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Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone

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Abstract. Due to fire suppression policies, timber harvest, and other management practices over the last century, many low- to mid-elevation forests in semiarid parts of the western United States have accumulated high fuel loads and dense, multi-layered canopies that are dominated by shade-tolerant and fire-sensitive conifers. To a great extent, the future status of western US forests will depend on tree species' responses to patterns and trends in fire activity and fire behavior and postfire management decisions. This is especially the case in the North American Mediterranean-climate zone (NAMCZ), which supports the highest precipitation variability in North America and a 4- to 6-month annual drought, and has seen greater-than-average increases in air temperature and fire activity over the last three decades. We established 1490 survey plots in 14 burned areas on 10 National Forests across a range of elevations, forest types, and fire severities in the central and northern NAMCZ to provide insight into factors that promote natural tree regeneration after wildfires and the differences in postfire responses of the most common conifer species. We measured site characteristics, seedling densities, woody shrub, and tree growth. We specified a zero-inflated negative binomial mixed model with random effects to understand the importance of each measured variable in predicting conifer regeneration. Across all fires, 43% of all plots had no conifer regeneration. Ten of the 14 fires had median conifer seedling densities that did not meet Forest Service stocking density thresholds for mixed conifer forests. When regeneration did occur, it was dominated by shade-tolerant but fire-sensitive firs (*Abies* spp.), Douglas-fir (*Pseudotsuga menziesii*) and incense cedar (*Calocedrus decurrens*). Seedling densities of conifer species were lowest in sites that burned at high severity, principally due to the biotic consequences of high severity fire, for example, increased distances to live seed trees and competition with fire-following shrubs. We developed a second model specifically for forest managers and restoration practitioners who work in yellow pine and mixed conifer forests in the central NAMCZ to assess potential natural regeneration in the years immediately following a fire, allowing them to prioritize which areas may need active postfire forest restoration and supplemental planting.

Key words: fire severity; fire suppression effects; fire-stimulated shrubs; forest resilience; forest restoration; natural regeneration; postfire conifer regeneration model; seed tree.

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Introduction

Fire plays an important ecological role in many forest ecosystems, including creation and maintenance of landscape structure, recycling of nutrients, biodiversity regulation, and both consumption and production of forest fuels (Agee 1993, Covington and Moore 1994, Sugihara et al. 2006). Many plants in western US forests have evolved traits that allow them to persist in a variety of fire regimes, including fire-resistant bark, self-pruning limbs, and sexual and/or asexual regeneration (i.e., seeder and/or resprouter species; Pausas et al. 2004). However, the frequency, size, and severity of wildfires across much of the western United States are increasing (Lenihan et al. 2008, Miller et al. 2009, Westerling et al. 2011, Miller and Safford 2012, Safford et al. 2012), potentially altering tree and woody shrub responses. Forest managers need to understand what limits and promotes natural conifer regeneration in the postfire environment, especially following high severity fires, so that forests might be better managed for long-term sustainability and resilience in a changing world (Brown et al. 2004, Crotteau et al. 2014).

In seasonally dry western forests, fire severity (defined here as basal area mortality from fire) and frequency are major drivers of plant community structure and forest successional patterns (Diaz-Delgado et al. 2003, Collins et al. 2007, Keeley 2009, Pierce and Taylor 2011). In the North American Mediterranean-climate zone (NAMCZ; southwestern Oregon, most of California, northwesternmost Mexico), yellow pine (*Pinus ponderosa* and *P. jeffreyi*) and mixed conifer (together we refer to these here as "YPMC") forests historically experienced frequent low and moderate severity fires (Stephens and Collins 2004, Beaty and Taylor 2007; Safford and Stevens, 2016), with mean fire return intervals of approximately 11–16 yr; at higher elevations, firs (*Abies* spp.) are more dominant, and pre-Euro-American fires were less common (FRIs ≥ 40 yr) and more severe (Van de Water and Safford 2011, Mallek et al. 2013). Frequent low to moderate severity fires in YPMC forests reduced fuel loads, fashioned landscape heterogeneity, exposed mineral soil, and released light, water, and nutrient resources that are critical to regenerating forests (North et al. 2009, Peterson et al. 2009, Franklin and Bergman 2011). Such fires have been promoted as a tool for restoring ecosystem structure and function to many degraded mid-elevation forests in the NAMCZ (Brown et al. 2004, Shatford et al. 2007, North et al. 2009). High severity fires are recognized as an integral part of the fire regimes in some forest ecosystems (Swanson et al. 2010), particularly for serotinous tree species that rely on high severity fires to open cones and release seeds in a favorable postfire environment rich in nutrients and low in competition. In YPMC and similar forests however, fires with extensive areas of high severity effects were historically uncommon (Mallek et al. 2013; Safford and Stevens, 2016) and have been shown to have negative impacts on soil, plant diversity, and forest regeneration (Miller et al. 2011, Collins and Roller 2013, DeSiervo et al. 2015, Stevens et al. 2015), in the latter case by removing seed sources, transforming some forest sites into shrubfields that persist for decades (Russell et al. 1998, Shatford et al. 2007).

Due to fire suppression policies, timber harvest, and other management practices over the last century, millions of hectares of YPMC forests in the western United States are in a state of high density, enhanced fuel loading, and dominance primarily by middle-aged cohorts of trees (McCreary 2001, Gray et al. 2005, Cocking et al. 2012). Past management has also changed forest species composition and structure by increasing the abundance of shade-tolerant and fire-sensitive species, while decreasing density of fire-resistant and shade-intolerant species like ponderosa pine and Jeffrey pine (Barbour et al. 2007; Safford and Stevens, 2016). Together, these factors are leading to a greater occurrence of high severity wildfires in YPMC forests, especially in the Southwest and the Sierra Nevada (Miller et al. 2009, Dillon et al. 2011, Miller and Safford 2012, Mallek et al. 2013). Climate change is expected to exacerbate this trend in most of the western United States (Lenihan et al. 2008, Safford et al. 2012), and future forest composition and ecosystem resilience will depend on how species respond to increased fire severity and management decisions in the postfire environment (Lloret et al. 2005, North et al. 2007).

