Stand-level spatial dependence in an old-growth Jeffrey pine – mixed conifer forest, Sierra San Pedro Mártir, Mexico

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Abstract: Descriptions of spatial patterns are important components of forest ecosystems, providing insights into functions and processes, yet basic spatial relationships between forest structures and fuels remain largely unexplored. We used standardized omnidirectional semivariance modeling to examine the spatial pattern of fuels and forest structure measured in a systematic nested plot grid covering 144 ha. Forest structure variables were spatially dependent at scales ranging from 62 to 572 m. Cross-variograms of fuels and forest structure showed both positive and negative correlations, ranging from 0.04 to 0.67. Notably, fine fuels were correlated positively and negatively with forest structure variables of white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) and Jeffrey pine (*Pinus jeffreyi* Balf.), respectively. Old-growth Jeffrey pine – mixed conifer forest within the study area exhibited both identifiable spatial correlations and high stand-level spatial heterogeneity, as demonstrated by the influence of outliers on the underlying spatial pattern. The spatial dependency of fuels with species-specific variables suggests that less common species may have a large influence in the characterization of forest attributes and that fuel classifications may be improved by accounting for the spatial distributions of overstory species. Spatial correlations have many applications to forest management, including the classification and mapping of forest structure, establishing guidelines for fuel treatments, and restoration of old-growth forest ecosystems.

Résumé : La description des patrons spatiaux est une composante importante des écosystèmes forestiers qui fournit un aperçu des fonctions et des processus. Par contre, les relations spatiales fondamentales entre les structures forestières et les combustibles demeurent largement inexplorées. Nous avons utilisé la modélisation de la semi-variance omnidirectionnelle standardisée pour examiner le patron spatial des combustibles et celui de la structure forestière, mesurés au moyen de placettes emboîtées disposées selon une grille systématique couvrant une superficie de 144 ha. Les variables de la structure forestière étaient spatialement dépendantes à des échelles allant de 62 à 572 m. Des variogrammes croisés des combustibles et de la structure forestière ont montré qu'il y avait des corrélations tant positives que négatives, allant de 0,04 à 0,67. Notamment, les combustibles légers étaient corrélés positivement avec les variables de la structure de la forêt de sapin argenté (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) et négativement avec celles de la forêt de pin de Jeffrey (*Pinus jeffreyi* Grev. & Balf.). Il y avait des corrélations spatiales identifiables et une forte hétérogénéité spatiale à l'échelle du peuplement, démontrées par l'influence des observations aberrantes sur le patron spatial sous-jacent, dans les forêts anciennes mélangées de conifères et de pin de Jeffrey présentes dans l'aire d'étude. La dépendance spatiale des combustibles avec des variables propres à chaque espèce indique que les espèces moins communes pourraient exercer une grande influence sur la caractérisation des attributs forestiers et que la classification des combustibles pourrait être améliorée en tenant compte de la distribution spatiale des espèces dominantes. Les corrélations spatiales ont plusieurs applications en aménagement forestier, incluant la classification et la cartographie de la structure forestière en vue d'élaborer des directives pour le traitement des combustibles et la restauration des écosystèmes de forêt ancienne.

[Traduit par la Rédaction]

Introduction

Many biological phenomena exhibit spatial correlation (or spatial dependence, e.g., Isaaks and Srivastava 1989; Rossi et al. 1992), usually expressed in the form of patches and gradients. Spatial dependence is the relationship of environmental data across space; values of variables from nearby locations are more likely to be similar than values observed at more distant locations. In old-growth coniferous forests of the western United States, this type of patterning is evident at multiple ecological and spatial scales, illustrated by the diversity in ectomycorrhizal fungal communities (Lilleskov et al. 2004), variation in tree-ring growth (Meko et al. 1993), growth, biomass, and arrangement of trees (Biondi et al. 1994; Chen et al. 2004), distribution of tree canopies (Cohen et al. 1990; Van Pelt and Franklin 2000), and fire synchrony across landscapes (Kellogg et al. 2008). These studies utilized one geostatistical method recognized as

Received 9 February 2009. Resubmitted 7 February 2010. Accepted 27 May 2010. Published on the NRC Research Press Web site at cjfr.nrc.ca on 17 August 2010.

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doi:10.1139/X10-122

semivariance analysis, a branch of applied spatial statistics (Isaaks and Srivastava 1989) that quantitatively estimates, models, and predicts spatial patterns of regionalized variables.

Research on spatial patterns in frequent-fire old-growth conifer forests is relevant for several reasons. First, given the decline in the distribution of these forests (Barbour et al. 2002; Youngblood et al. 2004; Abella et al. 2007), descriptions of spatial patterns will help to accurately define these types of ecosystems (Kaufmann et al. 2007). Second, spatial patterns can provide insights into ecosystem processes such as growth and mortality, regeneration, and disturbance history (Barbour et al. 2002; Boyden et al. 2005; Sánchez Meador et al. 2009), information that may be obscured in forest sites that have undergone changes as a result of Euro-American settlement activities (Stephens and Ruth 2005; Abella et al. 2007). Lastly, these sites serve as a source of information for reference conditions (reviewed in Swetnam et al. 1999; Sánchez Meador et al. 2010), providing a context for guiding management decisions to protect the remaining intact stands and manipulate sites that are in need of silvicultural and fuel reduction treatments (Stephens and Fulé 2005; Abella et al. 2007).

Spatial dependence is an important component to characterizing vegetation mosaics, utilizing recent advances in aerial photography and remote sensing. Improvements in the ability to map the distribution of biomass, or fuels, across landscapes (reviewed in Arroyo et al. 2008) have applicability to many important elements of forest and wildland fire management: development of fuel classifications, fire spread prediction models, and post-disturbance changes in vegetation patterns (Keane et al. 2001; Reich et al. 2004; Rollins et al. 2004; Jia et al. 2006). In forest ecosystems, one limitation of these methods is the ability to quantify variation in vegetation and fuel characteristics not captured in forest structure classifications. Challenges lie in the discrimination of various fuel components as a result of overstory tree canopies obstructing direct views of the ground and surface fuels too small to detect with imagery (Keane et al. 2001; Reich et al. 2004). Using geostatistical tools to describe stand-level fuels–forest structure spatial relationships would provide another source of information to improve classification and modeling accuracy (Keane et al. 2001; Reich et al. 2004; Rollins et al. 2004).

