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RESEARCH ARTICLE

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Fine-scale Patchiness in Fuel Load Can Influence Initial Post-fire Understory Composition in a Mixed Conifer Forest, Sequoia National Park, California

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ABSTRACT: Many forests, including the mixed-conifer forest of the Sierra Nevada, California, historically experienced a fire regime that generated considerable within- and among-fire environmental variability. Fire suppression has resulted in a heavier, more continuous fuel bed, which can cause today's prescribed fires to be considerably more homogeneous. To evaluate the potential importance of variability in fire severity on post-fire plant communities, I conducted an experiment to test whether understory species respond differently to sites burned under a heavy fuel load versus sites that burned under a light fuel load. Woody fuel was added or removed from small forest plots in order to manipulate the fire severity during prescribed fire. The fuel load manipulations affected which species survived fire as well as which species germinated after fire. Seven species (*Chimaphila menziesii, Chrysolepis sempervirens, Osmorhiza chilensis, Pyrola picta, Phacelia hydrophylloides, Rubus parviflorus,* and *Smilacina racemosa*) were unable to survive fire in either treatment. Four species (*Bromus laevipes, Galium sparsiflorum, Rubus glaucifolius,* and *Symphoricarpos mollis*) survived more often on sites that were burned under a light fuel load. Several fire-stimulated species (*Calystegia malacophylla, Cryptantha sp., Gayophytum eriospermum, Solanum xanti, Arctostaphylos patula, Ceanothus parvifolius,* and *Lotus crassifolius*) germinated after fire regardless of fuel load, but others (*Claytonia perfoliata, Ceanothus cordulatus, Prunus emarginata,* and *Ribes tularense*) appeared more often on the light fuel treatments. Seedlings of *Abies concolor* germinated more often on the sites that burned under heavy fuel conditions. The varying responses of different species suggest that small-scale variations in fuel load may cause heterogeneous patterns of surface fire severity, which in turn may contribute to maintaining floral diversity in the mixed-conifer forest understory. In order to conserve native understory plant diversity, fire management efforts to restore these forests might consider spatial heterogeneity in fire severity as a management objective.

Index terms: mixed-conifer, prescribed fire, Sierra Nevada, spatial heterogeneity, understory diversity

INTRODUCTION

In many areas of the western United States, the suppression of natural fires has produced heavy buildup of dead wood and dense trees and has dramatically altered forest structure and composition. Fuel accumulations in affected forests are associated with both a rise in fuel biomass and an increased spatial continuity of fuels (Miller and Urban 2000a). Therefore, fires in areas affected by fire suppression are not only more intense, but they are also likely to exhibit less within-fire patchiness than pre-European settlement fires would have. For example, the extensive barren landscapes produced by intense wildfires, such as large areas of the Rodeo-Chediski fire (Arizona, 2002) and the Hayman fire (Colorado, 2002), are homogeneous at a large scale, and may not produce the range of post-fire habitat conditions necessary for the reestablishment of all species. Less attention has been given to the possibility that prescribed fires, systematically ignited under mild weather conditions, might also lack the variability in fire severity required to restore the native understory community.

Efforts are currently underway to ameliorate heavy fuel conditions in western forests using mechanical thinning and prescribed fire (Western Governors' Association 2001; Healthy Forests Restoration Act 2003). Our understanding of the effects of these treatments on biodiversity and ecosystem functioning in these forests, while growing, remains incomplete. Recent studies on restoration methods have focused on the importance of fire for restoring historical forest structure and for tree regeneration (Mutch and Parsons 1998; Mast et al. 1999; Stephenson 1999; Bailey and Covington 2002; Miller and Urban 2000b; Waltz et al. 2003; North et al. 2007). Several papers have begun to shed light on herb and shrub responses to restoration treatments (Collins et al. 2007; Knapp et al. 2007; Korb et al. 2007; Wayman and North 2007). However, isolating the effects of fire severity per se on understory plant communities has been difficult because fire severity is correlated with factors such as canopy cover and soil moisture that affect both fire severity and understory species distributions (North et al. 2005; Knapp et al. 2007).