Forest managers are faced with difficult decisions in the first years following a wildfire. Will natural regeneration meet restocking objectives across the burned landscape? If not, which species should be planted? At what absolute and relative densities should they be replanted? What sorts of site preparation and vegetation control should be undertaken, if any? Supplemental planting in the wake of severe wildfires has long been a common practice to help meet silvicultural goals and can expedite forest recovery (Helms and Tappeiner 1996, Brown et al. 2004). However, due to the excessive size of many contemporary wildfires coupled with a lack of restoration funds, replanting is often prohibitively expensive across large swaths of severely burned forest (Palmer et al. 1997, Crotteau et al. 2014). Although models are useful tools for land managers to better understand revegetation dynamics and help predict forest recovery, there is a scarcity of postfire regeneration models that integrate biotic and abiotic factors.

This study examines the biotic and abiotic factors that influence conifer regeneration success across multiple fire sites and years. Previous research has shown that natural conifer regeneration is most limited by propagule arrival, the availability of bare mineral soil and safe microsites that mitigate heat stress, and available moisture in the first few years of recolonization of burned landscapes (Hobbs et al. 1992, Zald et al. 2008, Irvine et al. 2009, Pierce and Taylor 2011). Although a number of studies have examined the effects of a single fire on specific species (Harvey et al. 2011, Pierce and Taylor 2011, Dodson and Root 2013, Crotteau et al. 2013, 2014), few have tracked species-specific responses across multiple fires spanning a range of elevation, annual precipitation, forest types, and fire severities (Shatford et al. 2007, Collins and Roller 2013). Single-fire and single-species studies have limited application in understanding forest community assembly and succession in the postfire environment. Similarly, current models based on single fires do not capture the high variability present in low- and mid-elevation forests in the NAMCZ. In a recent study that analyzed regeneration patterns after multiple fires, Collins and Roller (2013) found that conifer regeneration was highly variable, and 80% of their plots had no tree regeneration. However, the five fires in that study burned within 30 km of each other and thus represent a relatively small proportion of geographic variability in these diverse forests.

This study is unique in its size and scope, examining factors that promote and limit multiple species conifer regeneration in the postfire environment across many fire sites, forest types, and fire severities. We investigated postfire conifer and shrub regeneration 5–11 yr after fire in 14 large (>400 ha) wildfires that occurred between 1999 and 2007 on National Forest lands in the central and northern NAMCZ, which corresponds to central and northern California. The objectives of this study were to (1) quantify postfire conifer tree regeneration across a range of environmental conditions, (2) develop statistical models to link environmental, biotic, and abiotic variables with conifer regeneration success, (3) develop a model that forest managers can use in the field to predict conifer seedling density after wildfires, and (4) explore whether natural regeneration alone will meet forest stocking objectives. Understanding forest recovery and regeneration processes after severe fires will give insight into the mechanisms that drive ecological change after such disturbances, which is critical to appropriately implementing management strategies on National Forest lands in a shifting and increasingly variable climate.

Methods

Study sites

Our study was conducted on 14 fires that burned in 10 National Forests in California (see Table 1, Fig. 1). Most of the fires occurred between 2002 and 2007, with the exception of the Pendola Fire (1999). Sampled fires were all in excess of 405 ha (1000 acres) in size, ranging from 477 ha to 37,886 ha. Elevations ranged from 470 to 2300 m, over a latitudinal extent of approximately 600 km. Mean annual precipitation ranges across the study sites from approximately 380 to 1640 mm/yr. Mean maximum (July) temperatures range from 22.7° to 29.3°C, and mean minimum (January) temperatures range from −4.7° to 4.5°C (Thorne et al. 2015).

Forest type and dominant species

Each fire spanned a range of elevations and climatic conditions that support a variety of different forest types. We stratified our analyses by forest type, using the Classification and Assessment with Landsat of Visible Ecological Groupings (CALVEG) vegetation classification system (USDA 2013). The CALVEG classification system is based upon the National Vegetation Classification System (NVCS) and is at a finer scale than most classification systems focused on fire regimes. We categorized the CALVEG vegetation types in our plots into five broadly defined forest types based on similarity in climate, species assemblages, and relationships with fire (Table 2). We also

Table 1. Summary of fires and forest type.

Fire year	Fire name	National forest	Area burned (ha)	Year sampled	MEG plots	DMC plots	MMC plots	YP plots	FIR plots	All forest types
1999	Pendola	Plumas, Tahoe	4975	2010–2011	140	38	0	1	0	179
2002	Showers	Lake Tahoe Basin	294	2009	0	0	17	0	0	17
2003	Spanish	Mendocino	2333	2010	15	112	11	6	12	156
2004	Deep	Sequoia	480	2009	15	0	0	2	0	17
2004	Freds	Eldorado	1716	2009	4	100	16	2	11	133
2004	Power	Eldorado	5144	2009	9	109	28	13	5	164
2004	Straylor	Lassen	985	2009	0	0	0	56	0	56
2004	Sims	Shasta-Trinity, Six Rivers	1192	2010	96	3	1	0	0	100
2005	Harding	Tahoe	477	2010	0	0	15	47	0	62
2006	Bar	Klamath, Shasta-Trinity	37,886	2011	27	10	53	3	0	93
2006	Bassetts	Tahoe	874	2011	0	1	44	0	67	112
2006	Ralston	Eldorado, Tahoe	2385	2011	18	60	0	13	0	91
2007	Antelope	Plumas	9022	2012	0	30	46	50	0	126
2007	Moonlight	Plumas	18,216	2012	0	26	99	53	6	184
Totals					324	489	330	246	101	1490

