition. Elevation and TWI were important factors in physical models of regeneration at both sites, and neighborhood variables (i.e., resprouter cover and aspen cover) held their place in competing biotic models. In the best combined models, subsequent disturbance added important information at both sites, and physical and biotic predictors were retained.

The biotic model had the best fit for La Mesa; fit of all models was improved when a spatial variable was added based on r and ρ (Table 3). Saddle Mountain combined model was the best fit and the addition of a spatial variable likewise contributed to better fit (Table 4). Lower values of ρ for Saddle Mountain

Table 2 Landscape characteristics of the study areas calculated within fire perimeters

For patch size, the mean is followed by minimum and maximum values in parentheses

Landscape characteristics	La Mesa	Saddle Mountain
Total area burned (ha)	5,745	4,060
High severity (%)	34	48
High-severity patches (n)	190	45
High-severity patch size (ha)	10 (0.08, 634)	43 (0.11, 947)
Lower-severity-patches (n)	150	96
Lower-severity-patch size (ha)	25 (0.01, 3673)	22 (0.01, 2047)

Table 3 The AIC and Δ AIC are given for competing physical, biotic, and combined models (Δ AIC \leq 4) resulting from analysis of La Mesa data

Model		AIC	Δ AIC	Pearson's r	Lin's ρ
Disturbance					
Number of subsequent burns		721.80	NA	0.37 (0.39; 0.54)	0.19 (0.28; 0.36)
Physical model					
Elevation	TWI	709.79	0.00	0.33 (0.50; 0.55)	0.29 (0.38; 0.44)
Elevation	Topographic position	713.37	3.58		
Elevation	Topographic position	713.64	3.85		
Biotic model					
Organic ground cover		708.57	2.24		
Organic ground cover	Resprouter cover	706.34	0.00	0.86 (0.88; 0.86)	0.68 (0.82; 0.81)
Combined					
Number of subsequent burns elevation	TWI	701.32	1.83		
Elevation	TWI	699.48	0.00	0.60 (0.73; 0.78)	0.50 (0.53; 0.57)

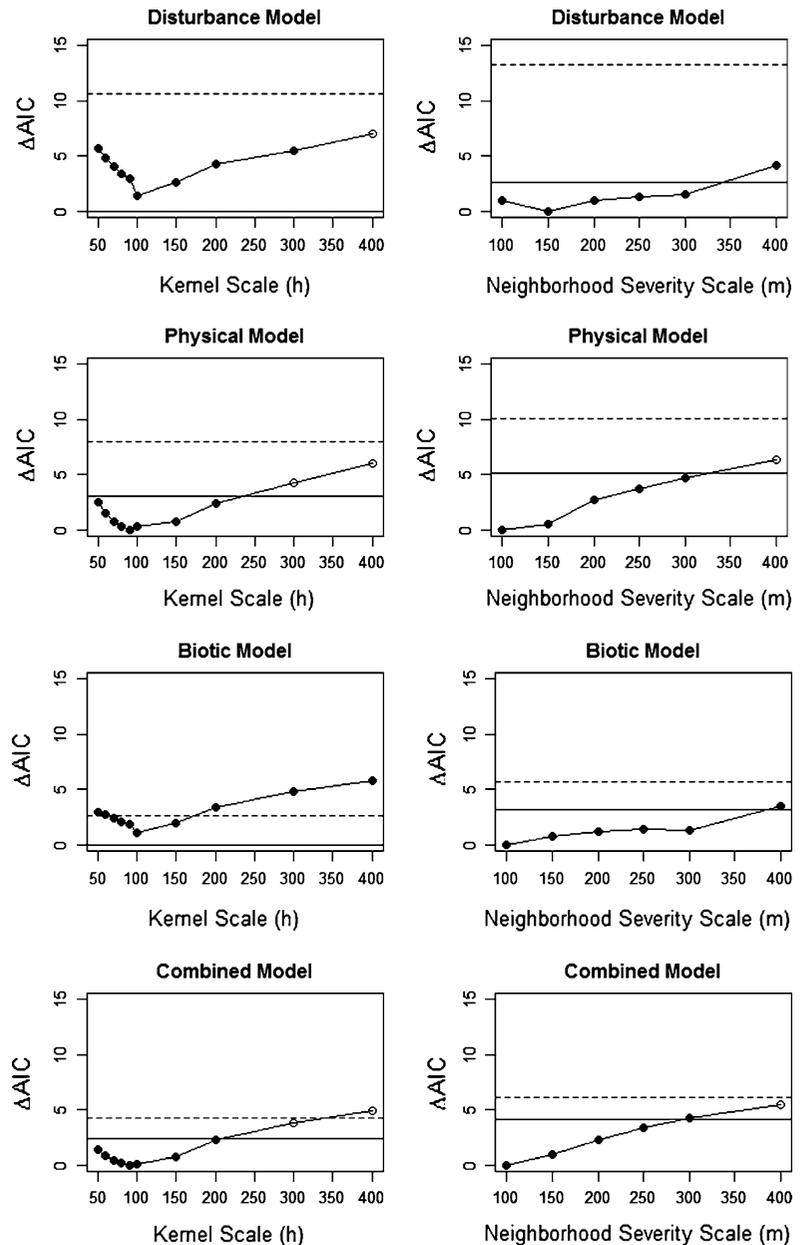
The best physical, biotic, and combined models, as well as the disturbance model, were used to test the benefit of adding a spatial variable (see Fig. 3). Pearson's correlation coefficient (r) and Lin's concordance correlation coefficient (ρ) are presented as goodness of fit measures for the best models. Given in parentheses are the values of these statistics for models with seed dispersal and neighborhood severity added at the best scale (kernel model; neighborhood severity model)