Although many studies have examined forest spatial patterns, few have explored the basic spatial structures of surface fuels and forest structure at stand scales in dry conifer forests of western North America. Old-growth Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) – mixed conifer forests in the Sierra San Pedro Mártir (SSPM), northwestern Mexico, are unique within the California floristic province in that systematic suppression of wildfire has been implemented only since the early 1970s (Stephens et al. 2003; Skinner et al. 2008). This is in contrast with forests in the western United States, which have largely experienced fire suppression for over 100 years (Stephens and Ruth 2005). As such, these forests still exhibit open, heterogeneous characteristics (Stephens 2004; Stephens and Gill 2005; Stephens and Fry 2005; Stephens et al. 2007), making them an ideal reference site to examine spatial structures through a geostatistical approach. Using semivariance analysis on data collected from a grid of forest inventory plots, our objectives were to (*i*) quantify the amount of variation in fuels and forest structure variables that is spatially dependent and the distance in which that relationship occurs and (*ii*) quantify the spatial codependency of fuels variables with forest structure variables. Our initial hypotheses were that the relatively low, patchy fine fuel loads found in the SSPM (Stephens 2004) would be positively correlated across the study area, although the correlation may be weak (van Mantgem and Schwilk 2009). Similarly, coarse fuels would be positively correlated but at larger scales. Whereas fine fuels are continuously deposited throughout the stand, coarse fuels are usually created by various disturbance events (Lundquist and Beatty 2002) resulting in small, sparsely scattered patches of high fuel loads (Stephens 2004; Youngblood et al. 2004; Stephens et al. 2007). Old-growth ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) forests, ecologically and morphologically similar to Jeffrey pine dominated forests, exhibit spatial aggregation of trees (Harrod et al. 1999; Youngblood et al. 2004; Sánchez Meador et al. 2009). We hypothesized that forest structure variables (i.e., canopy cover, tree density, basal area, and species composition) would show a similar pattern at variable spatial scales.

Study area

The study was conducted in the SSPM National Park (31° 37′N, 115°59′W) within the SSPM, approximately 120 km southeast of Ensenada, Mexico. The SSPM is located in the southern margin of the North American Mediterranean climate zone (Minnich et al. 2000) but is distinguished from similar forests in California by a larger proportion of precipitation falling during the summer (Stephens et al. 2003). The average annual precipitation at the closest weather station (980 m above sea level, 1959–2005), approximately 20 km southwest of our study site, was 29.2 cm. Summer and winter average temperatures were 24.5 and 12.1 °C, respectively. The precipitation on the forest plateau (2200–2600 m above sea level) was much higher; averages calculated from a temporary weather station installed at Vallecitos Meadow (1989–1992), 1.2 km east of our study site (2500 m above sea level), were 55 cm (Minnich et al. 2000).

Conifer forests in the SSPM, comprising approximately 40 000 ha, are similar to portions of the eastern Sierra Nevada, Lake Tahoe Basin, and southern California mountains (Minnich et al. 1995; Stephens 2001; Barbour et al. 2002; Everett 2008). The most common forest types are *P. jeffreyi*, *P. jeffreyi* – mixed conifer, and mixed white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) forests (Minnich and Franco 1998). Substrate in the SSPM is mostly granitic with some areas of metamorphic rock. Soils in the study area are derived from diorite parent materials and are shallow, well to excessively drained, and relatively acidic (Franco-Vizcaíno et al. 2002; Stephens and Gill 2005). Chemical and textural properties of the soils are similar to typical granite-derived soils in comparable forests in California (Potter 1998).

The SSPM has experienced livestock grazing at varying intensities over the last 200 years (Minnich and Franco 1998). Additionally, fire has been an important ecological component in *P. jeffreyi* – mixed conifer forests, occurring relatively frequently up through as recent as 1980 (fire return interval of 5.7–14.5 years; Stephens et al. 2003). However, in many areas of the forest, fire has been absent for the last several decades because of increasing suppression efforts.

Methods

To examine spatial relationships at the stand scale, we used data collected from a systematic square grid of 0.1 ha circular forest inventory plots. The initial installation consisted of 49 plots (7 × 7 grid) on a 200 m spacing and covered 144 ha. The starting point was chosen randomly in an area with a north- to northwest-facing aspect ranging from 0% to 20% slope. Sampling was densified in a random 16 ha portion of the initial grid (3 × 3 grid) by installing 112 plots, which reduced the spacing between plots to 25 m (Fig. 1). Plot locations were not precisely located at grid points because of poor GPS equipment and reception; however, plot locations were installed without bias.

Fuel and forest structure variables were sampled in plots following the methods described in Stephens (2004), Stephens and Gill (2005), and Stephens et al. (2007). Surface and ground fuels were sampled using the line intercept method (Brown 1974) in all 161 plots. As a result of the large number of zero observations in the 1–1000 h size classes, a new variable was created and identified as wood: the summation of all woody dead and downed fuels (1–1000 h size classes). Percent canopy cover, measured using a site tube (Stephens et al. 2007), was sampled in the nested grid of 121 plots (25 m minimum plot spacing). Stand structure variables (live and dead tree density, basal area, and species composition) were sampled in the original grid and the nested, 100 m spacing grid for a total of 65 plots.

Analysis

Geostatistics provide a means for characterizing and predicting spatially explicit data. One commonly used method, semivariance modeling, involves calculating the variance for a pair of observations of a variable as a function of their separation distance (Isaaks and Srivastava 1989). Formulating for multiple pairs at various distance classes (or lags) provides a measure of spatial correlation of a variable across the sampled area. A semivariogram (called variogram for simplicity) graphically describes the spatial variability of a variable by plotting semivariance as a function of lag distance classes. The semivariance values are estimated using the formula

$$[1]\qquad \widehat{\gamma}(h) = \frac{1}{2n(h)} \sum_{S_i - S_j = h} (y_i - y_j)^2$$

where $\widehat{\gamma}(h)$ is the semivariance estimator, h is the lag distance, $n(h)$ is the number of pairs separated by h, s_i and s_j are the locations of points i and j, and y_i and y_j are the values of variable y at these locations. Spatial dependence is evident when semivariance values increase with distance until an asymptote is reached, identified as the partial sill (C). The sill approximates the variance of the sample population; beyond this point the data are no longer spatially correlated. The apparent y-intercept of the variogram, the nugget effect (or nugget variance, C_o), is defined as the value at which spatial variability is unaccounted for because of the lower limits of the spatial sampling distance or random sampling error. The ratio of the partial sill (C) to the total sill ($C + C_o$) is the structural variance and represents the amount that can be considered spatially dependent (Rossi et al. 1992). Semivariance modeling can be extended to pairing the values of two different variables (y and z) at different locations to examine how they covary spatially. This is accomplished through the cross-variogram estimated by the function

