Patterns of pine regeneration following a large, severe wildfire in the mountains of southern California

Janet Franklin and Erin Bergman

Abstract: We examined establishment patterns of pines following a large, severe wildfire in the Peninsular Ranges of southern California, USA. The October 2003 Cedar Fire caused 98% pine mortality. In this study, we asked (*i*) where did seedlings establish and survive in formerly forested areas of the Cuyamaca Mountains 5 years following the high severity fire and (*ii*) what factors were associated with the spatial pattern of seedling establishment? Factors analyzed were pre-fire vegetation type, fire severity, post-fire vegetation characteristics, topography (slope, aspect, and elevation), and mapped soil type. We used a unique belt-transect survey method following the existing trail network that resulted in a representative sample of post-fire environments. Almost 1300 100 m × 20 m quadrats were searched in 2008–2009, one third of which supported juvenile pines. Regeneration primarily consisted of Coulter pine (*Pinus coulteri* D. Don), a weakly serotinous pine that was establishing at densities of 5–2320/ha on half of the quadrats where it had occurred pre-fire. *Pinus coulteri* regenerated in areas burned at high severity where pre-fire pine cover was high and its abundance was positively associated with higher elevation and cover of bare soil. In contrast, minimal regeneration of nonserotinous pines occurred patchily in areas that were not severely burned.

Résumé : Nous avons étudié les patrons d'établissement du pin à la suite de grands feux de forte intensité dans les chaînes péninsulaires du sud de la Californie, aux États-Unis. Le feu Cedar, en octobre 2003, a provoqué la mort de 98 % des pins. Dans cette étude, nous nous sommes demandés (*i*) où se sont établis et ont survécu les semis dans les anciennes zones forestières des montagnes Cuyamaca 5 ans après le feu de forte intensité et (*ii*) quels étaient les facteurs associés au patron spatial d'établissement des semis? Les facteurs qui ont été analysés sont le type de végétation avant le passage du feu, l'intensité du feu, les caractéristiques de la végétation après le feu, la topographie (pente, orientation et altitude) et le type de sol cartographié. Nous avons utilisé une méthode unique d'inventaire par transect en bande qui suivait le réseau existant de sentiers, ce qui a produit un échantillon représentatif des habitats après feu. Parmi les quelque 1300 quadrats de 100 m × 20 m examinés en 2008 et 2009, le tiers comportait des pins au stade juvénile. La régénération était surtout composée de *Pinus coulteri* D. Don, un pin faiblement sérotineux qui s'est établi à des densités variant de 5 à 2 320 semis à l'hectare dans la moitié des quadrats où il était présent avant le feu. *Pinus coulteri* s'est établi aux endroits où le feu a été très intense et où le couvert de pin avant le feu était élevé, alors que son abondance était positivement associée à l'altitude et au couvert de sol nu. À l'opposé, une régénération minimale de pins non sérotineux s'est établie de façon sporadique dans les endroits qui n'ont pas été sévèrement brûlés.

[Traduit par la Rédaction]

Introduction

Large, intense forest fires have become increasingly prevalent in western North America in recent decades primarily in response to climate (although fire exclusion, harvesting, and fuels treatment may also play a role), and this trend will likely continue (Westerling et al. 2006; Millar et al. 2007; Miller et al. 2009). Understanding a forest's ability to regenerate after a severe, stand-replacing fire is therefore vital to making effective management decisions, especially concerning the need for forest restoration and salvage logging (Beschta et al. 2004; Stephens and Ruth 2005; Hutto 2008). While widespread globally, conifer forests are locally restricted to the upper elevations of southern California's Mediterranean-type environment. Information on post-fire recovery in these forest systems is particularly lacking. The 2003 Cedar Fire in the mountains of San Diego County, USA, provided a unique opportunity to examine patterns of conifer forest regeneration following a large, severe fire and to better understand forest dynamics in a landscape subjected to extensive, infrequent natural disturbance (Turner et al. 1998).

Starting 25 October 2003, the Cedar Fire burned approximately 113 000 ha over a 10 day period. Most of the burned area comprised chaparral shrublands (Keeley et al. 2004). However, this study focuses on the 10 520 ha Cuyamaca Rancho State Park (CRSP) because, of the 5700 ha of conifer forest burned in the Cedar Fire, almost all of it occurred within CRSP. Vegetation in the CRSP exhibits an array of life forms (grassland 10% of the area, shrubland 49%, woodland 8%, and forest 32%) and is composed of species with different life histories and fire responses. These life forms occur in a fine-scaled spatial mosaic typical of many Mediterranean-type ecosystems. This forest–shrubland ecotone has probably experienced a heterogeneous fire regime (Agee 1998; Schoennagel et al. 2004). Therefore, large, stand-replacing fires in the study area, while historically uncommon and poorly understood, may not be unprecedented (Keeley and Zedler 2009). Recent studies have shown that the combined spatial heterogeneity of both vegetation and disturbance strongly affects patterns of post-fire succession (Turner et al. 1997; Keeley 1998; Crawford et al. 2001; Haire and McGarigal 2008). The purpose of this study was to determine if there were geographical patterns of post-fire pine establishment in conifer forests burned by the megafire and to identify factors associated with the spatial patterns and abundances of establishing pines 5 years after the fire.

Wildfires can promote seedling recruitment in pines by decreasing competition from other species (Mirov 1967), although pine species have a variety of responses to fire. Among the pines found in the study area, Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), ponderosa pine (*Pinus ponderosa* P. & C. Lawson), and sugar pine (*Pinus lambertiana* Dougl.) are nonsprouting, nonserotinous pines. *Pinus jeffreyi*, *P. ponderosa*, and Coulter pine (*Pinus coulteri* D. Don) have thick bark when mature and self-pruning protects them from fire-caused mortality (e.g., they are "fire resisters" when large), while *P. lambertiana* is more susceptible to fire-caused death as an adult (Keeley and Zedler 1998; Borchert et al. 2002). Further, while pines generally establish in high-light environments on mineral soils with little litter cover, some species such as *P. lambertiana* have a greater degree of shade tolerance (Keeley and Zedler 1998).

Pinus coulteri is endemic to the California Floristic Province and is found in the mountains of southwest California and northern Baja California, Mexico. Cone serotiny in this species is highly variable (Vale 1979); *P. coulteri* individuals have primarily nonserotinous cones when found in woodland populations, but in chaparral, *P. coulteri* has a higher proportion of serotinous cones (Borchert 1985). In chaparral, branches extend near the ground whereas in the woodland habitat, self-pruning occurs (Zobel 1953). When crown fires move through *P. coulteri* stands embedded in chaparral, synchronized seed release from closed cones often follows. As a result, pine populations in chaparral tend to be even-aged, while populations in woodland environments tend to have a more uneven-aged structure because seeds are continuously being dispersed (Borchert 1985) and can establish in the interval between fires. *Pinus coulteri* reaches maturity around 10 years and in a woodland environment will produce seeds every 3–6 years (Krugman and Jenkinson 1974). *Pinus coulteri* has the largest seeds with wings in the Pinaceae and, unlike the other two members of the subsection Sabinianae,

Torrey pine (*Pinus torreyana* Parry ex Carr.) and gray pine (*Pinus sabiniana* Dougl. ex Dougl.), which are wingless, *P. coulteri* seeds are wind dispersed although they are not carried great distances (Borchert et al. 2003; Johnson et al. 2003).

Several species of small mammals and birds are important seed dispersers and predators for all pines found in the study area (Vander Wall 1992; Borchert et al. 2003; Johnson et al. 2003; Thayer and Vander Wall 2005). Animals scatter hoard pine seeds, which, if they fail to relocate them, sometimes results in seedling establishment (Vander Wall et al. 2006). Distances that seeds are scatter hoarded range from tens of metres for rodents to several hundreds of metres, or even kilometres, for corvids.