Notes: We collected data on 14 fires located in 10 National Forests. Plots were installed across the fire severity gradient, determined a priori based on severity classification maps developed by the Remote Sensing Lab (USFS). Plots were established across a range of aspects, slopes, and elevations. Forest types are: MEG, mixed evergreen; DMC, dry mixed conifer; MMC, moist mixed conifer; YP, yellow pine; FIR, fir.

established a rule set based on postfire local species dominance (presence of hardwoods, black oak, and/or Douglas-fir) recorded at the plot level to differentiate between mixed conifer types (both moist and dry) and mixed evergreen forest types. Plots that were dominated by hardwoods and lower elevation Douglas-fir were classified in the mixed evergreen forest type (22%). Dry mixed conifer (<1000 mm annual precipitation) forests had a higher yellow pine component, while moist mixed conifer (>1000 mm annual precipitation) generally had a greater number of firs (Safford and Stevens, 2016). Of the 1490 surveyed plots, 55% were classified as mixed conifer forest types (dry and moist), and a further 17% were classified as yellow pine forest (Table 1). Due to the small sample size, red fir and white fir forest types were combined into a fir forest type (7%).

This study focuses on conifer species common to the majority of our study sites (Table 3) and includes ponderosa pine (PIPO) and Jeffrey pine (PIJE), sugar pine (*P. lambertiana,* PILA), western incense cedar (*Calocedrus decurrens*, CADE), Douglas-fir (*Pseudotsuga menziesii,* PSME), white fir (*Abies concolor,* ABCO), and red fir (*A. magnifica,* ABMA). These conifer species differ ecologically in their tolerance for shade, drought, and resistance to fire. The shade-intolerant but fire-resistant ponderosa pine and Jeffrey pine have thick bark when young that aids their survival in frequent fire ecosystems (Safford and Stevens, 2016). These two species also self-prune their lower limbs, offering protection of the canopy from flames burning in surface fuels (Franklin and Bergman 2011). Sugar pine has slightly thinner bark when young, is somewhat more susceptible to fire-caused mortality, and has an intermediate tolerance for shade (Burns and Honkala 1990). However, once mature, sugar pine typically has thicker bark than the both ponderosa and Jeffrey pines (Safford and Stevens, 2016). The shade-tolerant but fire-sensitive white fir, red fir, and western incense cedar are able to regenerate under full shade but are often killed by fires that yellow pines survive (Zald et al. 2008, Cocking et al. 2014). Douglas-fir has an intermediate tolerance for shade and intermediate sensitivity to fire.

Broadleaf ("hardwood") tree species include black oak (*Quercus kelloggii*), canyon live oak (*Q. chrysolepis*), Pacific madrone (*Arbutus menziesii*), tanoak (*Notholithocarpus densiflorus*), and big-leaf maple (*Acer macrophyllum*). Most of the hardwood (non-conifer) species resprout from their root crowns after being top-killed by fire (Plumb and Gomez 1983). In contrast, the conifer species are reliant on seed recruitment (obligate seeders) and establishment from seed trees that survived the fire or were located outside the fire perimeter. Dominant shrubs in our study sites include deerbrush (*Ceanothus integerrimus*),