$$[2]\qquad \widehat{\gamma}_{yz}(h) = \frac{1}{2n(h)} \sum_{S_i - S_j = h} (y_i - y_j)(z_i - z_j)$$

where $\widehat{\gamma}_{yz}(h)$ is the cross-variance estimator of the two variables y and z. Contrary to univariate variograms, cross-variogram values can be negative when the correlation between the two variables is negative. Variogram plots were fitted with three theoretical models: exponential, Gaussian, and spherical; determination of the best model fit was based on minimizing the residual sum of squares. For comparative purposes, parameters used in the variogram modeling (minimum and maximum lag distance, lag tolerance) were the same for all variables (canopy cover, fuels, percent composition of *P. jeffreyi* and *A. concolor*, live tree and snag density, density of *P. jeffreyi* and *A. concolor*, live tree and snag basal area) analyzed at the particular spatial resolution. Furthermore, to allow for comparisons at a common scale, all variograms were standardized by dividing the univariate semivariance (eq. 1) by the overall sample variance (Rossi et al. 1992) and the bivariate semivariance (eq. 2) by the product of the square root of the semivariance of each variable (Xu et al. 2004). However, in the bivariate analysis, standardized cross-variograms range between –1 and 1. Positive values indicate positive correlations and negative values indicate negative correlations between y and z and 0 means no correlation (Xu et al. 2004).

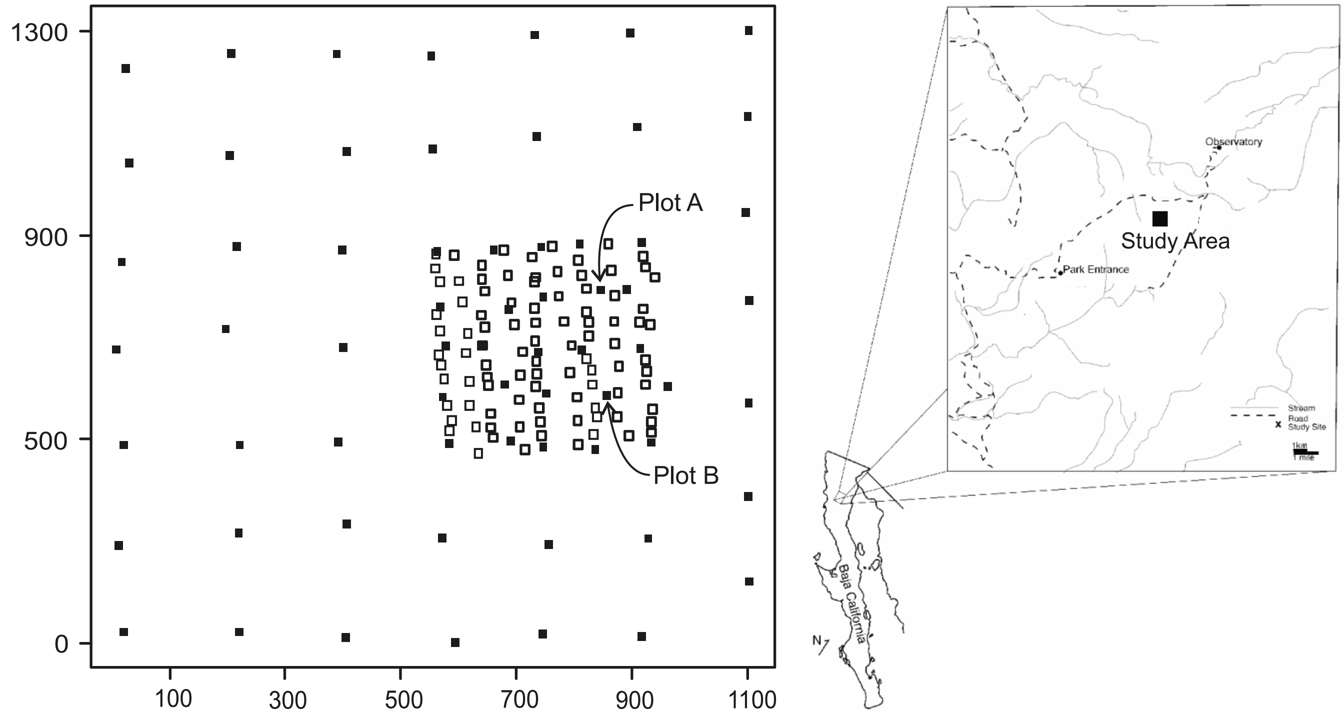
Analysis was performed using the gstat spatial package (Pebesma 2004) in R statistical computing software (R Development Core Team 2005). A requirement in semivariance modeling is the assumption of stationarity, the expectation that variance is due to separation distance only. Although normality of the data is not strictly required, serious violations such as high skewness or large outliers can violate the assumption and impair the variogram structure invalidating the results (Rossi et al. 1992; Basu et al. 1997). Environmental data are often observed to be lognormal or otherwise skewed and a transformation is needed to stabilize variance. Exploratory analyses (i.e., directional variograms, variogram cloud and squared difference box plots) were run to evaluate the distribution of the data and to detect spatial trends, defined as large-scale variation. Where trend was present, residuals from least squares regression were used in further analyses.

Results

Univariate spatial patterns

This forest is dominated by *P. jeffreyi* and as a result, forest structure attributes sampled for less common tree species (*Pinus contorta* Dougl. ex Loud. and *Pinus lambertiana* Dougl.) contained many zero observations, prohibiting spatial analysis. The range in observations varied greatly for

Fig. 1. Location (in metres) of forest inventory plots used in the analysis of spatial dependence in an old-growth *Pinus jeffreyi* – mixed conifer forest. The study area (144 ha) was located in the Sierra San Pedro Mártir National Park, northern Baja California, Mexico. Fuels were measured in all plots (open squares) and forest structure variables were measured in the solid squares.



the variables analyzed (Table 1). As expected, many frequency distributions were skewed with outliers; the number of plots with zero observations for a variable ranged from 0% to 40%. Canopy cover and live basal area exhibited near normal distributions and were not transformed. For most of the other forest structure variables, a logarithmic transformation sufficed in inducing normality and reducing the magnitude of the outliers. Owing to the large number of plots that were purely *P. jeffreyi*, the distribution of percent composition for this species was left skewed; however, transformations did not improve the stationarity assumptions in the exploratory analysis and, therefore, the untransformed data was used. Except for litter, all of the fuels variables were strongly right skewed with one to several outliers. Distributions for fine fuels and wood were near normal after a logarithmic transformation except for small spikes representing plots where no fuels were present. The larger fuels variables (100 and 1000 h) exhibited strong bimodal distributions because of the high number of plots in which fuel transects intersected no large fuels.