Fire histories based on dendrochronological analysis of fire scars from CRSP and nearby mountain peaks indicate that most fires occurred in midsummer through autumn (scars in dormant wood) and that fire frequency decreased around the mid-20th century (Skinner et al. 2006; Everett 2008). The 2003 Cedar Fire was a severe crown fire throughout much of the forested landscape of CRSP (Goforth and Minnich 2008), resulting in almost 100% conifer mortality except for small, scattered patches (Franklin et al. 2006).

Based on the pine ecology and fire history of the study area, we expected the spatial distribution of post-fire pine seedling establishment and survival to be related to the local severity of the fire, the proximity of unburned forest patches acting as seed sources, the efficacy of seed dispersal, and the fire response of the pine species in CRSP. Specifically, we expected that, because it can be serotinous, *P. coulteri* would likely regenerate in areas that it dominated before the fire even, if it was severely burned, and establish seedlings in the growing season immediately following the fire. On the other hand, we expected little regeneration by the other three pine species in severely burned sites (all adults killed) as well as those distant from any seed source, although these nonserotinous pines may have established in any year following the fire.

Methods

Study area and species

CRSP (32° 56′N, 116°34′W) is located in the Cuyamaca Mountains, Peninsular Ranges, California, USA. The area has a Mediterranean-type climate with primarily hot, dry summers and cool, moist winters with some convective summer precipitation. Average annual precipitation is 800 mm, minimum temperature is 4.3 °C, and maximum temperature is 19.1 °C (1948–2005, Western Regional Climate Center). CRSP spans an elevation range of 740–1996 m and supports a mosaic of chaparral, pine and oak woodland, mixed coniferous forest, grasslands, and riparian vegetation (California Department of Parks and Recreation 1986). The dominant conifers in the forested portions of CRSP are *P. jeffreyi* below 1500 m and *P. coulteri* between 1250 and 1700 m (Krofta 1995). Mixed conifer forest, defined by the presence of incense cedar (*Calocedrus decurrens* (Torr.) Florin) and white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) with occasional *P. lambertiana* and *P. ponderosa*, occurs above 1600 m. A key geographical pattern of forest types in CRSP is that lower-elevation *P. jef-*

Fig. 1. Juvenile pine distribution at Cuyamaca Rancho State Park based on a 2008 survey of 1230 quadrats. Each symbol represents the presence of juvenile pine in a quadrat. The park (solid line) was divided into east and west areas (broken line) based on the distribution of post-fire pine species: *Pinus coulteri* (triangles) and *Pinus lambertiana* (squares with a dot) on the west side and *Pinus jeffreyi* (circles) on the east side. Crosses are quadrats surveyed throughout formerly forested areas where no juvenile pines were found.
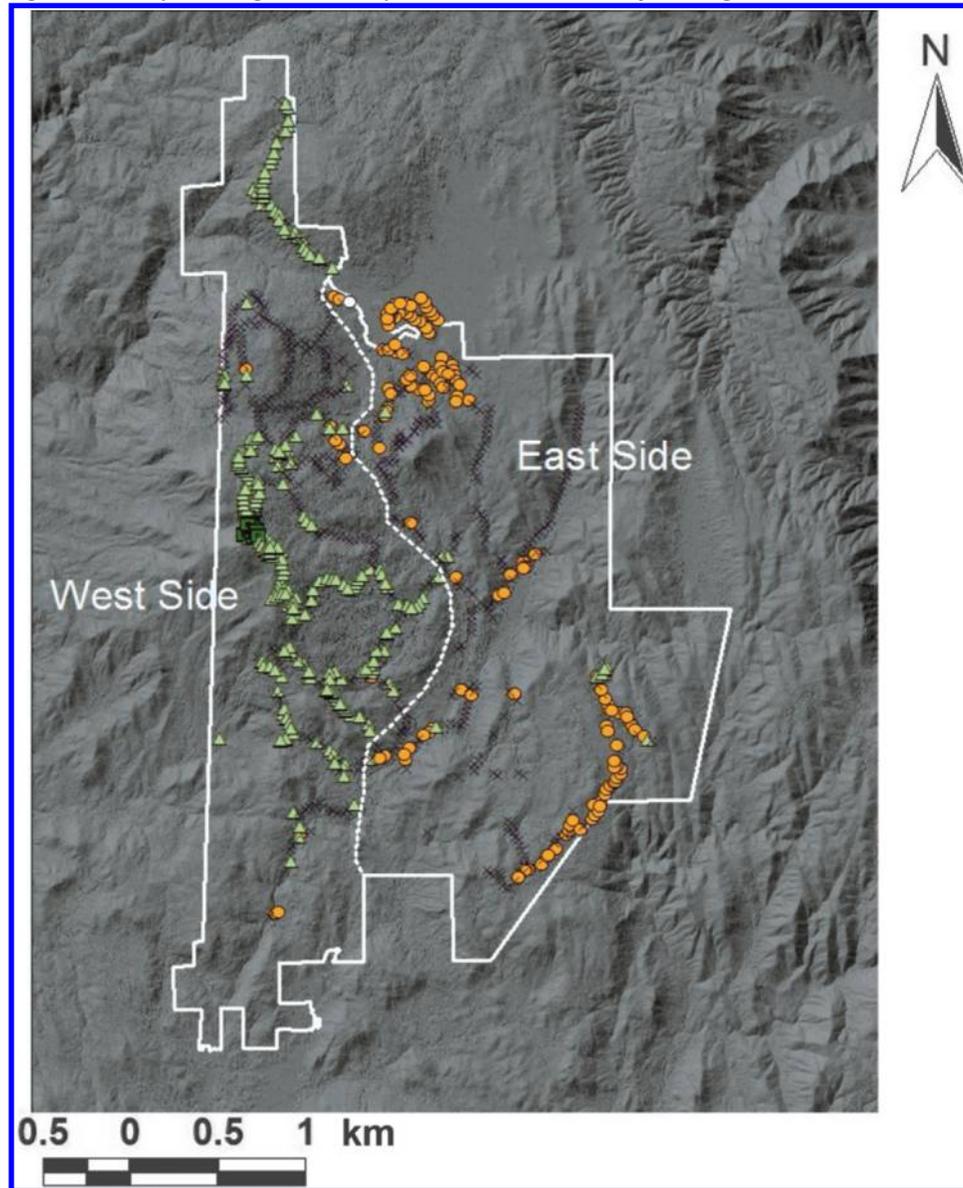
freyi woodland is found in the central (Sweetwater River Valley) and southeastern portions of CRSP, in the rain shadow of the Cuyamaca Mountains, while the mid- to higher-elevation *P. coulteri* woodland and mixed conifer forest is found in the western part of CRSP, on the slopes of the Cuyamaca Mountains (Fig. 1).

In addition to species-specific fire response, other factors examined for their influence on pine establishment included post-fire vegetation cover, topography, and soil type. We expected that shade-intolerant pines would be establishing in areas with little or no post-fire vegetation whereas species that are more shade tolerant (e.g., *P. lambertiana*) would regenerate in a variety of site conditions. Elevation, slope angle, and slope aspect are correlated with plant distributions owing to their relationship with temperature, radiation balance, and available moisture (Beers et al. 1966; Meentemeyer et al. 2001) and these topographic factors were correlated with the pre-fire distribution of tree species in the study area (Krofta 1995). Therefore, we examined these factors because our imperfect knowledge of pre-fire forest composition was based on generalized vegetation maps and post-fire observations (forensic botany). We also suspected that underlying soil type may have influenced patterns of pine establishment and survival.

Data collection methods

Earlier post-fire vegetation surveys in CRSP were based on a stratified random sample of forty 1 ha plots but this design

detected virtually no pine regeneration (Franklin et al. 2006; Franklin 2010). On the other hand, extensive field reconnaissance suggested that regeneration was extremely patchy, so we devised a sampling method based on strategies used to detect rare plants (Keith 2000) to describe spatial patterns of pine regeneration over the large and inaccessible study area. In 2008, 5 years post-fire, we established belt transects along every trail and fire road ("trails" hereafter for brevity) that intersected formerly forests areas of CRSP. Trails were used for rapid movement allowing us to survey large areas because the extremely high density of off-trail vegetation (Franklin 2010) made random sampling virtually impossible. The belt-transect strategy was our only means of conducting a spatially extensive survey with reasonable effort (supplementary material, Fig. S1).[1] In another study of post-fire seedling establishment, Turner et al. (2003) used a similar sampling strategy. They confirmed in their study area that an extensive network of trails thoroughly sampled the topographic and other major environmental gradients.