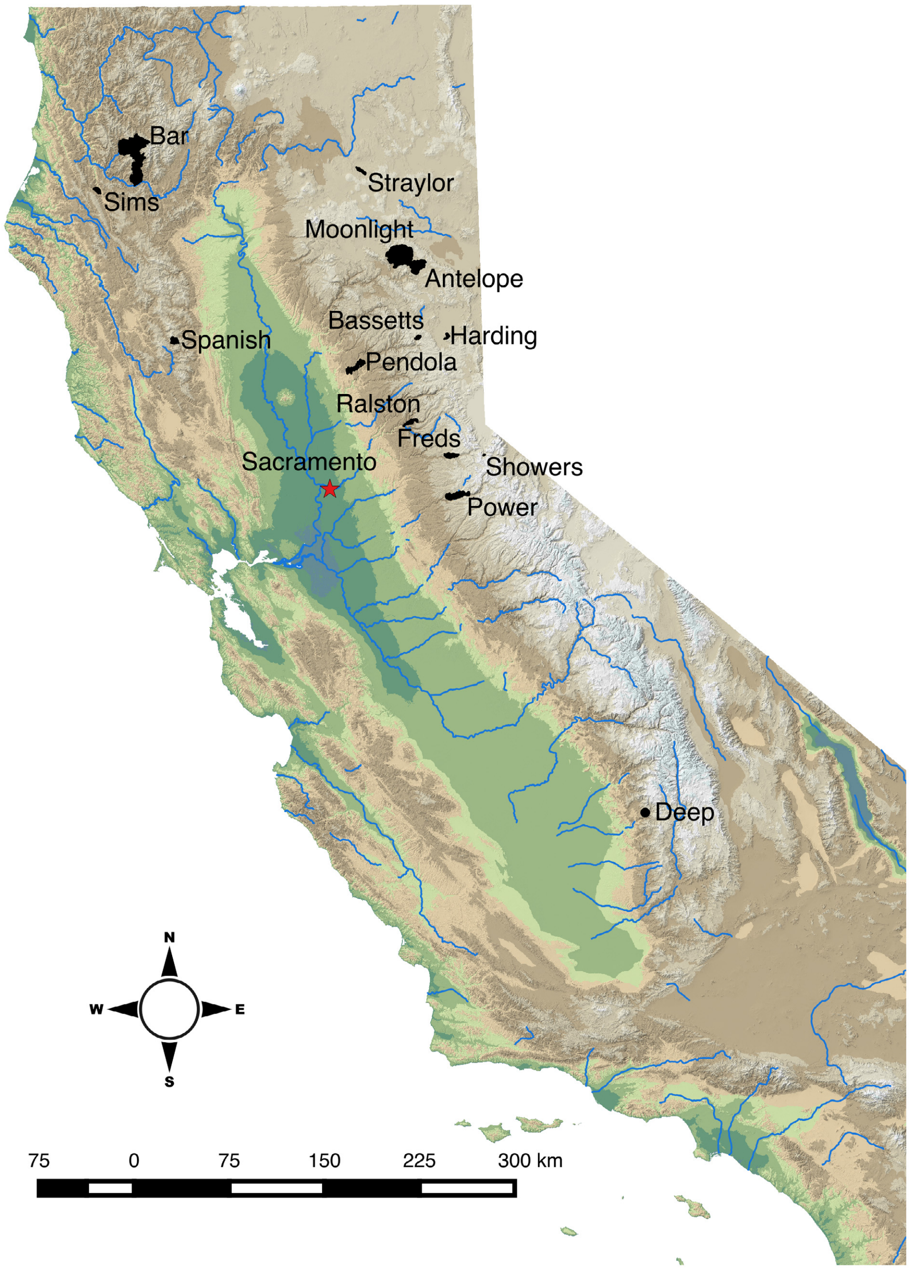

Fig. 1. Map of field sites. Data were collected on 10 National Forests and 14 wildfires between 2009 and 2012. Black polygons represent the fire perimeters. See Table 1 for detailed information about sampled fires and corresponding forest types.

mountain whitethorn (*C. cordulatus*), whiteleaf manzanita (*Arctostaphylos viscida*), greenleaf manzanita (*A. patula*), Sierra gooseberry (*Ribes roezlii*), bitter cherry (*Prunus emarginata*), chokecherry (*P. virginiana*), and California blackberry (*Rubus ursinus*).

Field data collection

Data were collected during four field seasons from 2009 to 2012, mostly surveying fires 5 yr after they burned (Fig. 1). Four of the 14 fires were sampled outside of the five-year span, including the Pendola (11 yr), Spanish and

Table 2. Forest types based on pre-Euro-American settlement fire regimes (PFR).

Forest type	Mean FRI (yr)	Mean min. FRI (yr)	Mean max. FRI (yr)	Dominant tree species
Mixed evergreen	29	15	80	*Quercus* spp. *Arbutus menziesii* *Notholithocarpus densiflorus* *Pseudotsuga menziesii*
Dry mixed conifer	11	5	50	*Pinus ponderosa* *P. lambertiana* *Calocedrus decurrens* *Abies concolor* *Quercus kelloggii*
Moist mixed conifer	16	5	80	*A. concolor* *P. menziesii* *C. decurrens* *Pinus lambertiana* *P. ponderosa*
Yellow pine	11	5	40	*P. ponderosa* *P. jeffreyi* *P. lambertiana* *Q. kelloggii*
Fir	40	15	130	*A. concolor* *Abies magnifica*

Notes: Forest types are based on species composition and were determined by extracting vegetation layers from the CALVEG classification maps and subsequently binning them into five broad vegetation types. Forest type was further validated by plot-level species dominance. FRI, Fire Return Interval. *Source:* Barbour et al. (2007) and Van de Water and Safford (2011).

Showers (7 yr), and Sims fires (6 yr). We sampled fires, and areas within fires, that had not been salvage harvested or replanted since the fire. Our project began as a collaboration with the Forest Service Pacific Southwest Region silviculture staff to determine rates of natural regeneration in fires that had not been replanted after fire and where enough time had passed that planting would be logistically and financially prohibitive. We focused on burned areas 5 yr after fire because the National Forest Management Act (Hoberg 2004) and Forest Service regulations (e.g., Forest Service Handbook 2409.13-21.42) require that productive forest be restocked within 5 yr after a major stand altering event, such as major tree harvest or a stand-replacing fire. Five years is also a forestry "rule of thumb" threshold beyond which burned areas require

Table 3. Conifer tree species and ecological tolerances.

Group	Species	Scientific name	Symbol	Elevation (m)	Seed weight (g)	Ecological tolerance		
						Shade	Drought	Fire
Firs	White fir	*Abies concolor*	ABCO	300–2100	0.015–0.055	High	Low	Low
	Red fir	*Abies magnifica*	ABMA	1700–2300	0.015–0.07	High	Low	Low
Incense cedar	Incense cedar	*Calocedrus decurrens*	CADE	600–2100	0.015–0.07	High	Low	Low
Douglas-fir	Douglas-fir	*Pseudotsuga menziesii*	PSME	300–2100	0.01–0.02	Intermediate	Intermediate	Intermediate
Pines	Ponderosa pine	*Pinus ponderosa*	PIPO	300–1800	0.02–0.07	Low	High	High
	Jeffrey pine	*Pinus jeffreyi*	PIJE	1500–2400	0.08–0.2	Low	High	High
	Sugar pine	*Pinus lambertiana*	PILA	1000–2000	0.15–0.3	Low	High	Intermediate

Notes: Conifer species are grouped by similarities in tolerance to shade, drought, and fire. Red fir and white fir are grouped together (firs) due to the relatively small contribution of red fir seedlings to total conifer regeneration. Incense cedar and Douglas-fir each form their own group with unique ecological tolerances. Pines, comprised of ponderosa, Jeffrey, and sugar pines, share similar ecological tolerances to shade, drought, and fire. *Source:* Safford and Stevens (2016).