For the fuels variables that could be modeled at the 25 m minimum plot spacing, only litter exhibited a spatial structure using residuals from a linear model (Table 2; Fig. 2). Variograms for the woody fuel components (1–1000 h), which were absent in many of the plots, indicated a lack of spatial structure, i.e., a constant semivariance over all distances. Percent canopy cover had the overall smallest range (62.2 m) of all variables analyzed with 59.2% of the variability spatially dependent (Fig. 2). Analyzed at the larger 100 m minimum plot spacing, variograms for snag basal area and snag density were not spatially structured and the range was beyond the scale of the study area, respectively. For live tree density, there was no spatial structure using residuals from a linear model; however, exploratory analysis identified one large outlier plot (plot A; Figs. 1 and 3), which had a density that that was 71% larger than the average of the surrounding eight plots on the grid, which inflated the first lag in the variogram (Fig. 2). After removing plot A, 16% of the variation was spatial dependent using a spherical model (range = 342.9 m, nugget = 0.87, sill = 1.03). Percent composition of *P. jeffreyi* was spatially dependent at the largest range for all univariate analysis. The range in the variogram for *P. jeffreyi* density extended beyond the study area; however, exploratory analysis identified two large outlier plots (plots A and B; Fig. 1) that were 50%–71% larger than the average of the surrounding eight plots on the grid (Fig. 3). Upon removal of plots A and B, the model structure increased to 32.9% (range = 326.4 m, nugget = 0.73, partial sill = 1.08). For *A. concolor*, 25.5% and 30.9% of the sample variance for percent composition and live density, respectively, was spatially dependent at smaller ranges compared with *P. jeffreyi* composition (Table 2; Fig. 2).

Bivariate spatial patterns

Cross-variograms indicated that canopy cover, analyzed at the 25 m minimum plot spacing, was weakly correlated with fuels (litter, 1 and 10 h fuels, and wood), ranging from 37 to 162.7 m (Tables 3 and 4; Figs. 4 and 5). At the 100 m minimum plot spacing, litter was positively correlated with live tree density, snag density, and live basal area. However, the correlation with live tree density was slightly negative at the

Table 1. Fuels and forest structure characteristics in an old-growth *Pinus jeffreyi* – mixed conifer forest in the Sierra San Pedro Mártir, northern Baja California, Mexico.

Variable	No. of plots	Average (1 SE)	Median	Range (m)	Zero observations (%)
Litter (trees·ha^{-1})	161	10.6 (0.7)	8.7	0.9–40.2	0
1 h fuels (trees·ha^{-1})	161	0.1 (0.0)	0	0–1	17.5
10 h fuels (trees·ha^{-1})	161	0.7 (0.1)	0.4	0–7	12.5
100 h fuels (trees·ha^{-1})	161	1.5 (0.2)	0.7	0–11.7	40.0
1000h fuels (trees·ha^{-1})	161	17.9 (2.6)	3.1	0–210.8	38.1
Wood (trees·ha^{-1})*	161	20.1 (2.7)	6.1	0–213.4	1.9
Canopy cover (%)	121	26.8 (1.1)	26.0	0–56	2.5
Pinus jeffreyi composition (%)	65	73.0 (3.2)	77.8	0–100	1.5
Abies concolor composition (%)	65	19.3 (2.5)	14.3	0–68.4	30.8
Pinus jeffreyi density (trees·ha^{-1})	65	106.3 (8.6)	80	0–290	1.5
Abies concolor density (trees·ha^{-1})	65	31.7 (4.9)	20	0–160	30.8
Live density (trees·ha^{-1})	65	151.9 (10.1)	150	30–450	0
Snag density (snags·ha^{-1})	65	4.8 (0.7)	2.5	0–22.5	28.1
Live basal area (m^2·ha^{-1})	65	20.1 (1.1)	18.7	5.7–50.7	0
Snag basal area (m^2·ha^{-1})	65	1.6 (0.2)	1.1	0–5.9	28.1

Note: Variables were measured in a nested grid of plots covering 144 ha where the minimum separation distance (spacing) between plots ranged from 25 to 200 m (see Fig. 1). 1 SE, 1 standard error of the average.

*Wood is the sum of all woody dead and downed fuels (1–1000 h size classes).

Table 2. Standardized variogram model parameters for fuels and forest structure in an old-growth *Pinus jeffreyi* – mixed conifer forest.

Variable	Variable transformation	Model	Range (m)	Nugget (C_o)	Sill (C)	Model structure $C/(C + C_o)$
Litter	Residual log(x + 1)	Spherical	392.7	0.80	1.06	24.6
1 h fuels	*					
10 h fuels	*					
100 h fuels	*					
1000 h fuels	*					
Wood	*					
Canopy cover	na	Spherical	62.2	0.41	1.00	59.2
Pinus jeffreyi composition	na	Spherical	572.1	0.73	1.21	39.8
Abies concolor composition	log(x + 1)	Spherical	390.5	0.75	1.01	25.5
Pinus jeffreyi density	†					
Abies concolor density	Residual log(x + 1)	Spherical	404.3	0.75	1.09	30.9
Live tree density	*					
Snag density	†					
Live basal area	na	Exponential	367.9	0.65	1.19	45.3
Snag basal area	*					

Note: Variograms are given in Fig. 2. na, not applicable.

*Horizontal line; pure nugget effect indicating no spatial structure detected.