In this study, we tested our sample to verify that it was representative of important environmental gradients (Gillison and Brewer 1985; Austin and Heyligers 1989). Trails were divided into 100 m segments in a geographic information system (GIS). Each segment was used to define the midline of 20 m × 100 m quadrats (supplementary material, Fig. S2).[1] In the field, each quadrat was located using a global positioning system (GPS) and delineated using a laser range finder or a tape measure, and the entire area was thoroughly searched for juvenile pines by at least two field workers (the trail itself was not included in the quadrat area; the two halves of the quadrat extended 10 m from each edge of the trail). "Juvenile pines" in this study refers to seedlings and saplings that established after the 2003 fire, i.e., those that were up to 4 years old in 2008. To maximize the detection of juvenile pines, we placed two additional 20 m × 100 m quadrats, one on each side, of any quadrat containing at least one juvenile in a form of adaptive cluster sampling (Thompson and Seber 1996).

Next, this entire sample was overlain onto a map of 16 environmental strata that were defined by combinations of elevation, slope, aspect, and fire severity, via classification and overlay of GIS maps, to determine if the sample gave proportional representation to all of the strata (supplementary material, Fig. S3).[1] Finally, to achieve a proportional sample for statistical inference of the factors associated with pine establishment, we assigned additional randomly located quadrats to environmental strata that were undersampled. No environmental strata were undersampled by >5%; however, two large classes were undersampled by 3%–4.6% (supplementary material, Table S1)[1] and 41 additional quadrats were randomly located within those two strata to reduce the undersampling to <3% in all classes, increasing the overall sample size by about 3%.

It was difficult to distinguish the species of juvenile *P. coulteri, P. jeffreyi*, and *P. ponderosa* past the distinctive cotyledon stage because all have three needles per fascicle and look similar. In those cases where they could not be positively identified, three-needled juveniles were assigned a species label based on the cones or seeds found nearest to them.

Pine juveniles found in quadrats with no cones were recorded as an unknown species (seven cases) and excluded from analyses. This imperfect method added some noise to our analyses, but it was a reasonable approach to classifying juveniles given the scope of our survey.

Juvenile abundance was based on stem counts within quadrats. Height was measured or estimated to the nearest 10 cm and then averaged for each species in each quadrat. Clumps of juveniles were a clear indication that seedlings germinated from animal caches. In this study, we defined a clump as two or more seedlings spaced <2 cm apart at the root collar (S. Vander Wall, personal communication, 9 April 2008). Nevertheless, these estimates of juveniles originating from seed caches were conservative, since many seedlings also germinate from single-seed caches (Borchert et al. 2002).

Environmental correlates of juvenile establishment that were measured in the field were vegetation cover and fire severity. Cover, the proportional area of the ground covered by the vertical projection of the canopy (Jennings et al. 1999), was visually estimated for shrubs and herbs. Nonoverlapping cover of substrate (bare soil) and leaf litter were also visually estimated. In addition, pre-fire tree cover was roughly estimated based on density of (burned) adult trunks. The percent cover of dominant species in each vegetation stratum (those together comprising 90% of cover) was also recorded. All cover estimates were made by at least two observers who divided the quadrats into 10 m × 10 m sections and then summed the estimates for each section. While these were large quadrats, we consider this method to have yielded reliable estimates of relative cover.

In the field, fire severity was recorded based on fire effects on the adult pines in each quadrat using three ordered classes: low, moderate, and high severity. High severity was defined by no living adult pines. Moderate severity was assigned if some green needles were found on at least one adult pine in the quadrat. Low severity was designated if 50% or more of the adult pines in the quadrat were still alive. Although this classification is very coarse compared with others (Hessburg et al. 2007; McKenzie et al. 2007), a more detailed field assessment of fire severity was not possible because the observations were made 4–5 years post-fire. Field data were primarily collected in May–June 2008 and the supplemental random sample was collected in April 2009.

Environmental data gathered from maps were also examined for their correlation with pine regeneration. Digital vegetation, soil, fire severity, and terrain maps were overlain onto quadrat locations to extract values for pre-fire vegetation type, soil type, mapped fire severity, elevation, slope, and aspect. Classes for categorical mapped variables were aggregated based on their similarity, creating classes that were more evenly represented in the sample. For example, the vegetation types annual grass, perennial grass, and wet meadow were combined into one life form category, "grass" (details in Bergman 2009).

Fire severity within the burn area was mapped from pre-fire and post-fire Landsat-5 Thematic Mapper scenes (Wahab-Twibell 2008). This map, while of coarser spatial resolution than our field assessment, provided an alternative

---

[1]Supplementary data are available with the article through the journal Web site (http://www.nrcresearchpress.com/cjfr).

estimate of fire severity that was based on imagery collected directly after the Cedar Fire. Average elevation, slope, and aspect for each quadrat were derived from a 10 m resolution digital elevation model. Aspect was transformed for subsequent analysis (because it is on a circular scale) using these formulas: Northness = cos(aspect) and Eastness = sin(aspect) (Beers et al. 1966).

Data analysis

The abundance of juveniles was mapped and the average height of juveniles, number of whorls, and number cached were compared for the east versus the west side of CRSP and among different species of pine. The division of the study area into east and west regions (Fig. 1) differentiated *P. coulteri* dominated forest on the west side from *P. jeffreyi* forest on the east side (California Department of Parks and Recreation 1986). The survey revealed that only *P. coulteri* was abundant enough for statistical analysis of factors related to juvenile establishment.

Abundance data were zero inflated, with a larger proportion of zeros than expected from the standard error models used with generalized linear models (GLMs) (Barry and Welsh 2002), a common problem with species abundance data (McCullagh and Nelder 1989). Analysis of abundance was therefore based on a subset of observations, only those quadrats with *P. coulteri* abundance greater than zero. Abundance data were right skewed and a natural logarithm transformation was used (Quinn and Keough 2002).

Simple linear regressions and generalized additive models (GAMs) were developed for abundance data, while simple logistic regression models and GAMs were used for occurrence (presence and absence) data to test the relationship of each individual predictor to each response variable and to suggest nonlinear response functions prior to fitting stepwise multiple regression models. Predictors that had P values <0.05 in the simple models were then included in a stepwise multiple logistic regression model of *P. coulteri* occurrence. The Bayesian information criterion was used as the model selection criterion (Quinn and Keough 2002). Then, a multiple GAM (with binominal error distribution specified to estimate a logistic model) was fit using the variables selected in the logistic regression to characterize nonlinear responses in the multiple-predictor model of occurrence (Yee and Mitchell 1991).

A stepwise multiple linear regression was developed in the same way for the log-transformed abundance data. A multiple GAM was fit using the Poisson distribution to describe the error function of the untransformed count data to characterize nonlinear response functions. All GAMs used splines as the smoothing function with 4 target degrees of freedom (Wood 2006).

Because of the spatially contiguous nature of the belt-transect data, spatial autocorrelation of each statistical model's residuals was calculated within neighborhoods (spatial lags) defined by the two nearest quadrats of any observation based on Moran's I statistic (Moran 1948) whose significance was estimated by Monte Carlo simulation. Diagnostics were calculated for the model of abundance to indicate the nature of spatial dependence in the model; these included the simple Lagrange multiplier (LM) test for error dependence (LMerr), the simple LM test for a missing spatially lagged

dependent variable (LMlag), variations of these tests that are robust to the presence of the other (RLMerr and RLMlag), and a test for both (SARMA, which is LMerr + RLMlag) (Anselin and Rey 1991). Then, because both kinds of spatial dependence effects were detected, spatial error and spatial lag linear models were estimated and their fit and coefficients were compared with those of the nonspatial model.