Table 4 The AIC and Δ AIC are given for competing physical, biotic, and combined models (Δ AIC \leq 4) using the data from Saddle Mountain

Model		AIC	Δ AIC	Pearson's r	Lin's ρ
Disturbance					
Number of subsequent burns		394.46	NA	0.36 (0.66; 0.82)	0.06 (0.20; 0.24)
Physical					
Elevation	TWI	389.38	2.00		
Elevation	Heat load	387.62	0.24		
Elevation		387.38	0.00	0.51 (0.71; 0.76)	0.11 (0.21; 0.20)
Biotic					
Rock ground cover		390.98	0.00	0.50 (0.67; 0.77)	0.11 (0.19; 0.22)
Rock ground cover	Aspen cover	392.85	1.86		
Combined					
Number of subsequent burns	Elevation	382.31	1.98		
Rock ground cover					
Number of subsequent burns	Elevation	380.33	0.00	0.66 (0.65; 0.81)	0.20 (0.23; 0.23)

The best physical, biotic, and combined models, as well as the disturbance model, were used to test the benefit of adding a spatial variable (see Fig. 4). Pearson's correlation coefficient (r) and Lin's concordance correlation coefficient (ρ) are presented as goodness of fit measures for the best models. Given in parentheses are the values of these statistics for models with seed dispersal and neighborhood severity added at the best scale (kernel model; neighborhood severity model)

Fig. 3 La Mesa model comparisons: ΔAIC values for disturbance, physical, biotic, and combined models without inclusion of a spatial variable are represented by a *dashed line* and ΔAIC with addition of distance to lower severity edge is shown as a *solid horizontal line*. The ΔAIC values for models where a seed dispersal kernel or neighborhood severity variable was added are shown as a *curved line*; significant scales ($P < 0.05$) are marked with a *filled circle*, non-significant scales with an *open circle*