†No asymptote; range beyond the scale of study or trend present.

first lag. After removing plot A (Fig. 3), the litter – live tree density cross-variogram model structure increased by 6.4% (range = 233.5 m, nugget = –0.19, sill = 0.30), and the semivariance at the first lag increased to a positive value (Fig. 3). Comparing litter with the composition and density of *A. concolor*, cross-variograms showed a weak positive correlation with 51.9% of the variation spatially dependent. Conversely, density of *P. jeffreyi* was negatively correlated with litter but only at the first lag. Removing plots A and B only slightly modified the spatial structure (range = 163.8 m, nugget = –0.46, sill = 0.03, model structure = 52%).

The variation in 1 h fuels was spatially dependent with species composition, but the correlation was positive with *A. concolor* and negative with *P. jeffreyi* within ranges of 117.6 m (Table 3; Fig. 4). Similar to litter, 1 h fuels were positively correlated with live tree density except for the first lag. Removing the large outlier plot (A) in live tree density resulted in a positive nugget value (0.14) and a much larger range (273 m) (sill = 0.17, model structure = 19.1). Snag variables showed a similar negative relationship to 1 h fuels.

For both species density variables, cross-variograms showed negative correlations with 10 h fuels, although the range was slightly larger for *P. jeffreyi* (Table 4; Fig. 5). Removing plots A and B from *P. jeffreyi* density resulted in no spatial structure. For 10 h fuels and live tree density, removing plot A decreased the model structure 48.9% (range = 422.9 m, nugget = –0.30, sill = –0.15).

Fig. 2. Standardized sample and modeled variograms for fuels and forest structure variables in an old-growth *Pinus jeffreyi* – mixed conifer forest. Model parameters are given in Table 2.

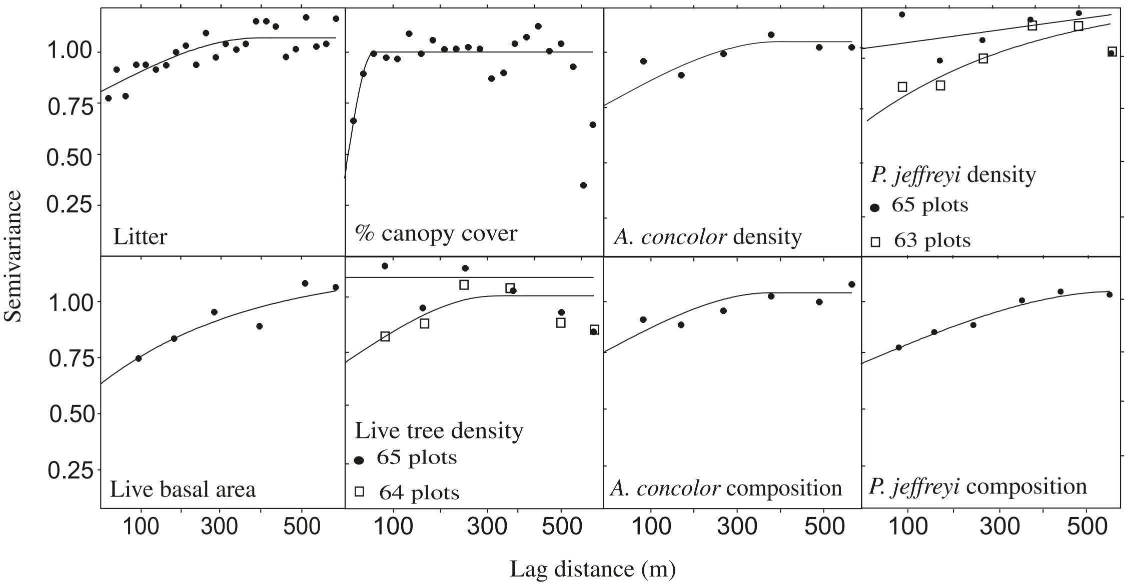
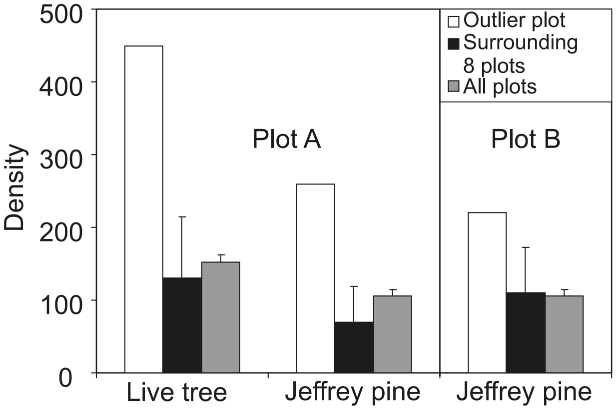


Fig. 3. Density (trees·ha^{-1}) of outlier plots (A and B) identified in semivariance analysis compared with the average density of the surrounding eight plots in the grid and the overall average density for the study area (N = 65).



Wood was positively correlated with snag density and snag basal area. There was no notable change in the wood – live tree density spatial structure after removing the high-density outlier plot A (Fig. 5). Canopy cover also showed a positive relationship with wood but only for the first lag. Cross-variograms of wood with live basal area and species variables either showed a lack of spatial structure or the relationship was beyond the range of the study area (Table 4).

Variables of larger fuel components (100 and 1000 h) contained a large number of zero observations at the 100 m spacing, which prohibited analysis.

Discussion

Fuels and forest structural attributes exhibited either various levels of spatial dependence over a wide range of spatial scales, no correlation suggesting a random pattern, or a spatial structure that was larger than the study area. This suggests that patch heterogeneity is a characteristic feature of Jeffrey pine – mixed conifer forests in the SSPM. It should be noted that whereas the spatial structure within the identified distance is implied to be continuous within the stand, patterns described here were generated using data from discrete circular forest inventory plots. Correlations at scales smaller than those analyzed in this study are one explanation for the proportion of sample variance not spatially structured (Isaaks and Srivastava 1989). Indeed, several (cross-) variograms identified spatial correlations at only the first or second lags. In a fuels-limited system such as this (Stephens 2004), line-intercept transects that are used to quantify fuels need to be relatively long to capture the variation in surface and ground fuels (Brown 1974). Our line transects were 13 m long, so a spacing of 25 m was the smallest plot grid that we could install to avoid overlap. Additional study areas that examine spatial forest characteristics will allow generalities to be developed and comparisons of vegetation mosaics in similar forests elsewhere.