Spatial autocorrelation was also detected in logistic regression residuals, and therefore, an autocovariate regression model of presence–absence was estimated (Augustin et al. 1996). A new explanatory variable, the autocovariate, was created based on the inverse-distance weighted average of the neighboring values of the response variable (juvenile presence–absence) for each observation (the average number of quadrats with juveniles present within 100 m). The neighborhood distance was defined as 100 m, corresponding roughly to maximum dispersal distances for *P. coulteri* as well as the average distance between neighboring quadrats. Spatial modeling was carried out using the spdep (Bivand 2002) package in the R statistical software (R Development Core Team 2007).

Results

Patterns of regeneration

In total, 1271 quadrats were surveyed in areas of CRSP that supported adult pines pre-fire. Of these, at least one juvenile pine was found in 435 of the quadrats and a total of 7032 juvenile pines were recorded. Within quadrats where juveniles were detected (count was nonzero), their density ranged from 5 to 2320/ha (average ± 1 SD: 86 ± 186/ha), and across all quadrats, average juvenile density was 28 ± 115/ha. Pre-fire (1992) average seedling densities of 28/ha were reported for the study area (Krofta 1995).

On the west side (Fig. 1), 46% of 880 quadrats contained juvenile pines (overall density 41 ± 138/ha). We recorded 6564 *P. coulteri* and 348 *P. lambertiana* juveniles but only 30 *P. jeffreyi* on the west side, and cached (clustered) individuals comprised 12% of all individuals (Table 1). On the east side, 391 quadrats were surveyed, only 6% of them with juveniles (91 juveniles total, overall density 1 ± 7/ha), mostly *P. jeffreyi*. On the east side, no cached juveniles were found and no cached *P. jeffreyi* juveniles were found anywhere. No *P. ponderosa* juveniles were positively identified in this study, although living adults and cones were found on the Burnt Pine and Azalea Glenn Trails. Our extensive survey revealed the spatial heterogeneity of pine regeneration in CRSP. Some areas (Conejos Trail and Airplane Ridge) have locally high densities of *P. coulteri* juveniles, while other areas (Middle Peak) show very little pine regeneration (supplementary material, Fig. S4).[1]

Pinus coulteri juveniles were taller, with more whorls, and cached more frequently than *P. jeffreyi* and *P. lambertiana* (Table 2). All *P. lambertiana* juveniles occurred in a cluster of 18 quadrats near Cuyamaca Peak (Fig. 1) and were found in mixed conifer forest on stony supan loam soils in areas of low to moderate burn severity with high forest canopy cover at 1850–1900 m elevation. Most *P. jeffreyi* juveniles were located in east-side *P. jeffreyi* forest on sandy soils between elevations of 1240 and 1534 m where fire severity ranged from high to low.

Table 1. Frequency and count of juvenile pines found in surveyed quadrats in the west versus east sides (Fig. 1) of Cuyamaca Rancho State Park.

Survey	Total	West	East
Plots surveyed	1271	880	391
Plots with juveniles (cached)	433 (101)	409 (101)	24 (0)
No. of juveniles (cached)	7032 (835)	6941 (835)	91 (0)
No. of *Pinus coulteri* (cached)	6574 (777)	6563	11
No. of *Pinus lambertiana* (cached)	348 (58)	348	0
No. of *Pinus jeffreyi* (cached)	110 (0)	30	80

Note: Frequency and number of cached individuals (as defined in the text) shown in parentheses.

Table 2. Summary of condition of juveniles and the environment in surveyed quadrats in the west versus east sides (Fig. 1) of Cuyamaca Rancho State Park.

	West		East	
Variable	Mean	Range	Mean	Range
Height, all juveniles (cm)	78	5–200	38	10–70
Height, juvenile *Pinus coulteri* (cm)	75	20–200		
Height, juvenile *Pinus lambertiana* (cm)	20	6–60		
Whorls, all juveniles (*N*)	3	0–5	2	0–3
Whorls, *Pinus coulteri* (*N*)	3	0–5		
Whorls, *Pinus lambertiana* (*N*)	1	0–3		
Cover, adult pine (%)	20	0–95	16	0–65
Cover, *Ceanothus palmeri* (%)	27	0–100	9	0–60
Cover, trees (%)	51	0–100	41	0–90
Cover, shrubs (%)	50	0–100	37	0–100
Cover, herbs (%)	34	0–100	59	0–100
Cover, bare soil (%)	13	0–95	4	0–100
Elevation (m)	1475	1105–1962	1455	1235–1690

Note: Cover of trees is an estimate of pre-fire conditions and cover of shrubs, herbs, and bare soil is based on post-fire (2008) visual assessment.

Table 3. Multiple logistic regression of *Pinus coulteri* presence and absence, contrasting coefficients, and their significance for nonspatial logistic regression versus autologistic model (autocovariate is the frequency of *P. coulteri* juvenile neighbors).

	Logistic regression			Autologistic regression		
Predictor	Coefficient	SE	*P*	Coefficient	SE	*P*
Adult pine cover	0.047	0.006	<0.001	0.035	0.007	<0.001
Ceanothus palmeri cover	–0.022	0.003	<0.001	–0.011	0.004	0.006
VEG, Coulter pine	1.641	0.444	<0.001	0.458	0.626	0.464
VEG, shrub	1.086	0.415	0.009	0.289	0.597	0.627
VEG, Jeffrey pine	0.270	0.391	0.498	–0.249	0.566	0.660
VEG, mixed conifer	–0.226	0.420	0.590	–0.422	0.461	0.490
VEG, oak–hardwood	–0.207	0.440	0.639	–0.131	0.627	0.834
Fire severity, high	1.809	0.408	<<0.001	1.198	0.505	0.018
Fire severity, mid	1.063	0.437	0.015	0.699	0.536	0.193
Elevation	0.003	0.001	<<0.001	0.001	0.001	0.236
Autocovariate				3.916	0.261	<<0.001

Note: VEG, mapped pre-fire vegetation categories (with their names given). Fire severity based on field estimates.

Factors related to occurrence of *P. coulteri* juveniles

Pinus coulteri occurrence (presence) was most likely in areas of high field-estimated fire severity, high elevation, high pre-fire cover of adult pine and post-fire exposure of bare soil, and low post-fire cover of the dominant shrub Palmer ceanothus (*Ceanothus palmeri* Trel.) ($P < 0.05$). Oc-currence was also associated with some soil and vegetation types (details in Bergman 2009). Northness, Eastness, slope, cover of herbs, and total pre-fire tree cover were not significantly related to *P. coulteri* occurrence.

The stepwise multiple logistic regression of *P. coulteri* occurrence retained pre-fire cover of pine, post-fire *C. palmeri*