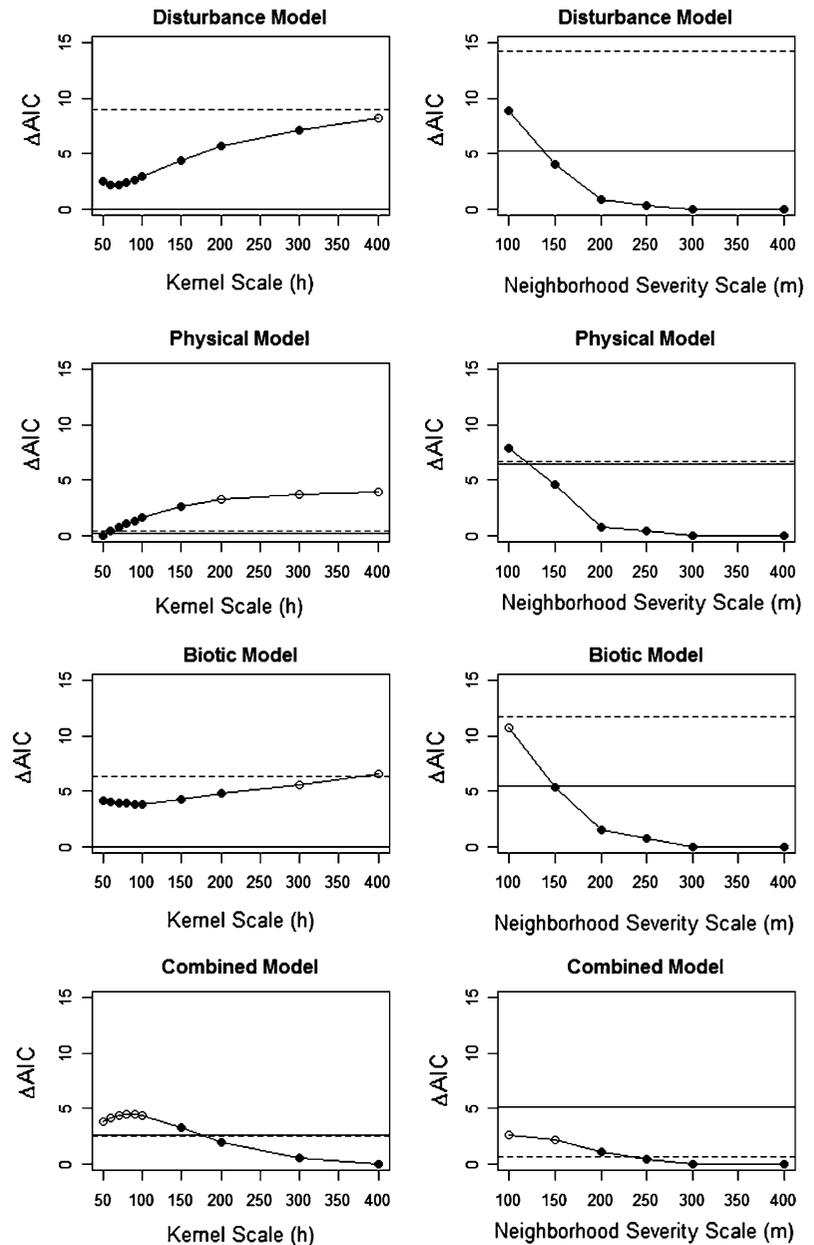
models could reflect poor agreement, but evaluation of the influence of the small sample of non-zero values ($n = 26$) and influence of data homogeneity (Atkinson and Nevill 1997) would be necessary to further assess these results.

Particular scales in seed dispersal kernel and neighborhood severity models added significant information to disturbance, physical, biotic and combined models for La Mesa. Kernel scales where $h = 90$ or 100 provided the most improvement over

original models, but several scales were significant ($P < 0.05$) in all models (Fig. 3). Biotic and combined models showed the least improvement through addition of a kernel variable. The best scale for neighborhood severity fell between 100 and 150 m; the full model at the best scale represented a major improvement over original models ($\Delta AIC \geq 6$).

La Mesa models containing distance to edge of lower severity were close competitors with the best seed dispersal kernel and neighborhood severity

Fig. 4 Saddle Mountain model comparisons: Δ AIC values for disturbance, physical, biotic, and combined models without inclusion of a spatial variable are represented by a *dashed line* and Δ AIC with addition of distance to lower severity edge is shown as a *solid horizontal line*. The Δ AIC values for models where a seed dispersal kernel or neighborhood severity variable was added are shown as a *curved line*; significant scales ($P < 0.05$) area marked with a *filled circle*, non-significant scales with an *open circle*



models, with one exception (Fig. 3). The distance model Δ AIC was approximately five units greater than the best physical-neighborhood severity model at 100 m; thus, the distance model was not well supported by the data. All other models with the distance variable were within three Δ AIC units of the best scaled variable model.

Saddle Mountain models also exhibited improvement when seed dispersal kernel or neighborhood

severity predictors were added, with some exceptions (Fig. 4). The most model improvement was noted when the seed dispersal kernel at $h = 60$ was added to the disturbance model. Biotic, physical, and combined models showed little or no improvement at any kernel scale, even though kernel predictors were often significant ($P < 0.05$). Models with neighborhood severity, however, were generally better than original models at Saddle Mountain