Here I define fire severity as the magnitude of the ecological effects of fire. Under the condition that fuels are completely consumed, higher fuel loads tend to result in higher fire severities relative to lighter fuel loads because of the increased temperature and duration of heat pulse into the soil, greater fuel consumption, and increased vegetation mortality (Reinhardt et al. 2001; Knapp and Keeley 2006). Variation in fire severity can create spatial heterogeneity in the environment by generating gradients in soil conditions, light availability, and microclimate. This heterogeneity may facilitate the establishment of a variety of specifically adapted species (Grubb 1977). Fire sensitive plants, for example, may survive only on sites that were unburned or lightly burned, whereas some fire stimulated species might require high fire temperatures to scarify and germinate. Under fires of high temperature or duration, seed banks may be killed such that only plants able to disperse to the site after fire, and tolerate its seedbed conditions, are able to establish. If plants respond differently to variation in fire severity, a more heterogeneous burn should lead to a more diverse suite of species after fire. If species diversity conservation is a management goal, as it is in many areas currently slated for restoration treatments, learning how herbaceous diversity depends on fire-generated heterogeneity should be a top priority.

Here I test the prediction that individual species respond differently to fire severity in Sierra Nevada mixed-conifer forests. I conducted experimental manipulations of fuel loads on small forest floor areas to produce burns that would release different amounts of heat and create patches of different fire severities. I added woody fuel to create high severity burning conditions and removed woody fuel to create light severity burning conditions. I assessed plant community composition in each plot before and one year after a prescribed fire. If species composition varies based on pre-fire fuel loading, the argument could be made that spatial heterogeneity in fire severity is important for maintaining understory diversity in this forest. In such a case, homogeneous prescribed fires might not adequately restore plant community composition.

METHODS

Study area

The experimental fuel manipulations were conducted within a 500-m x 1000-m area of forest in the Tar Gap area of the East Fork of the Kaweah watershed in Sequoia National Park. Slopes were predominately west facing at elevations between 2000 and 2300 meters. The region experiences a Mediterranean climate with cold, wet winters and warm, dry summers. Before European settlement, mixed-conifer forests on west-facing slopes experienced a mean fire return interval of about 14 years (Kilgore and Taylor 1979), with most fires occurring in the late summer to fall dry period (Caprio and Swetnam 1995). The study area had not burned since the Park started keeping fire records in 1921.

Abies concolor (Gord. & Glend.) Lindl. ex Hildebr. (white fir) is the dominant tree species in this forest, with *Pinus lambertiana* Dougl. (sugar pine), and *Calocedrus decurrens* [Torr.] Florin. (incense cedar) occurring as less frequent components of the overstory. The understory is composed of a sparse yet diverse assemblage of shrub and herb species. In the absence of fire, populations of many understory plants are constrained to small areas within canopy gaps, while other species have greatly reduced adult populations compared to the abundance of seed in the seed bank (Rocca 2004). Many of the shrubs, including *Lotus crassifolius* [Benth.] Greene (big deervetch), *Prunus emarginata* [Dougl. ex Hook.] D. Diert. (bitter cherry), *Ribes tularense* [Coville] Fedde (sequoia gooseberry), *Arctostaphylos patula* Greene (greenleaf manzanita), and several *Ceanothus* species (ceanothus) germinate from the seed bank following fire, and are collectively referred to as "fire-stimulated shrubs" hereafter.

Experimental design and data collection

Within the study area, ten 4-m x 4-m sites were chosen for experimental fuel manipulation. Each site was chosen to be free of obstacles such as tree boles and rock outcrops (which would affect the area available for plant growth). All sites were covered by enough needle litter and fine woody fuel to carry fire, and were spaced at least 50 meters apart.

A randomized-block experiment tested the effects of fire severity on post-fire community composition. Each 4-m x 4-m site (block) was divided into four 2-m x 2-m quadrants (Figure 1a). Two quadrants were randomly assigned to a "heavy" fuel treatment and two to a "light" fuel treatment. For the quadrants in the heavy fuel treatment, woody fuel was added to approximate the highest fuel loads observed in these forests, or approximately 10 kg dry woody fuel/m^2, with a fuel size class distribution roughly equivalent to that created by a fallen tree crown. Light fuel treatments were created by removing all woody fuel in the 10-hour size class or larger (> 0.65 cm diameter), leaving approximately 0.1 kg fine woody fuel/m^2 and enough litter to ensure the area would burn mildly (Figure 1b).

Understory plant composition was surveyed before the fire, in late July 2002. Prior to fuel manipulations, all understory plant species were recorded within the central square meter of each 2-m x 2-m treated quadrant (Figure 1a) leaving an unsampled buffer around the edges of each treatment area. Newly germinated shrub seedlings were counted, and other understory species were recorded as present or absent. Seedlings of trees were tallied by species.