Fig. 2. Results of a multiple generalized additive model for *Pinus coulteri* juvenile presence–absence based on smoothing splines for continuous variables showing the response function (and standard error (broken lines)) relating the log-odds ratio of juvenile occurrence (*y*-axes) to each predictor (*x*-axes). For categorical variables, horizontal lines show the median and 5th and 95th percentiles. The "rug" at the bottom of each plot shows the distribution of values of the response variable. ADULT_PINE, estimated pre-fire pine cover (%); CEAN_PALME, post-fire cover of the shrub *Ceanothus palmeri* (%); VEG_TYPE, mapped vegetation class (CP, Coulter pine; G, grass; JP, Jeffrey pine; MC, mixed conifer; OH, oak–hardwood; S, shrub); FIRE_FIELD, fire severity class estimated in the field (high, low. and mid (moderate)); ELEVATION, elevation (m).
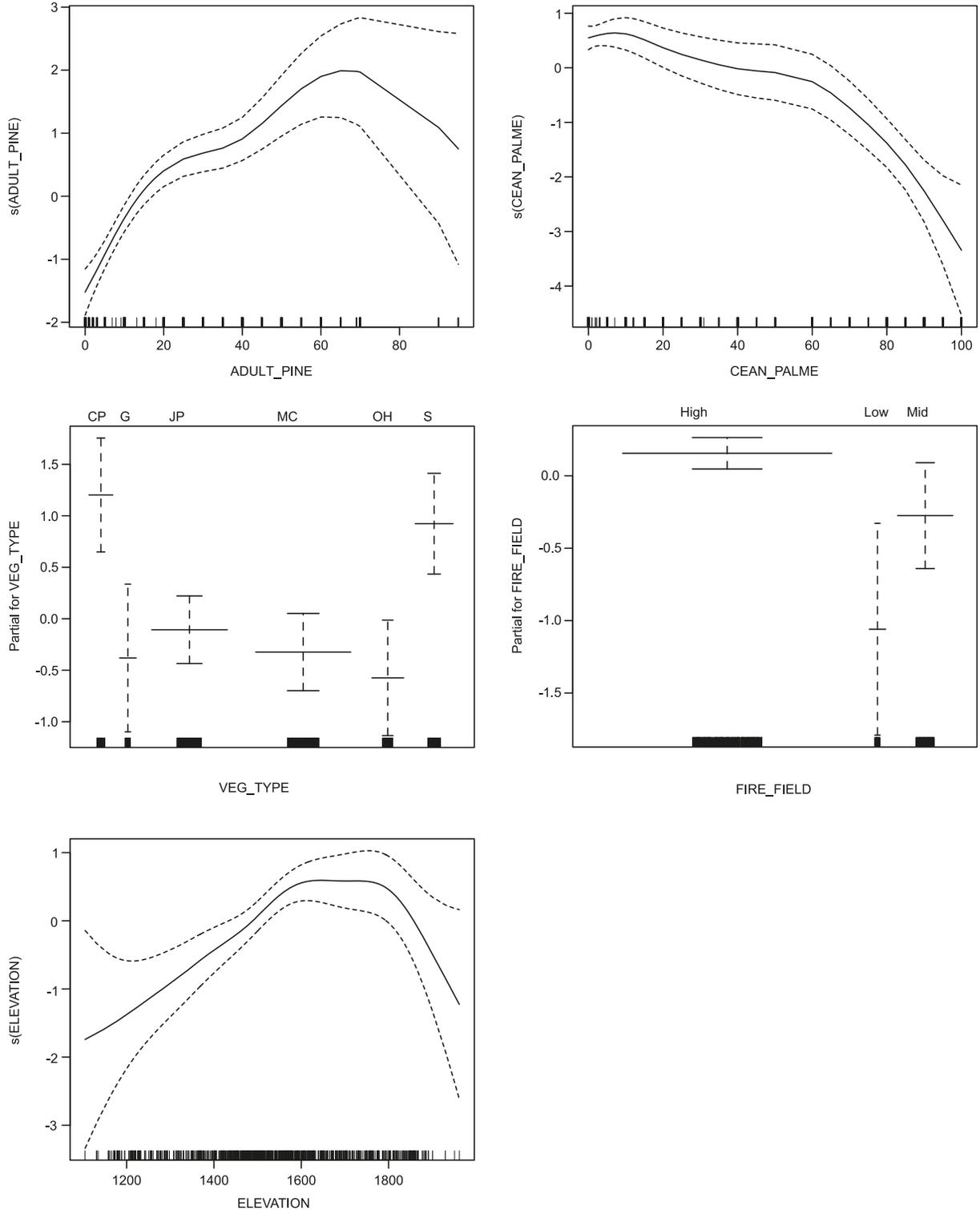
Table 4. Coefficients of nonspatial and spatial (error and lag) linear models of *Pinus coulteri* abundance and their significance.

Predictor	Coefficient	SE	*t* or *z*	*P*
Generalized linear model (AIC = 1196)				
Intercept	–2.371	0.675	–3.512	<0.001
Bare soil cover	0.017	0.004	4.352	<<0.001
Ceanothus palmeri cover	–0.008	0.003	–3.343	<0.001
Elevation	0.003	0.0004	5.465	<<0.001
Spatial error model (AIC = 1182)				
Intercept	–2.169	0.803	–2.700	0.007
Bare soil cover	0.0189	0.005	4.031	<<0.001
Ceanothus palmeri cover	–0.008	0.003	–2.659	0.008
Elevation	0.002	0.0005	4.334	<<0.001
Spatial lag model (AIC = 1172)				
Intercept	–1.276	0.686	–1.860	0.063
Bare soil cover	0.013	0.004	–3.360	<0.001
Ceanothus palmeri cover	–0.006	0.002	–2.287	0.022
Elevation	0.001	0.0005	2.929	0.003
Lag abundance	0.335	0.064	5.251	<<0.001

cover, pre-fire vegetation type, fire severity, and elevation as predictors (Table 3). This model had moderate discriminative ability (area under curve of receiver operating characteristic plot = 0.82), and considerable variability in juvenile occurrence remained unexplained (adjusted R^2 = 0.25). The multiple GAM based on the same predictors (area under curve = 0.85, adjusted R^2 = 0.30) revealed that the relationships between the likelihood of juvenile presence and the three continuous predictor variables were significantly nonlinear (P << 0.001 based on a χ^2 test). The response to *C. palmeri* cover was negative but nonlinear, becoming more steeply negative when shrub cover is >60% (Fig. 2). The location of pre-fire mapped *P. coulteri* forest was positively associated with juvenile establishment (Table 3); *P. coulteri* juveniles were positively associated with high fire severity (estimated in the field) and most likely to establish where there were intermediate values of pre-fire pine cover (50%–80%) and at 1600–1800 m elevation (Fig. 2).

Residuals from the multiple logistic regression and GAM were significantly (P < 0.001) spatially autocorrelated up to 200–400 m distance based on Monte Carlo simulation. The coefficient of an autocovariate of *P. coulteri* juvenile occurrence was significant and positive: quadrats with juveniles were found near other quadrats with juveniles (Table 3). Cover of pre-fire adult pine in the quadrat was still significantly positively related to juvenile occurrence, cover of post-fire *C. palmeri* remained significantly negatively correlated, and high fire severity remained weakly positively associated in the autologistic model. However, all environmental predictors were less significant than in the nonspatial model (Table 3), as is expected from theory (Fortin and Dale 2005). Vegetation type and elevation were no longer significantly related to juvenile occurrence once the nearby occurrence of other juvenile pines was accounted for. The occurrence of juveniles was concentrated along ridges and at high elevations on the west side of CRSP, but it is not possible to determine if elevation (or the physical factors it acts as a surrogate for) was actually a causal factor. The entire study

area is within the range of elevations at which *P. coulteri* was found in CRSP pre-fire (Krofta 1995).

### Factors related to abundance of *P. coulteri* juveniles

Many of the same predictors were related to the abundance *P. coulteri* as to presence, with cover of bare soil and elevation being the most important. Northness was also positively related to abundance. The final stepwise GLM (adjusted R^2 = 0.37) indicated that only elevation and percent cover of bare soil cover were strongly positively correlated and *C. palmeri* cover negatively correlated with abundance of juveniles (Table 4). The Poisson GAM of abundance (adjusted R^2 = 0.38) indicated that relationships between the juvenile abundance and the predictor variables were significantly nonlinear (P << 0.001 based on a χ^2 test). The response curves (Fig. 3) suggest that in those plots where *P. coulteri* juveniles are present, the relationship of abundance to bare soil cover is strongly positive up to 25%, above which abundance remains high. The relationship between *C. palmeri* cover and juvenile abundance is steeply negative between 0% and 20%, above which abundance remains low. Elevation had a positive, nearly linear relationship to abundance.

Residuals from the linear models of abundance model were spatially autocorrelated at 100 m distance (one lag). The diagnostic tests indicated both spatial lag and spatial error dependence (P < 0.001). The spatial error and spatial lag models that were developed both had lower Aikake's information criterion than the linear model, and spatial autocorrelation in the residuals of the spatial lag model was no longer significant. Estimated coefficients and their significance values were lower than for the GLM, but the magnitude of the change was small, and all three variables remained significant predictors (P < 0.05) (Table 4). This suggests that the results of the GLM are robust in spite of spatial autocorrelation.