Several live forest structure variables exhibited spatial dependence, ranging from 62.2 m for canopy cover (measured at the 25 m plot spacing) to 342.9–572.1 m for species composition, species density, and basal area (measured at the 100 m plot spacing). Relatively short-range seed dispersal in Jeffrey pines as well as post-dispersal seed caching from small mammals (Vander Wall and Joyner 1998) promotes spatial patches in forest structure (Stephens and Fry 2005). Stand dynamics in this arid environment are regulated by periodic environmental disturbances such as fire, occurring relatively frequently in low to moderate intensities (Minnich et al. 2000; Stephens et al. 2003). Fires tend to vary in behavior; spreading according to the arrangement and availability of fuels, resulting in an irregular, convoluted burn pattern, which, in turn, further perpetuates a patchy fuel and forest structure pattern (Miller and Urban 1999; Collins et al. 2007; Stephens et al. 2008; van Mantgem and Schwilk 2009). Although these results support our initial hypothesis of a patchy forest pattern across the study area, spatial information in other old-growth Jeffrey pine – mixed conifer for-

Table 3. Standardized cross-variogram model parameters of fuels and forest structure in reference to litter and 1 h fuels in an old-growth *Pinus jeffreyi* – mixed conifer forest.

Variable	Model	Range (m)	Nugget (C_o)	Sill (C)	Model structure $C/(C + C_o)$
Litter					
Canopy cover	Spherical	162.7	0.15	0.29	48.8
Pinus jeffreyi composition	*				
Abies concolor composition	Gaussian	435.8	0.20	0.28	28.4
Pinus jeffreyi density	Spherical	160.0	–0.97	0.04	52.0
Abies concolor density	Gaussian	311.4	0.16	0.33	51.9
Live tree density	Exponential	56.7	–0.96	0.25	55.1
Snag density	Spherical	144.2	0.87	0.09	46.5
Live basal area	Gaussian	260.8	0.10	0.40	75.9
Snag basal area	Spherical	191.3	0.89	–0.04	50.7
1 h fuels					
Canopy cover	Gaussian	60.6	0.25	0.07	70.4
Pinus jeffreyi composition	Exponential	58.7	0.63	–0.33	60.3
Abies concolor composition	Exponential	117.6	–0.31	0.37	54.7
Pinus jeffreyi density	Spherical	484.2	0.03	0.09	65.8
Abies concolor density	Exponential	63.5	–0.88	0.34	27.7
Live tree density	Exponential	144.4	–0.61	0.17	21.8
Snag density	Exponential	141.8	–0.46	–0.04	93.9
Live basal area	Exponential	116.6	–0.64	0.67	50.9
Snag basal area	Gaussian	408.7	–0.23	–0.04	54.0

Note: Cross-variograms are given in Fig. 4.

*No asymptote; range beyond the scale of study or trend present.

Table 4. Standardized cross-variogram model parameters of fuels and forest structure in reference to 10 h fuels and wood (1–1000 h fuels) in an old-growth *Pinus jeffreyi* – mixed conifer forest.

Variable	Model	Range (m)	Nugget (C_o)	Sill (C)	Model structure $C/(C + C_o)$
10 h fuels					
Canopy cover	Spherical	37.0	–0.17	0.39	70.0
Pinus jeffreyi composition	*				
Abies concolor composition	Spherical	144.0	–0.17	–0.07	60.0
Pinus jeffreyi density	Exponential	159.2	–0.68	–0.14	91.0
Abies concolor density	Spherical	144.0	–0.42	–0.28	68.4
Live tree density	Spherical	250.1	–0.67	–0.16	76.0
Snag density	Spherical	197.2	0.58	0.11	81.0
Live basal area	*				
Snag basal area	Spherical	214.1	0.61	0.04	93.4
Wood					
Canopy cover	Spherical	47.8	0.43	–0.14	56.0
Pinus jeffreyi composition	†				
Abies concolor composition	*				
Pinus jeffreyi density	*				
Abies concolor density	*				
Live tree density	Spherical	312.5	–0.12	0.19	61.8
Snag density	Spherical	311.9	–0.07	0.09	55.4
Live basal area	*				
Snag basal area	Spherical	160.0	–0.16	0.06	57.9

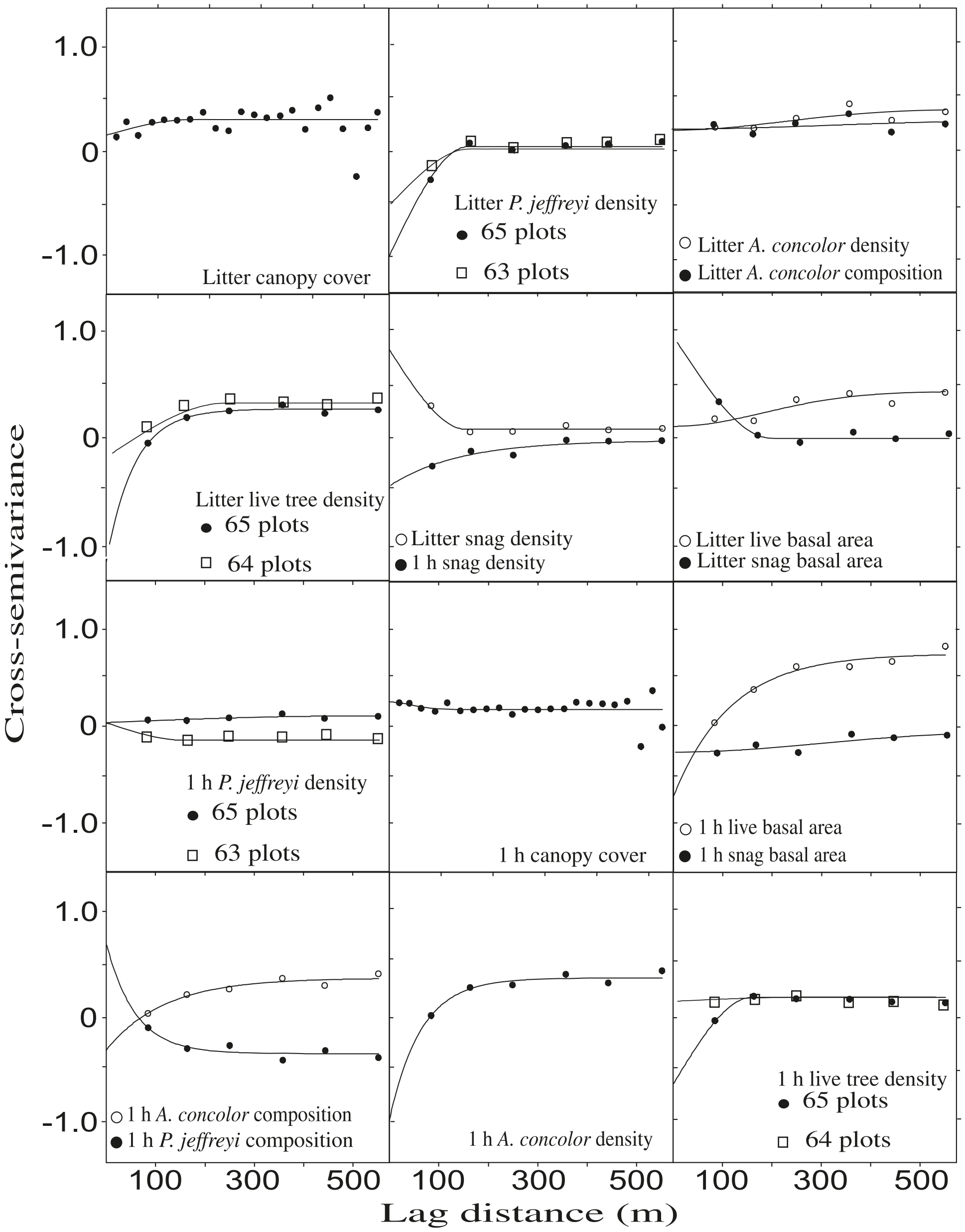
Note: Cross-variograms are given in Fig.5.