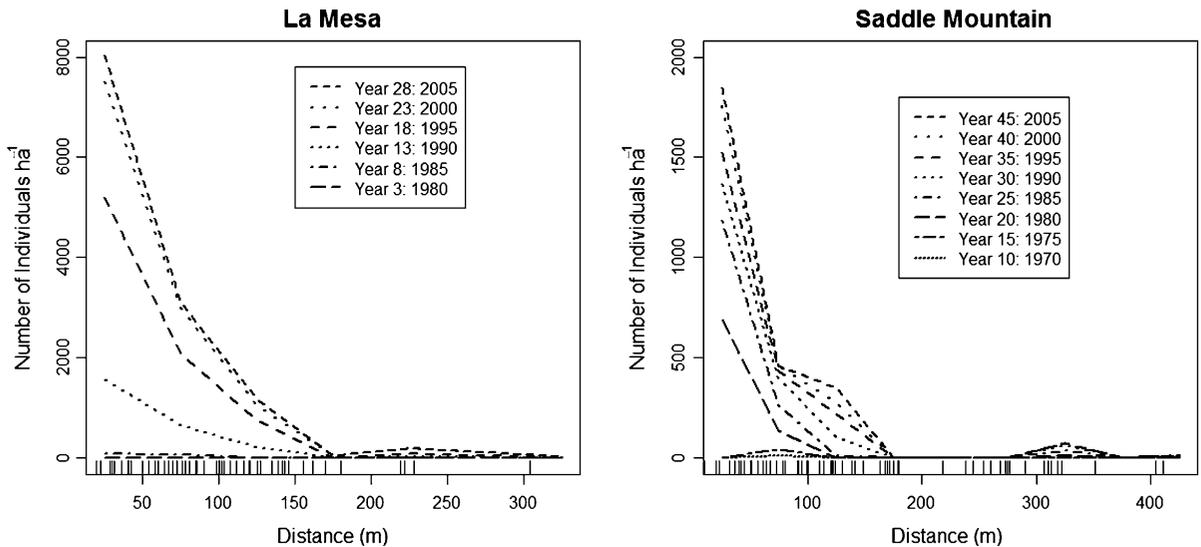


Fig. 5 Cumulative regeneration (number of individuals ha^{-1}) through time, plotted across the gradient of distance to edge of lower severity at La Mesa (left) and Saddle Mountain (right). Observations were binned within 50-m distance intervals.

(Fig. 4). Neighborhood severity scales that added the most information were 300–400 m. Combined models were an exception; ΔAIC was nearly the same with or without addition of a neighborhood severity predictor.

At Saddle Mountain, the addition of distance to edge of lower severity to original models resulted in ΔAIC values close to the best seed dispersal kernel models in most cases (Fig. 4). Biotic models containing a kernel variable showed marked improvement over the model with distance added; this was true across scales ($h = 50\text{--}100$; $\Delta\text{AIC} \approx 4$). The addition of neighborhood severity consistently produced models that were better supported than those containing distance to lower severity edge.

Total productivity and density of trees differed between the two sites, with cumulative total number of trees at lowest distances much greater at La Mesa ($\sim 8,000$ trees ha^{-1} at La Mesa; $\sim 2,000$ trees ha^{-1} at Saddle Mountain; Fig. 5). 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 1–8 at La Mesa, and year 1–15 at Saddle Mountain),

Vertical lines along the x-axis represent locations of field plots. Post-fire years correspond to the descending sequence of dashed lines

but approximately 5–15 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 the 2005 field season 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, indicated by narrow intervals between dashed lines (Fig. 5).

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 (Fig. 5). 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. 1988–1995). 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}).

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 our 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 we used to quantify spatial pattern all contributed unique information in relation to other factors, 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. In some cases, the inherent scaling of the distance variable provided a measure of spatial heterogeneity that was at least as good as the other, explicitly scaled variables. The neighborhood severity metric 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 that 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 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 et al. (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.

Our results indicated that spatial patterns of burning interact with subsequent disturbance, the physical environment, and the biotic neighborhood in complex ways. For example, the original biotic models at both sites were comparable to those with the added kernel variable at the best scale (Figs. 3, 4). Available seed sources are only one component of successful regeneration; neighborhood conditions, defined by resprouters that come back quickly after fire, evidently played an equally important role in determining ponderosa pine distribution. This interpretation is consistent with the idea that resprouters “capture” a site in areas of fire-induced tree mortality in some places (Allen et al. 2002; Savage and Mast 2005). However, models that incorporate spatial and temporal dynamics are necessary to fully understand 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 our estimates, either few seedlings originated or few survived until approximately 5–10 years post-fire at either site. Years 5–15 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 2000–2004. 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). Our 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 we employed approaches zero rapidly with distance, predicting spread of individuals from the frontier of the population (Clark et al. 1999). Theoretically, our data would be better fit with a fat-tailed kernel model that accommodates regeneration from long-distance dispersal.