Sequoia National Park personnel ignited the burn unit beginning on 10 October 2002. A strip headfire ignition pattern was employed, resulting in a relatively complete burn. The year following the fire, in early August 2003, the vegetation surveys were repeated. The 2003 growing season followed a winter with average precipitation and a heavier than normal spring snowpack due to late season storms and cool spring temperatures (California Department of Water Resources; Rockwell et al. 2005).

Analyses

The objective of this study was to describe the responses of individual species to fire severity; therefore, each species was analyzed separately using randomized-block ANOVA with site as a blocking factor and fuel treatment as the primary factor (two replicates of each treatment per block).

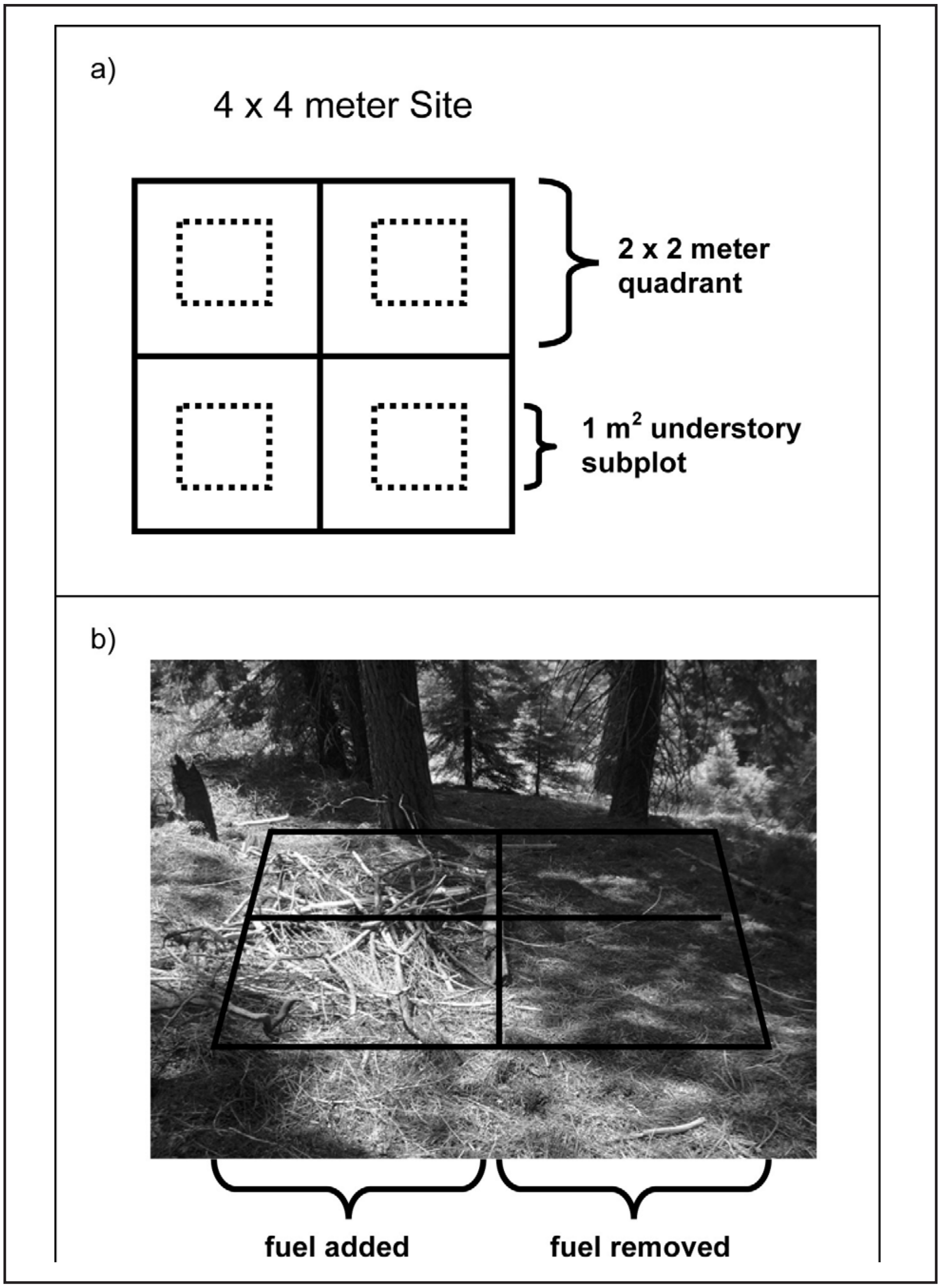

Figure 1. Experimental design. a) Schematic of randomized block design. 4 x 4 meter sites were divided into 4 quadrants. Two quadrants were randomly assigned to a "heavy" fuel treatment and two to a "light" fuel treatment. b) Photo of fuel manipulations. Both heavy fuel load treatments are on the left side of the plot, with light fuel load treatments on the right.