*No asymptote; range beyond the scale of study or trend present.

†Horizontal line; pure nugget effect indicating no spatial structure detected.

ests is lacking. Although described using different analytic methods, aggregation of live trees in patches of 0.02–0.30 ha were found in old-growth ponderosa pine forests in Washington (Harrod et al. 1999), Oregon and California (Getis and Franklin 1987; Youngblood et al. 2004), and Arizona (White 1985; Biondi et al. 1994; Sánchez Meador et al.

Fig. 4. Standardized sample and modeled cross-variograms for litter and 1 h fuels with forest structure variables in an old-growth *Pinus jeffreyi* – mixed conifer forest. Model parameters are given in Table 3.

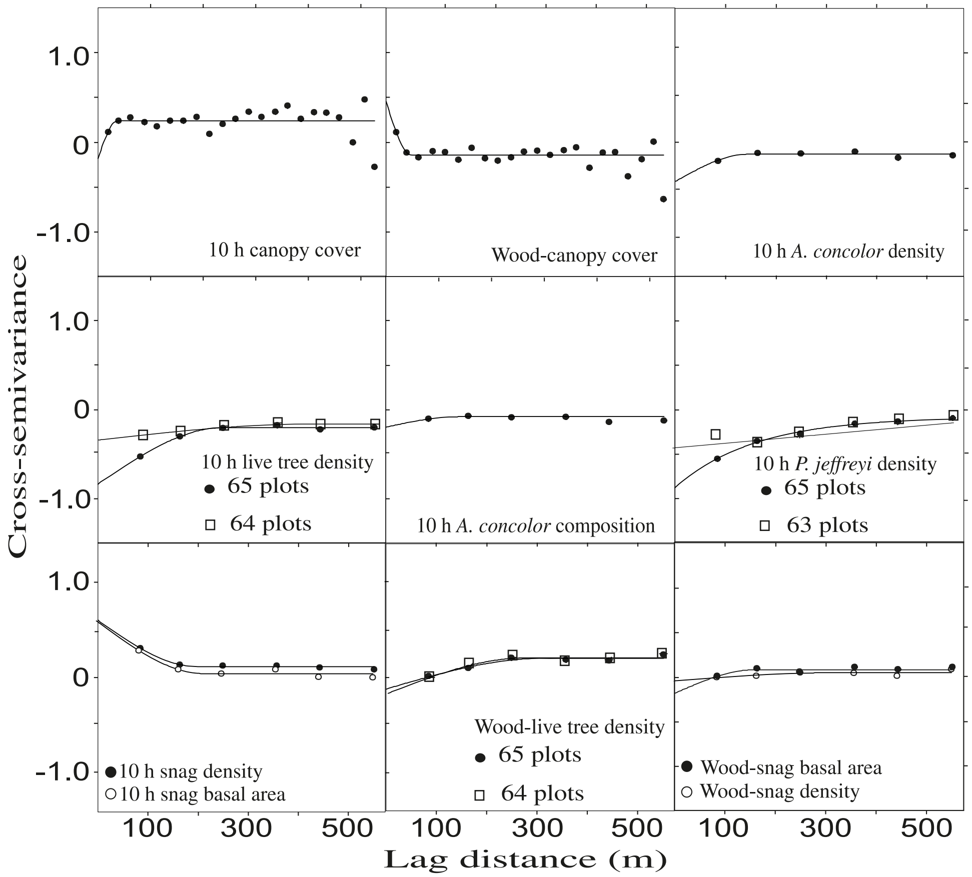


2009). However, a random pattern was found in Colorado (Boyden et al. 2005).

For live tree density, the exclusion of one or two outlier plots modified the amount of variation that was spatially dependent. Although there would be no justification for eliminating these outliers in the analysis of a designed experiment, noting the effect of their removal demonstrates the influence that outliers have on spatial structure (Basu et al. 1997) and emphasizes the fact that uncommon forest structural conditions may mask underlying forest spatial patterns. After removing two plots (density = 220–450 trees·ha^{-1}) located in what may be considered a regeneration patch (see Stephens and Fry 2005), variograms for live tree density and *P. jeffreyi* density were positively correlated. Although regeneration patches occupy a relatively small fraction of the total area (Stephens and Fry 2005), they are of mixed age and size and therefore contribute to the spatial variation in tree density in this forest.

Conversely, both snag variables showed no detectable spatial structure within the study area. Snags are relatively sparse in this forest and may be too rare to identify spatial patterns. Low snag density is a characteristic pattern in some old-growth ponderosa pine forests (Barbour et al. 2002; Youngblood et al. 2004; Boyden et al. 2005) and they can exhibit a clumped spatial pattern (Boyden et al. 2005). Given the multiyear drought the SSPM has been experiencing since 1999 (Stephens 2004), the low numbers of snags is surprising. Maloney and Rizzo (2002) found tree mortality caused by insects to be weakly density dependent. Although insects may show spatial patterns of activity resulting in localized clumps of mortality (Boyden et al. 2005), tree survivorship, species diversity, and distribution

Fig. 5. Standardized sample and modeled cross-variograms for woody fuels and 10 h fuels with forest structure variables in an old-growth *Pinus jeffreyi* – mixed conifer forest. Model parameters are given in Table 4.



in the SSPM (Stephens and Gill 2005) may promote a heterogeneous pattern of mortality.