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. Our 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 we observed, young forests could inhabit distances over 200 m from edge of lower severity in approximately 15 years from the date of our 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. Because our spatial methodologies differentiate this study from those using evidence from historical data and undisturbed sites, it is difficult to compare the forest structure we observed to reference conditions (Fulé et al. 1997; Moore et al. 1999). However, our observations at La Mesa and Saddle Mountain demonstrated that ponderosa pine forests with diverse density and age structure can naturally return after severe fire.

We encourage those concerned with restoration of areas burned in recent large fires to 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 have been solely defined by composition and structure (Fulé et al. 1997; Moore et al. 1999), 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-equilibrium systems, including large fires (Wallington et al. 2005). Our 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.

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References

- Agee JK (1998) The landscape ecology of western forest fire regimes. *Northwest Sci* 72:24–34
- Allen CD (1989) Changes in the landscape of the Jemez Mountains, New Mexico. Dissertation, University of California, Berkeley
- Allen CD, Savage M, Falk DA, Suckling KF, Swetnam TW, Schulke T, Stacey PB, Morgan P, Hoffman M, Klingel JT (2002) Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecol Appl* 12:1418–1433
- Atkinson G, Nevill A (1997) Comment on the use of concordance correlation to assess the agreement between two variables. *Biometrics* 53:775–777
- Baird M, Zabowski D, Everett RL (1999) Wildfire effects on carbon and nitrogen in inland coniferous forests. *Plant Soil* 209:233–243
- Beschta RL, Rhoades JJ, Kauffman JB, Gresswell R, Minshall GW, Karr JR, Perry DA, Hauer FR, Frissell CA (2004) Postfire management on forested public lands of the western United States. *Conserv Biol* 18:957–967
- Bonnet VH, Schoettle AW, Shepperd WD (2005) Postfire environmental conditions influence the spatial pattern of regeneration for *Pinus ponderosa*. *Can J For Res* 35:37–47
- Burnham KP, Anderson DR (2004) Multimodel inference. *Soc Methods Res* 33:261–304
- Choi YD (2007) Restoration ecology to the future: a call for a new paradigm. *Restor Ecol* 15:351–353
- Clark JS (1998) Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *Am Nat* 152:204–224
- Clark JS, Ji Y (1995) Fecundity and dispersal in plant-populations—implications for structure and diversity. *Am Nat* 146:72–111
- Clark JS, Beckage B, Camill P, Cleveland B, HilleRisLambers J, Lichter J, McLachlan J, Mohan J, Wyckoff P (1999) Interpreting recruitment limitation in forests. *Am J Bot* 86:1–16
- Clark JS, Lewis M, Horvath L (2001) Invasion by extremes: population spread with variation in dispersal and reproduction. *Am Nat* 157:537–554
- Clark JS, Lewis M, McLachlan JS, HilleRisLambers J (2003) Estimating population spread: what can we forecast and how well? *Ecology* 84:1979–1988
- Cooper CF (1960) Changes in vegetation, structure, and growth of south-western pine forests since white settlement. *Ecol Monogr* 30:130–164
- Covington WW (2000) Prescribed fire is not the issue. *J For* 98:48
- Covington WW, Fulé PZ, Hart SC, Weaver RP (2001) Modeling ecological restoration effects on ponderosa pine forest structure. *Restor Ecol* 9:421–431
- Delcourt HR, Delcourt PA, Webb T (1983) Dynamic plant ecology: the spectrum of vegetation change in space and time. *Quart Sci Rev* 1:153–175
- Dellasala DA, Williams JE, Williams CD, Franklin JF (2004) Beyond smoke and mirrors: a synthesis of fire policy and science. *Conserv Biol* 18:976–986
- Falk DA (2006) Process-centered restoration in a fire-adapted ponderosa pine forest. *J Nat Conserv* 14:140–151
- Franklin JF, Lindenmayer DB, MacMahon JA, McKee A, Magnusson J, Perry DA, Waide R, Foster DR (2000) Threads of continuity: ecosystem disturbances, biological legacies and ecosystem recovery. *Conserv Biol Pract* 1:8–16
- Frelich LE (2002) Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press, New York
- Frelich LE, Reich PB (1995) Spatial patterns and succession in a Minnesota Southern-Boreal forest. *Ecol Monogr* 65:325–346
- Fulé PZ, Covington WW, Moore MM (1997) Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecol Appl* 7:895–908
- Ginzburg LR, Jensen CXJ (2004) Rules of thumb for judging ecological theories. *Trends Ecol Evol* 19:121–126
- Guisan A, Edwards TC Jr, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol Modell* 157:89–100
- Haire SL, McGarigal K (2008) Inhabitants of landscape scars: succession of woody plants after large, severe forest fires in Arizona and New Mexico. *Southwest Nat* 53:146–161
- Hopkins RL (1990) Kaibab formation. In: Beus SS, Morales M (eds) Grand Canyon geology. Oxford University Press, New York, pp 225–245
- Kashian DM, Tinker DB, Turner MG, Scarpace FL (2004) Spatial heterogeneity of lodgepole pine sapling densities following the 1988 fires in Yellowstone National Park, Wyoming, USA. *Can J For Res* 34:2263–2276
- Kokaly RF, Rockwell BW, Haire SL, King TVV (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 Sens Environ* 106:305–325
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1983
- Lin L (1989) A concordance correlation coefficient to evaluate reproducibility. *Biometrics* 45:255–268
- Lindenmayer DB, Franklin JF (2002) Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington

- McCune B, Keon D (2002) Equations for potential annual direct incident radiation and heat load. *J Veg Sci* 13:603–606
- McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS: spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst, MA. www.umass.edu/landeco/research/fragstats/fragstats.html. Accessed Oct 2009
- Mielke PW Jr, Berry KJ (2001) Permutation methods: a distance function approach. Springer, New York
- Moore MM, Covington WW, Fulé PZ (1999) Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecol Appl* 9:1266–1277
- Moore MM, Huffman DW, Fulé PZ, Covington WW (2004) Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. *For Sci* 50:162–176
- NCDC (2006) National Climatic Data Center: southwest region moisture status. <http://www.ncdc.noaa.gov/oa/climate/research/2006/jun/st107dv00pcp200606.html>. Accessed Oct 2009
- Paine RT, Tegner MJ, Johnson EA (1998) Compounded perturbations yield ecological surprises. *Ecosystems* 1:535–545
- Pierce JL, Meyer GA, Jull AJT (2004) Fire-induced erosion and millennial-scale climate-change in northern ponderosa pine forests. *Nature* 432:87–90
- Reneau SL, McDonald EV (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 WH, Everham EH, Frelich LE, Moritz MA, Sparks RE (1998) Are large, infrequent disturbances qualitatively different from small, frequent disturbances? *Ecosystems* 1:524–534
- Savage M, Mast JN (2005) How resilient are southwestern ponderosa pine forests after crown fires? *Can J For Res* 35:967–977
- Savage M, Brown PM, Feddema J (1996) The role of climate in a pine forest regeneration pulse in the southwestern United States. *Ecoscience* 3:310–318
- Shatford JPA, Hibbs DE, Puettmann KJ (2007) Conifer regeneration after forest fire in the Klamath-Siskiyou: how much, how soon? *J For* 105:139–146
- Silverman BW (1986) Density estimation for statistics and data analysis. Chapman and Hall, New York
- Swetnam TW, Betancourt JL (1998) Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *J Clim* 11:3128–3147
- R Development Core Team (2009) R: a language and environment for statistical computing. <http://www.R-project.org>. ISBN-3-900051-07-0
- Turner MG, Hargrove WW, Gardner RH, Romme WH (1994) Effects of fire on landscape heterogeneity in Yellowstone-National-Park, Wyoming. *J Veg Sci* 5:731–742
- Turner MG, Romme WH, Gardner RH, Hargrove WW (1997) Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecol Monogr* 67:411–433
- Turner MG, Baker WL, Peterson CJ, Peet RK (1998) Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* 1:511–523
- Turner MG, Romme WH, Tinker DB (2003) Surprises and lessons from the 1988 Yellowstone fires. *Front Ecol Environ* 1:351–358
- Wallington TJ, Hobbs RJ, Moore SA (2005) Implications of current ecological thinking for biodiversity conservation: a review of the salient issues. *Ecol Soc* 10:10–16. <http://www.ecologyandsociety.org/vol10/iss1/art15/>. Accessed Oct 2009
- Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western US forest wildfire activity. *Science* 313:940–943
- White AS (1985) Presettlement regeneration patterns in a southwestern ponderosa pine stand. *Ecology* 66:589–594
- Wiens JA (1989) Spatial scaling in ecology. *Funct Ecol* 3:385–397
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York