For the species for which seedling counts were available (shrub and tree seedlings), a general linear model with a log link (i.e., Poisson regression) was fit. For the herbaceous species, logistic regressions on presence/absence were run. A term for pre-fire presence/absence was included in the models for each species that occurred on the study sites before the fire. Significance of explanatory factors was determined using chi-squared tests. All analyses were conducted in S-plus 7.0 (Insightful, Inc.).

Each experimental site burned across its entire area, as evidenced by coverage of ash and/or charred litter. While thermocouple measurements of heat pulse into the soil were not available for this study, visual inspection of the plots following fire suggested that the fuel manipulations influenced fire severity, as measured by fuel consumption, in a predictable manner. All woody fuels in the treated blocks were thoroughly consumed, while some litter and fine fuels remained charred but recognizable after fire in some of the light fuel areas.

RESULTS

Tree seedlings were rare in the sampled area. A total of 61 seedlings were counted across all sites before the fire, and all of these were killed regardless of fire severity treatment. Because all seedlings died, only first-year germinants could occur post-fire. Sixteen first-year seedlings were counted after the fire. All were *A. concolor* seedlings except for one *P. lambertiana* seedling, which was not considered in the analysis. Thirteen *A. concolor* seedlings occurred on the heavy fuel quadrants while two occurred on the light fuel quadrants, suggesting that the more severely burned sites are the more suitable for *A. concolor* germination ($P = 0.0027$, Poisson ANOVA).

Seedlings of six fire-stimulated shrub species had germinated one year after the fire (Table 1). Three species showed significant treatment preferences; *Ceanothus cordulatus* Kellogg (whitethorn), *P. emarginata,* and *R. tularense* preferred the light fuel sites ($P = 0.0018$, $P = 0.0055$, and $P < 0.0001$ respectively, Poisson ANOVA). Only one fire-stimulated shrub, *R. tularense*, occurred anywhere in the study area before fire; seedlings of this species were more likely to be found where the species occurred before the fire ($P < 0.0001$, Poisson ANOVA).

Twenty-one other (herb and non-fire-stimulated shrub) species were observed before and/or after the fire. Table 2 arranges all the herb, shrub, and tree species along a gradient from fire sensitive to fire tolerant, along with results of statistical tests. Six species, *Chimaphila menziesii* (R. Br. ex D. Don) Spreng (little prince's pine), *Chrysolepis sempervirens* (Kellogg) Hjelmqvist (bush chinquapin), *Pyrola picta* Sm. (white-veined wintergreen), *Phacelia*

Table 1. Mean seeding count per quadrant, by treatment, for six fire-stimulated shrub species, with p-values for a treatment effect. Species with significant treatment effects are highlighted in bold.

Species	mean seedling count: Light fuel	Heavy fuel	p-value
greenleaf manzanita (*Arctostaphylos patula*)	1.05	0.55	0.075
snow bush (*Ceanothus cordulatus*)	**0.35**	**0.00**	**0.00**
littleleaf ceanothus (*Ceanothus parvifolius*)	0.55	0.70	0.55
big deervetch (*Lotus crassifolius*)	0.15	0.15	0.54
bitter cherry (*Prunus emarginata)*	**0.80**	**0.20**	**0.01**
sequoia gooseberry (*Ribes tularense*)	**2.25**	**0.70**	**<0.0001**

hydrophylloides Torr. ex A. Gray (waterleaf phacelia), *Rubus parviflorus* Nutt. (thimbleberry), and *Smilacina racemosa* (L.) Desf. (false Soloman's-seal), were found before the fire but disappeared completely after the fire, and one nearly disappeared (*Osmorhiza chilensis* Hook. & Arn. [mountain sweetcicely]). The other fourteen species were observed after the fire and were separated into three categories: (1) those that were present before the fire ("fire survivors," eight species), (2) those that represented appearances of new species ("fire-stimulated herbs," five species), and (3) those that were present before fire but also often appeared in new places after fire (one species).