Discussion

Severe fire has not extirpated pine populations at CRSP. *Pinus coulteri* is patchily regenerating where *P. coulteri* for-

Fig. 3. Results of a multiple generalized additive model for *Pinus coulteri* juvenile abundance based on smoothing splines showing the response function relating the log abundance (Poisson model) of juvenile abundance (*y*-axes) to each predictor (*x*-axes). The "rug" at the bottom of each plot shows the distribution of values of the response variable. SUBSTRATE, bare ground cover (%); ELEVATION, elevation (m); CEAN_PALME, post-fire cover of the shrub *Ceanothus palmeri* (%).
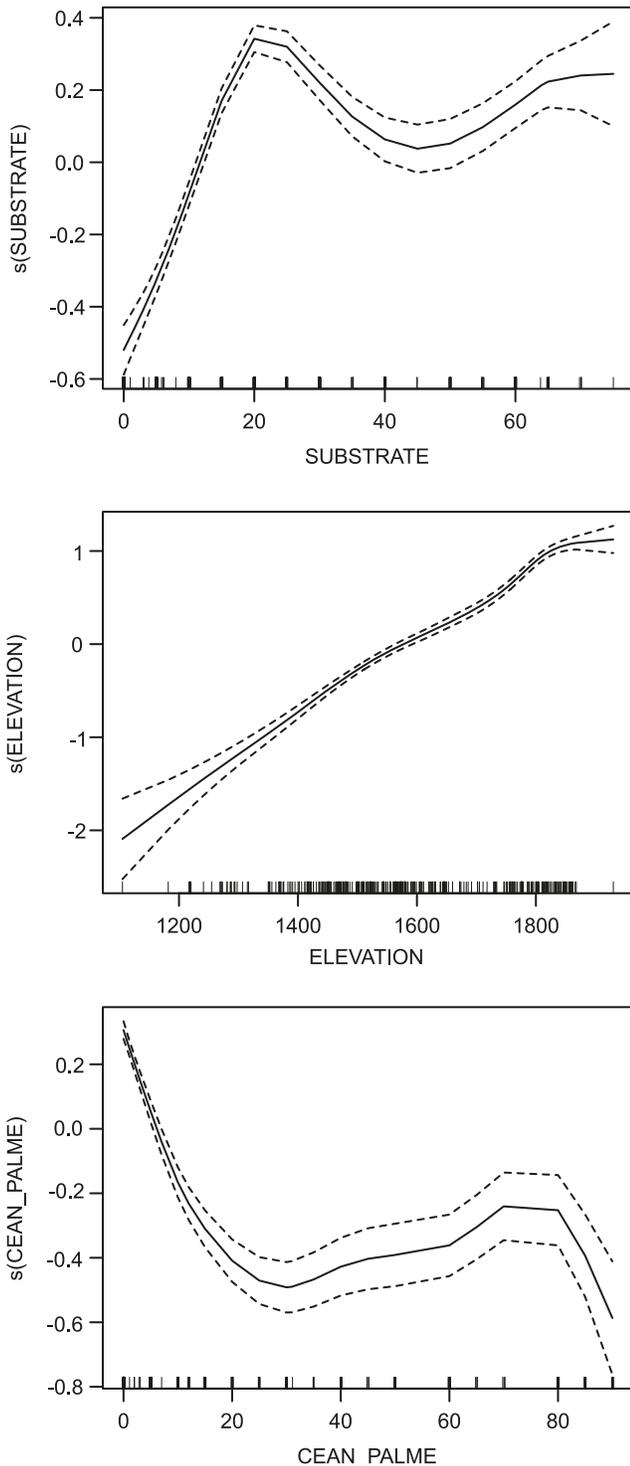
est was found pre-fire, at high elevations, and in areas free from high *C. palmeri* cover where bare soil was prevalent. Even though *P. lambertiana* and *P. jeffreyi* do not share the same fire adaptations as *P. coulteri*, they did survive in small pockets where the fire burned at a low severity. The map of juvenile pines will allow forest restoration programs to avoid tree planting in areas where natural regeneration is occurring (Savage and Mast 2005). Tree planting began in limited areas of CRSP soon after the Cedar Fire to restore the scenic nature and recreational value of the park.

Pinus coulteri in the Cuyamaca Mountains occupies transitional habitats between chaparral and conifer woodlands, and variation in cone serotiny can be complex and dependent on nearby vegetation (Borchert 1985; Wells 2001). Almost all juvenile pines located in the survey were *P. coulteri*, and they were most likely to be found where pre-fire pine cover ranged from 50% to 70% and where adult mortality was complete. The positive correlation between the establishment of *P. coulteri* juveniles and fire severity class, as well as the fact that most establishment was confined to the first post-fire growing season (larger number of whorls), suggests that trees in these woodland populations were serotinous and that recruitment depended on close proximity to a protected aerial seed bank.

In spite of the approximate nature of the estimation methods for some variables (visual estimates of cover in large plots), relationships between *P. coulteri* establishment and environmental factors were detected, although they should be interpreted cautiously. The probability of finding *P. coulteri* juveniles declined with increasing cover of *C. palmeri*, suggesting that competition from these shrubs may be inhibiting pine establishment (e.g, Conard and Radosevich 1982). However, the lack of observed regeneration in dense shrub cover may have been the result of our failure to detect it due to impaired visibility. In our study, some *P. coulteri* were observed growing through *C. palmeri* shrubs and juvenile heights were often substantial (cf., Erickson and Harrington 2006). In spite of the overall negative correlation, we counted 100 *P. coulteri* juveniles in one quadrat with 80% cover of *C. palmeri*. *Ceanothus* species are nitrogen fixing and therefore important to ecosystem recovery because much of the nitrogen is volatilized by fire (Johnson 1995; Busse et al. 2007). Since pine regeneration was not observed on any specific soil type, and because pines frequently grow in nutrient-poor soils, nitrogen fixation by *C. palmeri* may not be necessary for regeneration of pines.

The proportion of *P. coulteri* juveniles originating from seed caches suggests that animal seed scatter hoarding contributed to pine establishment. *Pinus coulteri* juveniles were found in the greatest abundance where the cover of bare soil was highest. Although this pattern can be explained by their shade intolerance, directed dispersal often occurs in patches of bare soil with low cover by leaf litter (Vander Wall 1990; Briggs et al. 2009).

Pinus coulteri juveniles were most abundant at higher elevations in the study area. It is tempting to conclude that its distribution is related to higher moisture availability at upper elevations (Gworek et al. 2007). However, juveniles tended to occur where there were pre-fire adults, and when the proximity of other juveniles was considered, the effect of elevation on occurrence was insignificant (although elevation was still

positively related to abundance). While it is not possible to determine from our data if climate change is displacing regeneration upslope relative to the distribution of previous generations of *P. coulteri* (e.g., Xu and Yan 2001; Sanz-Elorza et al. 2003), knowledge of the elevation range over which these pines are successfully establishing is useful for guiding future forest management.

The lack of stronger correlations between regeneration patterns and mapped environmental variables was disappointing because it prevents development of predictive maps of habitat suitable for forest restoration (Franklin 2009). However, the extensive nature of our survey provides spatially explicit information about patterns of pine regeneration. Lack of relationship to mapped soil type probably resulted from lack of variability in the study area soils primarily derived from granitic substrates (see Bergman 2009). Vegetation and fire severity maps were somewhat coarse scaled and categorically generalized (Franklin et al. 2000, 2001), so much so that field observations at the quadrat scale, as approximate as they were 5 years after the disturbance, were more strongly correlated with regeneration patterns.

The lack of regeneration of *P. jeffreyi* in CRSP is related to both the size and severity of the Cedar Fire, i.e., the mortality of even very large trees over extensive areas, and the lack of serotiny in this species. Further, because *P. jeffreyi* has a masting habit, dispersing large numbers of seeds during a few weeks only every several years (Lanner 1998), this pine may be at a distinct disadvantage following large, severe stand-replacing fire (Savage and Mast 2005). However, even though much of the fire on the *P. jeffreyi* dominated east side was severe, patches did burn at lower severity, allowing for the survival of adult *P. jeffreyi* (Franklin et al. 2006). These patches likely will serve as nuclei of future forest regeneration.