The univariate variogram for litter was spatially dependent within a range of 392.7 m but 1 h fuels showed no spatial structure. Abundance of litter and 1 h fuels was positively correlated with *A. concolor* and negatively correlated with *P. jeffreyi* at much smaller scales. Average loads for litter and 1 h fuels were 18% and 48% lower in plots dominated (>50% composition) by *P. jeffreyi* compared with plots dominated by *A. concolor*, respectively. Whereas a patchy fuel structure is a characteristic feature of SSPM forests (Stephens et al. 2004), correlations with species-specific variables were not expected. These patterns are likely a result of species differences in the following factors: fuel accumulation and decomposition rates, fuel consumption during fires, needle and branch morphology (van Wagtendonk et al. 1998), and productivity (Fonda et al. 1998; Stephens 2001; Stephens et al. 2004).

The paucity of large, woody fuels in the SSPM resulted in no discernible spatial structure, which corresponds to the finding in potential standing woody debris in the form of snags. Our initial hypothesis was that various disturbance events (fire, insects, diseases, drought, wind; Lundquist and Beatty 2002) would create small, sparsely scattered patches of high fuel loads. The large number of plots with no fuels and the few plots with an abundance of large fuels supports this hypothesis. However, the overall range in cover of coarse wood (0%–8.4%; Stephens et al. 2007) would suggest that a smaller measurement scale (<100 m spacing) may be needed to detect finer scale patterns.

The spatial distribution of fuels attributes are highly variable, dependent upon numerous environmental variables including stand history, and not necessarily correlated with vegetation type (Keane et al. 2001; Falkowski et al. 2005). Although we found some patterns in fuels that were related to species composition, much more research on factors that influence fuels – forest structure relationships are needed. Including a measure of spatial dependence that explains some of the variation in the characterization of forest structure and fuels should improve ecosystem models. Coupling spatial models of environmental data with imagery has proven successful in characterizing and mapping of fuels across landscapes (Keane et al. 2001; Reich et al. 2004; Falkowski et al. 2005). Although these methods have many limitations including site-specific descriptions, parameterization, applicability to other methods, and short temporal use (Arroyo et al. 2008), it is apparent that fuels and forest structure classifications and modeling will be improved with a combination of technology (i.e., better image resolution) and statistical methods and a greater understanding of ecological relationships.

Management implications

Spatial relationships vary temporally, especially as stands develop and are exposed to various disturbances (Biondi et al. 1994; Youngblood et al. 2004; Boyden et al. 2005;

Sánchez Meador et al. 2009); thus, these data provide a baseline for monitoring changes (Hessburg et al. 1999). Patterns described here are from a relatively intact forest ecosystem, and although wildfires are still occurring in conifer forests within the SSPM National Park (e.g., Stephens et al. 2008), enhanced fire suppression efforts may adversely change the trajectory of stand dynamics.

Further research examining spatiotemporal relationships will increase our understanding of ecosystem processes and provide structural information for forests that are in need of restoration (Youngblood et al. 2004; Sánchez Meador et al. 2009). Forest managers are often supplied with empirical data on forest structure in the form of averages and standard errors, which may be used to develop management guidelines as targets for future forest conditions. As the ranges in the variability of spatial relationships are increasingly recognized and adequately described (e.g., near neighbor distances, patch size, and abundance; Sánchez Meador et al. 2009) as important components of forest structure and biological diversity (Landres et al. 1999), incorporation of the spatial structure should improve guidelines so that forests can be modified to conditions that can incorporate future environmental disturbances. Methods that portray the natural range in spatial patterns (Landres et al. 1999), including uncommon forest structures that contribute to spatial heterogeneity (e.g., high tree density patches found in this study), will help to convey important stand characteristic information to managers. Although simply recreating spatial patterns will not necessarily promote ecosystem resiliency (Millar et al. 2007), knowledge of these patterns and future research into the mechanisms that cause changes (Swetnam et al. 1999) will provide insight as to how processes may be allowed to function through the patterns created. Given the altered conditions of the majority of conifer forests in the western United States as a result of past fire suppression and (or) exclusion, timber harvesting, livestock grazing, and active fuel and forest structure management are considered necessary (Stephens and Ruth 2005), especially in forests that once burned frequently under low- to moderate-intensity fire regimes. While restoration treatments have been performed often with the aid of reference conditions (Hessburg et al. 1999; Stephens and Fulé 2005; Sánchez Meador et al. 2010), one challenge is how to communicate spatial variability to managers and incorporate the observed patterns at the appropriate management scale.

Conclusion

The use of geostatistical tools can aid in the quantification of the degree and scale of correlations of fuels and forest structure variables that may not be identified with traditional statistical methods. Many variables were spatially autocorrelated at various scales, and both positive and negative bivariate correlations were identified, providing information on stand-level patterns that are applicable to management and restoration efforts of old-growth forests. Some spatial patterns likely occur at larger scales than those in this study, as identified by variograms with sloped lines and evidence of periodicity. In a few cases, outliers strongly influenced the spatial pattern, demonstrating the affect of uncommon stand structures on depictions of forest conditions. Semivariance modeling is a useful tool for characterizing the spatial variability of forest attributes, providing information that can supplement models of forest and fuels attributes.

Acknowledgments

We thank all of the field crews that assisted in data collection on this project. Carl Skinner assisted in the production of Fig. 1. The logistical support of Ernesto Franco is sincerely appreciated. Statistical consultation was provided by Andrew Sánchez Meador. This project was supported by USDA Agricultural Experiment Station funds from the University of California, Berkeley. The research reported here was carried out under permits (NUM/SGPA/DGVS/3315, UM/SGPA/DGVS/04036, and NUM/SGPA/DGVS/04075) issued by the Mexican Ministry of the Environment (SEMARNAT) for the project “Cronología de incendios y cambios climáticos y de vegetacœn en los bosques de conÚferas mixtas de la Sierra de San Pedro MÃrtir, Baja California, Mexico.”

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