Of the fire survivors, *Bromus laevipes* Shear (woodland bromegrass), *Galium sparsiflorum* W. Wight (Sequoia bedstraw), *Rubus glaucifolius* Kellogg (glaucous-leaved raspberry), and *Symphoricarpos mollis* Nutt. (creeping snowberry) survived more often on light fuel sites, while *Arabis repanda* S. Watson var. *repanda* (Yosemite rockcress), *Pteridium aquilinum* (L.) Kuhn (hairy brackenfern), *Sambucus mexicana* C. Presl ex DC. (common elderberry), and *Silene lemmonii* S. Watson (Lemmon's campion) were not fire sensitive and were generally found in the same places before and after fire. *Apocynum androsaemifolium* L. (bitter dogbane) appeared to survive equally often after light fuel and heavy fuel treatments, but new appearances occurred more often on light fuel quadrants. Of the five fire-stimulated herbs, *Claytonia perfoliata* Donn. ex Willd. spp. *perfoilata* (miner's lettuce) appeared only on the light fuel sites after fire, while *Calystegia malacophylla* (Greene) Munz ssp. *malacophylla* (Sierra morning-glory), *Cryptantha sp*. (cryptantha species), *Gayophytum eriospermum* Coville (Coville's groundsmoke), and *Solanum xanti* A. Gray (chaparral nightshade) germinated on both light and heavy fuel load sites. No species, other than the tree seedlings of *A. concolor*, occurred more often on the heavy fuel areas after the fire.

DISCUSSION

Species responded differently to fuel load, most likely in response to the different fire severities created by each treatment. Species in the understory of this Sierra Nevada mixed conifer forest appear to take advantage of the variety of "regeneration niches" (Grubb 1977) created by a patchy surface fuel load (Table 2). Before European settlement of California, fires ignited by lightning or by Native Americans probably burned for weeks to months. Over this time period, fires would at times creep or smolder and at other times run along the forest floor or flare up to the canopy. The resulting burn pattern would include a variety of burn severities including unburned patches of ground, areas of sterilized mineral soil, and occasional canopy gaps (Kilgore and Taylor 1979). If this kind of heterogeneous burn pattern was typical during the evolutionary history of these species, the differential responses to fire severity observed in this study might represent adaptations to different fire-generated microsites. Regardless of the adaptive nature of differential responses to fire severity, this study suggests that a homogenous burn pattern, whether the result of wildfire or a prescribed fire conducted under very dry moisture conditions (Knapp and Keeley 2006), may lead to a loss of regeneration or survival microsites for some species.

Based on the results of this experiment, one could predict that homogeneously severe burns through heavy fuels are likely to favor shrubs and fire dependent annuals. Light burns may appear to support the highest post-fire species diversity because few species seem to explicitly require a severe surface fire environment. On the other hand, burns that are uniformly low to moderate in severity might fail to generate the high severity microsites required by some tree seedlings. Studies suggest that *Sequoiadendron giganteum* [Lindl.] Buschh. (giant sequoia) germinates and survives best on the ashy mineral soil created by the hottest fires (Harvey et al. 1980), and that seedlings of many mixed-conifer tree species germinate most often in the largest fire-created canopy gaps (Kilgore 1973; Demetry and Duriscoe 1996). The observation that one tree species, *A. concolor,* germinated more often on high severity burn sites supports these previous studies; however, longer term observations are needed to determine whether germination from this abundant and prolific seeder translates into successful seedling establishment. I was unable to determine the best microsites for tree regeneration for other tree species due to the small area sampled and, perhaps, because the prescribed burn did not generate the kind of intense fire that

Table 2. Understory species sorted along a gradient of fire sensitivity.