Table 4. Fire severity assessments.

Ocular estimate: Description	Ocular estimate: Fire severity class*	Fire severity label	Percentage basal area mortality	RdNBR: Fire severity class
Unburned	0	Unburned	0	1
Lightly burned, no sig. overstory mortality, patchy spatial burn pattern, groups of surviving shrubs/saplings	1	Low	0–10	2
		Low	10–25	3
Lightly burned, isolated overstory mortality, most saplings/shrubs dead	2	Low-moderate	25–50	4
Moderately burned, mixed overstory mortality, understory mostly burned to ground	3	High-moderate	50–75	5
High intensity, significant proportion (75–90%) of overstory killed, dead needles remaining on trees 1 yr later	4	High	75–90	6
High intensity burn, total/near total mortality of overstory, most needles consumed in fire	5	High	>90	7

Notes: Remotely sensed fire severity classification is based on the Relative difference in Normalized Burn Ratio (RdNBR) obtained from pre- and postfire LANDSAT images. Field-based ocular estimates were grouped in five fire severity classes based on the amount of tree basal area mortality. These are the inverse of the severity classes from the National Park Service Fire Monitoring Handbook, which codes high severity fire as "0" and no fire as "5."

major extra investment in site preparation to plant and planting in such locations is rarely undertaken.

Potential sites were identified by GIS pre-work in collaboration with USFS personnel. Large wildfires (>400 ha) are automatically assessed for fire severity by remote sensing analysis based on the Relative differenced Normalized Burn Ratio (RdNBR) between pre- and postfire LANDSAT imagery (Miller and Thode 2007). The vegetation burn severity maps are then classified into seven categories of severity that are defined by the percentage of tree basal area killed by fire (Table 4).

In Forest Service Region 5 (which includes California), "deforested" lands are considered those that lose >50% of their pre-fire basal area (basal area mortality classes 5–7, Table 4). These areas are identified for each large fire in Region 5, and then, "treatable" (as defined by the Forest Service; i.e., lands where planting is permitted) deforested acres are identified by overlaying information on land ownership (USFS and other), land suitability (general forest, wilderness, roadless areas, etc.), vegetation type, and slope (for more information, see http://www.fs.usda.gov/detailfull/r5/landmanagement/resourcemanagement/?cid=STELPRDB5362659). A 200 × 200 m grid was overlaid on each fire area in GIS, and field plots were located at the grid nodes that met our field sampling conditions (i.e., USFS lands, non-wilderness, and untreated after fire). Unburned control plots (fire severity class 0) were also added to each fire in a 400 m buffer on the outside of the fire perimeters or in large unburned patches within the fire, representing a mix of plot aspects, slopes, and elevations. These selection criteria resulted in a total of 1490 sample plots across the 14 fires.

Field plots were sampled using a fixed 4.4 m (14.3-ft) radius (area = 60 m^2 or 1/70 acre). Site characteristics were measured, including slope, aspect, dominant vegetation, and plot treatment history. We visually estimated percentage areal cover by bare ground, rock, basal vegetation, litter (which included fine woody debris <7.6 cm diameter), and coarse woody debris (>7.6 cm diameter). Above-ground cover was visually estimated as percentage of the plot area for conifers, hardwoods, shrubs, forbs, and grasses. Live and dead overhead (>2 m height) canopy covers were also visually estimated. The depths of litter and duff (fermentation layer) were recorded as an average of three representative readings in each plot. Woody plants were identified to species; herbaceous plants were simply recorded as graminoid or forb. Nomenclature is from Jepson and Hickman (2012). Species were recorded using codes from the USDA PLANTS database (USDA, NRCS 2009; http://plants.usda.gov/).

The diameter at breast height (dbh; taken at 1.37 m height) of each surviving tree with dbh > 2.5 cm (1″) was recorded. We recorded

Table 5. Summary of fires and fire severity class.

Fire year	Fire name	National forest	Area burned (ha)	UB plots	LW plots	LM plots	HM plots	HI plots
1999	Pendola	Plumas, Tahoe	4975	18	17	16	19	109
2002	Showers	Lake Tahoe Basin	294	0	0	1	6	10
2003	Spanish	Mendocino	2333	15	3	19	15	104
2004	Deep	Sequoia	480	0	0	0	5	12
2004	Freds	Eldorado	1716	9	1	5	21	97
2004	Power	Eldorado	5144	12	1	7	18	126
2004	Straylor	Lassen	985	0	1	1	4	50
2004	Sims	Shasta-Trinity, Six Rivers	1192	12	3	3	10	72
2005	Harding	Tahoe	477	7	1	12	13	29
2006	Bar	Klamath, Shasta-Trinity	37,886	11	11	11	14	46
2006	Bassetts	Tahoe	874	22	13	14	14	49
2006	Ralston	Eldorado, Tahoe	2385	13	26	17	14	21
2007	Antelope	Plumas	9022	10	11	27	19	59
2007	Moonlight	Plumas	18,216	10	28	22	14	110
Totals				139	116	155	186	894

Notes: See Table 5 for a description of fire severity classes. Fire severity classes are: UB, unburned; LW, low; LM, low-moderate; HM, high-moderate; HI, high.

distance and compass direction from plot center to the nearest potential seed source (a sexually mature tree that could be expected to produce seed for natural regeneration) for each conifer and hardwood tree species for which we found a seedling in the plot. If no seedlings were found in the plot, we recorded the closest potential conifer and hardwood seed tree. Our laser rangefinder had an effective range of approximately 200 m, and we recorded that distance for all situations where there was no visible seed tree.