The apparent differences in pine species response to fire emphasize that a "one size fits all" fire management strategy (Schoennagel et al. 2004; Noss et al. 2006) would not maintain all pine species in this landscape. Fire prevention will be required over the next several decades to protect both natural regeneration and any investment in restoration because additional fire in the early stages of forest recovery is most likely to reduce survival of small conifers as well as reestablishment of long-lived obligate seeders including serotinous *P. coulteri* and other species (Franklin 2010).

Acknowledgements

References

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

Anselin, L., and Rey, S.J. 1991. Properties of tests for spatial dependence in linear regression models. Geogr. Anal. **23**(2): 112–131. doi:10.1111/j.1538-4632.1991.tb00228.x.

Augustin, N., Mugglestone, M., and Buckland, S. 1996. An autologistic model for the spatial distribution of wildlife. J. Appl. Ecol. **33**(2): 339–347. doi:10.2307/2404755.

Austin, M.P., and Heyligers, P.C. 1989. Vegetation survey design for conservation: gradsect sampling of forests in North-eastern New South Wales. Biol. Conserv. **50**(1-4): 13–32. doi:10.1016/0006-3207(89)90003-7.

Barry, S.C., and Welsh, A.H. 2002. Generalized additive modelling and zero inflated count data. Ecol. Model. **157**(2–3): 179–188. doi:10.1016/S0304-3800(02)00194-1.

Beers, T.W., Dress, P.E., and Wensel, L.C. 1966. Aspect transformations in site productivity research. J. For. **64**: 691–692.

Bergman, E. 2009. Pine regeneration in Cuyamaca Rancho State Park, San Diego County, five years after a high severity crown fire. M.Sc. thesis, Department of Biology, San Diego State University, San Diego, Calif.

Beschta, R.L., Rhodes, J.J., Kauffman, J.B., Griesswell, R.E., Minshall, G.W., Karr, J.R., Perry, D.A., Hauer, E.R., and Frissell, C.A. 2004. Postfire management on forested public lands of the western United States. Conserv. Biol. **18**(4): 957–967. doi:10.1111/j.1523-1739.2004.00495.x.

Bivand, R. 2002. Spatial econometrics functions in R: classes and methods. J. Geogr. Syst. **4**(4): 405–421. doi:10.1007/s101090300096.

Borchert, M. 1985. Serotiny and cone-habit variation in populations of *Pinus coulteri* (Pinaceae) in the southern Coast Ranges of California. Madroño, **32**: 29–48.

Borchert, M., Schreiner, D., Knowd, T., and Plumb, T. 2002. Predicting postfire survival in coulter pine (*Pinus coulteri*) and gray pine (*Pinus sabiniana*) after wildfire in central California. West. J. Appl. For. **17**(3): 134–138.

Borchert, M., Johnson, M., Schreiner, D.S., and Vander Wall, S.B. 2003. Early postfire seed dispersal, seedling establishment and seedling mortality of *Pinus coulteri* (D. Don) in central coastal California, USA. Plant Ecol. **168**(2): 207–220. doi:10.1023/A:1024447811238.

Briggs, J.S., Vander Wall, S.B., and Jenkins, S.H. 2009. Forest rodents provide directed dispersal of Jeffrey pine seeds. Ecology, **90**(3): 675–687. doi:10.1890/07-0542.1. PMID:19341138.

Busse, M.D., Jurgensen, M.F., Page-Dumroese, D.S., and Powers, R. F. 2007. Contribution of actinorhizal shrubs to site fertility in a Northern California mixed pine forest. For. Ecol. Manag. **244**(1–3): 68–75. doi:10.1016/j.foreco.2007.03.040.

California Department of Parks and Recreation. 1986. Cuyamaca Rancho State Park General Plan. Colorado Desert District Headquarters, Borrego Springs, Calif.

Conard, S.G., and Radosevich, S.R. 1982. Post-fire succession in white fir (*Abies concolor*) vegetation of the northern Sierra Nevada. Madroño, **29**: 42–56.

Crawford, J.S., Wahren, C.H.A., Kyle, S., and Moir, W.H. 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. J. Veg. Sci. **12**(2): 261–268. doi:10.2307/3236610.

Erickson, H.E., and Harrington, C.A. 2006. Conifer–*Ceanothus* interactions influence tree growth before and after shrub removal in a forest plantation in the western Cascade Mountains, USA. For. Ecol. Manag. **229**(1–3): 183–194. doi:10.1016/j.foreco.2006.03.029.

Everett, R.G. 2008. Dendrochronology-based fire history of mixed-conifer forests in the San Jacinto Mountains, California. For. Ecol. Manag. **256**(11): 1805–1814. doi:10.1016/j.foreco.2008.04.036.

Fortin, M.-J., and Dale, M.R.T. 2005. Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge, U.K.

Franklin, J. 2009. Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge, U.K.

Franklin, J. 2010. Vegetation dynamics and exotic plant invasion following high severity crown fire in a southern California conifer forest. Plant Ecol. **207**(2): 281–295. doi:10.1007/s11258-009-9672-6.

Franklin, J., Woodcock, C.E., and Warbington, R. 2000. Multi-attribute vegetation maps of Forest Service lands in California supporting resource management decisions. Photogramm. Eng. Remote Sens. **66**: 1209–1217.

Franklin, J., Simons, D.K., Beardsley, D., Rogan, J.M., and Gordon, H. 2001. Evaluating errors in a digital vegetation map with forest inventory data and accuracy assessment using fuzzy sets. Trans. Geogr. Inf. Syst. **5**(4): 285–304.

Franklin, J., Spears-Lebrun, L.A., Deutschman, D.H., and Marsden, K. 2006. Impact of a high-intensity fire on mixed evergreen and mixed conifer forests in the Peninsular Ranges of southern California, USA. For. Ecol. Manag. **235**(1–3): 18–29. doi:10.1016/j.foreco.2006.07.023.

Gillison, A.N., and Brewer, K.R.W. 1985. The use of gradient directed transects or gradsect in natural resources survey. J. Environ. Manag. **20**: 103–127.

Goforth, B.R., and Minnich, R.A. 2008. Densification, stand-replacement wildfire, and extirpation of mixed conifer forest in Cuyamaca Rancho State Park, southern California. For. Ecol. Manag. **256**(1–2): 36–45. doi:10.1016/j.foreco.2008.03.032.

Gworek, J.R., Vander Wall, S.B., and Brussard, P.F. 2007. Changes in biotic interactions and climate determine recruitment of Jeffrey pine along an elevation gradient. For. Ecol. Manag. **239**(1–3): 57–68. doi:10.1016/j.foreco.2006.11.010.

Haire, S.L., and McGarigal, K. 2008. Inhabitants of landscape scars: succession of woody plants after large, severe forest fires in Arizona and New Mexico. Southwest. Nat. **53**(2): 146–161. doi:10.1894/0038-4909(2008)53[146:IOLSSO]2.0.CO;2.

Hessburg, P.F., Salter, R.B., and James, K.M. 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. Landsc. Ecol. **22**(Suppl. 1): 5–24. doi:10.1007/s10980-007-9098-2.

Hutto, R.L. 2008. The ecological importance of severe wildfires: some like it hot. Ecol. Appl. **18**(8): 1827–1834. doi:10.1890/08-0895.1. PMID:19263880.

Jennings, S.B., Brown, N.D., and Sheil, D. 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. Forestry, **72**(1): 59–74. doi:10.1093/forestry/72.1.59.

Johnson, D.W. 1995. Soil properties beneath *Ceanothus* and pine stands in the eastern Sierra Nevada. Soil Sci. Soc. Am. J. **59**(3): 918–924. doi:10.2136/sssaj1995.03615995005900030042x.