	FIRE SENSITIVE		FIRE TOLERANT		FIRE STIMULATED	
	Disappeared after fire	**Survived more often on light fuel plots**	**Post-fire occurrences match pre-fire**	**New occurrences more often on light fuel plots**	**New occurrences on both light and heavy fuel plots**	**New occurren more often o heavy fuel plo**
Other species	little prince's pine *(Chimaphila menziesii)*	woodland bromegrass*† *(Bromus laevipes)*	bitter dogbane*# *(Apocynum androsaemifolium)*		Sierra morning-glory *(Calystegia malacophylla)*	white fir* *(Abies concolor)*
	bush chinquapin *(Chrysolepis sempervirens)*	Sequoia bedstraw* *(Galium sparsiflorum)*	Yosemite rockcress† *(Arabis repanda)*	miner's lettuce‡ *(Claytonia perfoliata)*	cryptantha species *(Cryptantha sp.)*	
	mountain sweetcicely§ *(Osmorhiza chilensis)*	glaucous-leaved raspberry‡ *(Rubus glaucifolius)*	hairy brackenfern† *(Pteridium aquilinum)*		Coville's groundsmoke‡ *eriospermum)*	
	white-veined wintergreen *(Pyrola picta)*	creeping snowberry* *(Symphoricarpos mollis)*	common elderberry‡ *(Sambucus mexicana)*		chaparral nightshade *(Solanum xanti)*	
	waterleaf phacelia *(Phacelia hydrophylloides)*		Lemmon's campion‡ *(Silene lemmonii)*			
	thimbleberry *(Rubus parviflorus)*					
	false Soloman's-seal *(Smilacina racemosa)*					
Fire-stimulated Shrubs				snow bush* *(Ceanothus cordulatus)*	greenleaf manzanita *(Arctostaphylos patula)*	
				bitter cherry* *(Prunus emarginata)*	littleleaf ceanothus *(Ceanothus parvifolius)*	
				Sequoia gooseberry*† *(Ribes tularense)*	bid deervetch *(Lotus crassifolius)*	

* significant treatment effect ($p < 0.05$)

† significant pre-fire presence effect ($p < 0.05$)

‡ too few post-fire occurrences to analyze statistically

§ survived on 5 out of 18 quadrants, no significant treatment effect

displays characteristics of both columns

creates canopy openings.

The species that establish after fire fall into three general life history categories: (1) fire-stimulated shrubs (see Table 1), (2) annual forbs (*C. perfoliata*, *G. eriospermum*, and *Cryptantha sp.*, and (3) perennial forbs (*C. malacophylla*, and *S. xanti*). Because long-distance animal dispersal into the area is probably a relatively rare event given the burned forest understory (with sparse food availability) and the short time since fire, the animal dispersed shrub species likely germinated from the seed bank. At least two of the species showing reduced tolerances to more severe burn conditions, *R. tularense* and *A. androsaemifolium,* have smaller seeds than do many of the more heat tolerant shrubs including *A. patula*, *L. crassifolius*, and the *Ceanothus* species. Previous studies in chaparral have demonstrated that smaller seeded species are less tolerant of high temperature pulses than are large seeded species (Keeley et al. 1985). The annual forb *C. perfoliata,* which is also known to germinate from the seedbank after fire (Toth 1991), has small seeds that are also probably killed at high temperatures. The other annual forbs have small seeds favoring long distance dispersal and are likely to have arrived in the area after fire. These species are relatively common in unburned sites, yet they take advantage of the increased resource availability and reduced competition following fire (Keeley et al. 1985). The perennial forbs *C. malacophylla* and *S. xanti* were not common in the area before the fire and likely germinated from the soil seedbank.

The impacts of the two treatments on the forest floor environment, including the effects of fire severity on seedbed soil characteristics and the suppression of interspecific competition, should be most dramatic immediately after fire (Gebauer 1993). Therefore, fire-generated microenvironments should have the strongest influence on determining post-fire community composition during the initial post-fire period. The legacy of the initial post-fire plant community is likely to endure, especially for the fire-stimulated species, which germinate from the seedbank only during the first year after fire. The post-fire distribution of slow spreading, fire sensitive species is also likely to persist for many years following fire, while the post-fire spatial pattern of annuals and other readily dispersed species will be less apparent with increasing time-since-fire.

A central justification for structural and process restoration goals is the assumption that ecosystem health and biodiversity will follow from restoration of forest structure or the reintroduction of ecosystem processes such as fire (Landres et al. 1999; Stephenson 1999). Under current management strategies, however, spatial heterogeneity in fire effects is not stated as a process goal; nor is biodiversity preservation stated as a structural goal (National Park Service 2004). If the results from this small study prove to be characteristic for mixed-conifer forests more broadly, and when conservation of native biodiversity is an objective of forest management, burn prescriptions should promote spatial variability in fire effects, especially when fuels are heavy and continuous. Studies have shown that burning under relatively mild (moist) conditions creates a heterogeneous burn pattern, with lightly burned, severely burned, and unburned forest floor patches, even if fuel loads are homogeneous (Miller and Urban 1999; Rocca 2004; Knapp and Keeley 2006). This provides a potential strategy by which managers can reduce fuel load and continuity while generating a heterogeneous burn pattern.

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Monique Rocca received her Ph.D. from the Nicholas School of the Environment at Duke University. She is currently Assistant Professor of Wildland Fire Science at Colorado State University.

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