All postfire conifer and hardwood seedlings and saplings in each plot were counted, identified to species where possible, and aged by counting annual terminal bud scars (USDA 2008). For this study, we considered seedlings to be regenerating trees under 1.37 m height (dbh height), while saplings were trees greater than 1.37 m in height but less than 7.6 cm dbh (USDA 2008). The overall height and last year's growth of the tallest individual of each species were measured. Only completed growing seasons were counted as a full year of growth.

Postfire shrub regeneration was recorded within each plot by identifying species, measuring modal height, and estimating areal coverage as a percentage of the plot area; all cover values <1% were recorded as 0.5%. We used a variable radius plot with an English 20 BAF (basal area factor) gauge to calculate stand basal area (Grosenbaugh 1952); we tallied live and dead trees separately.

Fire severity assessment

A visual assessment of fire severity was recorded to account for local variability in severity at a finer scale than the 30 × 30 m LANDSAT pixels (Table 4). Field-based ocular estimates of fire severity in and immediately surrounding the field plots were compared to the remotely sensed RdNBR severity assessments and placed into one of six ordinal categories of fire severity based on thresholds of basal area mortality: (0) unburned (0% mortality), (1) low severity (0–25%), (2) low-moderate severity (25–50%), (3) high-moderate severity (50–75%), (4) high severity (75–90%), and (5) extremely high severity (>90%). We combined severity classes 4 and 5 into one high severity class (>75%) in the subsequent analysis (see Table 5 for plots in fire severity by fire).

Climate variables (mean annual precipitation, temperature maxima and minima) were obtained from climate surfaces developed by Thorne et al. (2015). Temperature minima and maxima were calculated as the maximum monthly temperatures averaged annually; maximum temperatures were averaged from April to September, and minimum temperatures were averaged from October to March. Time since last fire was extracted from Fire Return Interval Departure maps to identify the number of years since the last fire burned in control plots, as all other plots burned at the time of the fire (http://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=STELPRDB5327836; Safford and Van de Water 2014).

Data Analysis

Conifer stocking

A stocking analysis is a conventional forestry method used to assess the adequacy of natural and artificial regeneration and sets a median density threshold (i.e., must be met in at least 50% of the plots visited; Silvicultural Forest Handbook R5 1989). Stocking is defined as the degree of occupancy of land by regenerating trees and is measured in trees/unit area. Forest Service silvicultural goals for regenerating conifers in the study region are approximately 494 seedlings/ha (200 trees/acre) for mixed conifer forest types, and 740 seedlings/ha (300/acre) for fir forest types at a roughly 4.5 m spacing (Silvicultural Forest Handbook R5, USDA 1989). The recommended proportion of pines to shade-tolerant species in mixed conifer forests is 70:30 (R. Tompkins, USFS, *personal communication*) depending on site conditions, although any conifer species qualifies in the overall stocking analysis.

We corrected vertically projected regenerating seedling density estimates for slope. All saplings that regenerated since the fire (2.3% of all regenerating stems) were combined with counts of regenerating seedlings, as saplings were only present on the oldest fire (Pendola, 12-year-old fire) and in unburned controls and low severity plots of other fires. Species group summary statistics were compiled across and within fires, across and within forest types, and across a fire severity gradient to understand regeneration patterns.

Postfire conifer regeneration model

To better understand the factors that contribute most to successful postfire conifer regeneration, we developed generalized linear mixed models with nested random effects that integrated relevant abiotic and biotic variables for the five forest types that we sampled. We developed a second model for the mixed conifer + yellow pine forests (YPMC), as these forests comprise the majority of forested area in Sierra Nevada National Forests and experience by far the majority of contemporary fires. We combined mixed conifer and yellow pine because yellow pine had <250 plots, combining these forest types is common in the literature (e.g., Barbour and Minnich 1999, Miller and Safford 2012, Steel et al. 2015; Safford and Stevens, 2016) and there are strong successional relationships between them (Van Wagtendonk and Fites-Kaufman 2006; Safford and Stevens, 2016). Pairwise correlation graphs were generated to identify potential collinearity in the predictor variables. Temperature maxima were strongly correlated with elevation, so only elevation was used in the subsequent analyses. Distance to potential conifer seed tree was included as a five-level categorical variable, defined as follows: 0–30 m, >30–60 m, >60–120 m, >120–200 m, and >200 m. The first two levels reflect the dispersal rule of thumb that foresters often cite of "one or two tree lengths" (R. Tompkins, USFS, *personal communication*) or about 30 and 60 m. The final class reflects the fact that our laser rangefinder had a maximum range of approximately 200 m; hence, it represents locations with no visible seed tree. Note that actual mean distance to a viable seed tree is underestimated for high severity plots in Fig. 7, as about 19% of the high severity plots had no visible seed trees. See Appendix S1: Table S1 for a complete list of variables, how they were recorded, and any transformations that were employed.

Plot aspect and slope were transformed into a Topographic Index by multiplying the cosine of aspect by slope percentage (Stage 1976). Aspect was also transformed into northness (cosine of aspect), eastness (sine of aspect), and abs-aspect (the absolute value of 180 minus plot aspect) and compared in the subsequent models with the Topographic Index; only the abs-aspect variable was used in the final model selection as it showed the strongest statistical significance in the preliminary analysis. A solar insolation analysis was conducted in ArcGIS that combined field-based slope and aspect measurements with Digital Elevation Models to calculate heat load for each plot. Fire severity was treated as a categorical variable with five levels, as was forest type with five levels. Each plot was assigned to a fire, and plots were grouped according to spatial clusters nested within each fire. All other variables were continuous.