Johnson, M., Vander Wall, S.B., and Borchert, M. 2003. A comparative analysis of seed and cone characteristics and seed-dispersal strategies of three pines in the subsection Sabinianae. Plant Ecol. **168**(1): 69–84. doi:10.1023/A:1024470224134.

Keeley, J.E. 1998. Postfire recovery and management: the October 1993 large fire episode in California. *In* Large forest fires. *Edited by* J.M. Moreno. Backhuys Publishers, Leiden, The Netherlands. pp. 69–90.

Keeley, J.E., and Zedler, P.H. 1998. Evolution of life histories in *Pinus*. *In* Ecology and biogeography of *Pinus*. *Edited by* D.M. Richardson. Cambridge University Press, Cambridge, U.K. pp. 219–251.

Keeley, J.E., and Zedler, P.H. 2009. Large, high-intensity fire events in southern California shrublands: debunking the fine-grain age patch model. Ecol. Appl. **19**(1): 69–94. doi:10.1890/08-0281.1. PMID:19323174.

Keeley, J.E., Fotheringham, C.J., and Moritz, M.A. 2004. Lessons from the October 2003 wildfires in Southern California. J. For. **102**(7): 26–31.

Keith, D.A. 2000. Sampling designs, field techniques and analytical methods for systematic plant population surveys. Ecol. Manag. Restor. **1**(2): 125–139. doi:10.1046/j.1442-8903.2000.00034.x.

Krofta, D.M. 1995. Stand structure and composition of mixed conifer–hardwood forest in Cuyamaca Rancho State Park, San Diego County, California. M.Sc. thesis, Department of Biology, San Diego State University, San Diego, Calif.

Krugman, S.L., and Jenkinson, J.L. 1974. *Pinus* L. pine. *In* Seeds of woody plants in the United States. *Edited by* C.S. Schopmeyer. U. S. Dep. Agric. Agric. Handb. 450. pp. 598–638.

Lanner, R. 1998. Seed dispersal in *Pinus*. *In* Ecology and biogeography of *Pinus*. *Edited by* D.M. Richardson. Cambridge University Press, Cambridge, U.K. pp. 281–295.

McCullagh, P., and Nelder, J.A. 1989. Generalized linear models. Chapman and Hall, London, U.K.

McKenzie, D., Raymond, C.L., Kellogg, L.K.B., Norheim, R.A., Andreu, A.G., Bayard, A.C., Kopper, K.E., and Elman, E. 2007. Mapping fuels at multiple scales: landscape application of the Fuel Characteristic Classification System. Can. J. For. Res. **37**(12): 2421–2437. doi:10.1139/X07-056.

Meentemeyer, R., Moody, A., and Franklin, J. 2001. Landscape-scale patterns of shrub-species abundance in California chaparral: the role of topographically mediated resource gradients. Plant Ecol. **156**(1): 19–41. doi:10.1023/A:1011944805738.

Millar, C.I., Stephenson, N.L., and Stephens, S.L. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecol. Appl. **17**(8): 2145–2151. doi:10.1890/06-1715.1. PMID:18213958.

Miller, J.D., Safford, H.D., Crimmins, M., and Thode, A.E. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. Ecosystems (N.Y.), **12**(1): 16–32. doi:10.1007/s10021-008-9201-9.

Mirov, N.T. 1967. The genus *Pinus*. Ronald Press, New York.

Moran, P.A.P. 1948. The interpretation of statistical maps. J. R. Stat. Soc. B, **10**: 243–251.

Noss, R.F., Franklin, J.F., Baker, W.L., Schoennagel, T., and Moyle, P.B. 2006. Managing fire-prone forests in the western United States. Front. Ecol. Environ, **4**(9): 481–487. doi:10.1890/1540-9295(2006)4[481:MFFITW]2.0.CO;2.

Quinn, G.P., and Keough, M.J. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, U.K.

R Development Core Team. 2007. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Sanz-Elorza, M., Dana, E.D., Gonzalez, A., and Sobrino, E. 2003. Changes in the high-mountain vegetation of the central Iberian peninsula as a probable sign of global warming. Ann. Bot. **92**(2): 273–280. doi:10.1093/aob/mcg130. PMID:12814955.

Savage, M., and Mast, J.N. 2005. How resilient are southwestern ponderosa pine forests after crown fires? Can. J. For. Res. **35**(4): 967–977. doi:10.1139/x05-028.

Schoennagel, T., Veblen, T.T., and Romme, W.H. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. Bioscience, **54**(7): 661–676. doi:10.1641/0006-3568(2004)054[0661:TIOFFA]2.0.CO;2.

Skinner, C.N., Stephens, S., and Everett, R. 2006. Fire regimes of

forests in the peninsular and transverse ranges of southern California. Joint Fire Science Project 01B-3-3-18. Environmental Sciences - Policy and Management, University of California-Berkeley, Berkeley, Calif.

Stephens, S.L., and Ruth, L.W. 2005. Federal forest-fire policy in the United States. Ecol. Appl. **15**(2): 532–542. doi:10.1890/04-0545.

Thayer, T.C., and Vander Wall, S.B. 2005. Interactions between Steller's jays and yellow pine chipmunks over scatter-hoarded sugar pine seeds. J. Anim. Ecol. **74**(2): 365–374. doi:10.1111/j.1365-2656.2005.00932.x.

Thompson, S.K., and Seber, G.A.F. 1996. Adaptive sampling. John Wiley & Sons, New York.

Turner, M.G., Romme, W.H., Gardner, R.H., and Hargrove, W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecol. Monogr. **67**(4): 411–433. doi:10.1890/0012-9615(1997)067[0411:EOFSAP]2.0.CO;2.

Turner, M.G., Baker, W.L., Peterson, C.J., and Peet, R.K. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems (N.Y.), **1**(6): 511–523. doi:10.1007/s100219900047.

Turner, M.G., Romme, W.H., Reed, R.A., and Tuskan, G.A. 2003. Post-fire aspen seedling recruitment across the Yellowstone (USA) landscape. Landsc. Ecol. **18**(2): 127–140. doi:10.1023/A:1024462501689.

Vale, T.R. 1979. *Pinus coulteri* and wildfire on Mount Diablo, California. Madroño, **26**: 135–140.

Vander Wall, S.B. 1990. Food hoarding in animals. University of Chicago Press, Chicago, Ill.

Vander Wall, S.B. 1992. The role of animals in dispersing a "wind-dispersed" pine. Ecology, **73**(2): 614–621. doi:10.2307/1940767.

Vander Wall, S.B., Borchert, M.I., and Gworek, J.R. 2006. Secondary dispersal of bigcone Douglas-fir (*Pseudotsuga macrocarpa*) seeds. Acta Oecol. **30**(1): 100–106. doi:10.1016/j.actao.2006.02.004.

Wahab-Twibell, R.A. 2008. Setting the scene for wildfire severity mapping using biophysical, environmental and prior-disturbance controls. M.S. thesis, Graduate School of Geography, Clark University, Worcester, Mass.

Wells, M.L. 2001. Human-altered fire regimes and the development of stand structure in Macrocarpae pines. Ph.D. thesis, Department of Geography, San Diego State University, San Diego, Calif., and University of Californis-Santa Barbara, Santa Barbara, Calif.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., and Swetnam, T.W. 2006. Warming and earlier spring increase western US forest wildfire activity. Science, **313**(5789): 940–943. doi:10.1126/science.1128834. PMID:16825536.

Wood, S.N. 2006. Generalized additive models: an introduction with R. CRC Press, New York.

Xu, D., and Yan, H. 2001. A study of the impacts of climate change on the geographic distribution of *Pinus koraiensis* in China. Environ. Int. **27**(2–3): 201–205. doi:10.1016/S0160-4120(01)00083-6. PMID:11697670.

Yee, T.W., and Mitchell, N.D. 1991. Generalized additive models in plant ecology. J. Veg. Sci. **2**(5): 587–602. doi:10.2307/3236170.

Zobel, B. 1953. Geographic range and intraspecific variation of Coulter pine. Madroño, **12**: 1–7.