The dependent variable conifer seedling density, measured in regenerating stems/unit area (plot), was highly right-skewed, with 43% of the plots containing no conifer regeneration. Conifer

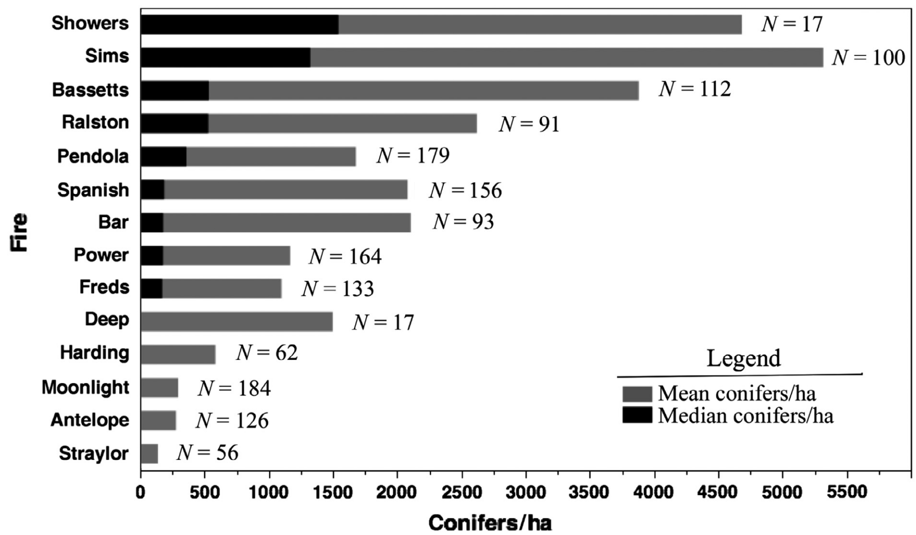

Fig. 2. Postfire conifer stocking across all forest types by fire. Refer to Table 1 for forest type plots by fire.

stem count data were analyzed with a zero-inflated generalized linear mixed model with the fire and cluster nested within fire specified as random effects. The use of the zero-inflated mixed model posits the zeroes as the result of two different processes: the binomial process and the count process (Zurr et al. 2013). We made the a priori decision to include the zero-inflation parameter to reflect two processes necessary to successful conifer regeneration: the arrival of viable seed (a binomial process) and the subsequent establishment and survival of seedlings (a count process). The excess zeroes in the count data may be result of a lack of viable seed arriving to the site as well as failure of seeds to germinate and survive after arrival. The data were modeled with a negative binomial distribution with a log link to account for strong overdispersion in the data, due to both the spike in zeros and the variance of the dependent variable being considerably greater than the mean (Potts and Elith 2006, Crotteau et al. 2014).

The predictive model building occurred in three segments, where similar explanatory variables were added to the model consecutively as a group (Appendix S1: Tables S3 and S4). The empty model included fire identity as a random effect, to account for within-fire variation. Cluster (a grouping of spatially close plots) was nested within fire to account for variation at the local scale. Subsequent groupings of variables were added to the empty model, and the best model was selected via AIC score, a measure that takes model fit into account and values parsimony in predictor variables (Potts and Elith 2006). All statistical tests were conducted in JMP and the R package glmmADMB (JMP version 9; SAS Institute; R version 1.13, Cary, North Carolina, USA).

Results

Conifer stocking across fires and forest types

Conifer regeneration in the studied fires was extremely heterogeneous, both among and within fires (Fig. 2, Tables 6 and 7). The overall mean conifer regeneration density (seedlings + saplings; hereafter we will refer to the combination as "seedlings") in the 14 fires we sampled was 1746/ha (±142 SE). However, over 43% of all plots had no regeneration and an additional 11% of plots had only one conifer seedling. Twenty-seven of 1490 plots (1.8% of the total) had seedling densities greater than three standard deviations above the mean of total conifer regeneration. When these plots were removed from the analysis, the mean conifer regeneration density aggregated across all fires dropped to 1166/ha (±68 SE).

The overall median density of conifer regeneration after fire was 176/ha. As with mean density, the median density varied tremendously among fires (Fig. 2, Table 7). For five of the 14 fires, the median seedling density was zero, and in four of

Table 6. Mean conifer densities by fire.

Fire	N^1	Pines	Firs	Douglas-fir	Incense cedar	Mean conifer seedlings + saplings/ha
Pendola	179	270	269	636	504	1679
Showers	17	1424	3260	0	0	4685
Spanish	156	399	827	797	59	2081
Deep	17	0	85	0	1414	1499
Freds	133	758	122	141	79	1100
Power	164	568	220	14	365	1167
Straylor	56	131	0	0	6	137
Sims	100	20	0	5288	10	5318
Harding	62	279	91	0	215	585
Bar	93	186	75	1845	0	2106
Bassetts	112	161	2810	354	556	3881
Ralston	91	767	261	708	885	2621
Antelope	126	164	14	77	24	278
Moonlight	184	103	136	25	32	295

Notes: See Table 4 for species composition of each of the four conifer groups. Mean conifer densities include both seedlings and saplings (2.3% of total conifer regeneration). N^1 is number of plots.

the remaining fires, the median density was <200/ha. Four fires had median densities >500/ha (Table 7). In these fires, the high mean and median densities were driven primarily by large numbers of shade-tolerant firs and incense cedar (Tables 6 and 7).

Ten of the 14 fires had median conifer seedling densities that did not meet Forest Service stocking density thresholds for mixed conifer forests (Fig. 3), and two of the five fires located in the fir forest type did not meet stocking thresholds for fir forests (Fig. 4). In mixed conifer forest, 12 of the fires did not meet Forest Service desired proportions of species (70% pines and 30% firs).

The four conifer groups were regenerating with near parity in dry mixed conifer forests (Fig. 5); pines and incense cedar showed their highest absolute densities in this forest type. Not surprisingly, firs had the highest seedling densities in the fir forest type, with a combined mean of 2493 (±777 SE) seedlings/ha. Also not surprisingly, Douglas-fir had greater regeneration success (1866 + 423 SE seedlings/ha) in the mixed evergreen forest than in other forest types. Seedling densities were generally low in the yellow pine forest type, but this was the only forest type in which pine (and incense cedar) regeneration was significantly higher than fir or Douglas-fir.

Table 7. Median conifer densities by fire.

Fire	N^1	Pines	Firs	Douglas-fir	Incense cedar	Median conifer seedlings + saplings/ha
Pendola	179	0	0	0	0	359
Showers	17	340	1001	0	0	1543
Spanish	156	0	0	0	0	186
Deep	17	0	0	0	0	0
Freds	133	0	0	0	0	171
Power	164	168	0	0	0	177
Straylor	56	0	0	0	0	0
Sims	100	0	0	1297	0	1323
Harding	62	0	0	0	0	0
Bar	93	0	0	0	0	178
Bassetts	112	0	334	0	0	533
Ralston	91	170	0	170	0	530
Antelope	126	0	0	0	0	0
Moonlight	184	0	0	0	0	0

Notes: Median conifer densities include both seedling and sapling density estimates. N^1 is number of plots.

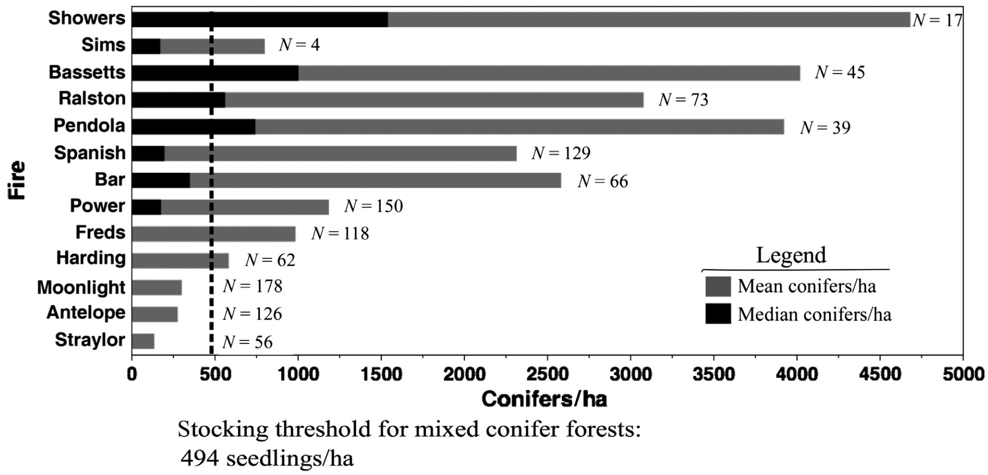

Fig. 3. Postfire conifer stocking in mixed conifer forest types by fire.

All forest types had a high percentage of plots with zero seedlings, especially in the YPMC types (mixed evergreen: 38%; moist mixed conifer: 41%; dry mixed conifer: 41%; yellow pine: 61%; fir: 32%). Although conifer establishment is highly stochastic and local geography influences regeneration success, plots with no conifer regeneration tended to be found in the interior of large, contiguous severely burned areas. Over 71% of plots with failed regeneration were burned with high severity; of these, 19% had no visible seed tree. The mean distance to potential seed tree in plots with no regeneration was 68.8 m (±2.8), and 37.0 m (±2.0) for plots with at least one regenerating conifer ($F = 89.9$, $P < 0.001$). Mean live basal area was also found to be approximately 200% greater in plots with at least one seedling than plots with no regeneration ($F = 74.2$, $P < 0.001$). Plots with failed regeneration had lower mean annual precipitation values: 966 mm as opposed to 1129 mm for plots with at least one seedling ($F = 104.9$, $P < 0.001$). Mean shrub cover was found to be higher (33%) in plots with no seedlings than in plots with conifer regeneration (23%; $F = 44.5$, $P < 0.001$). In general, plots with no regeneration were located in the interior of severely burned areas, farther from potential seed trees, in drier landscapes, and in areas with greater shrub presence.

Fire severity effects on conifer regeneration and other factors

Mean conifer seedling densities were unimodally related to fire severity: They were highest

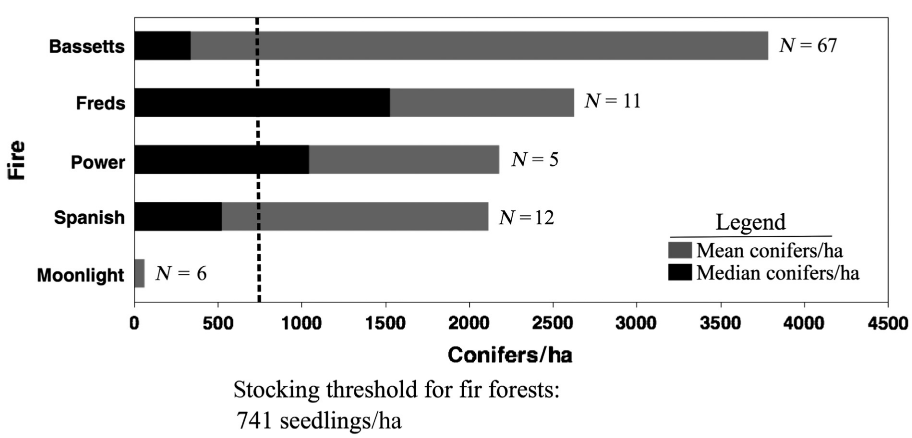

Fig. 4. Postfire conifer stocking in fir forest type by fire.

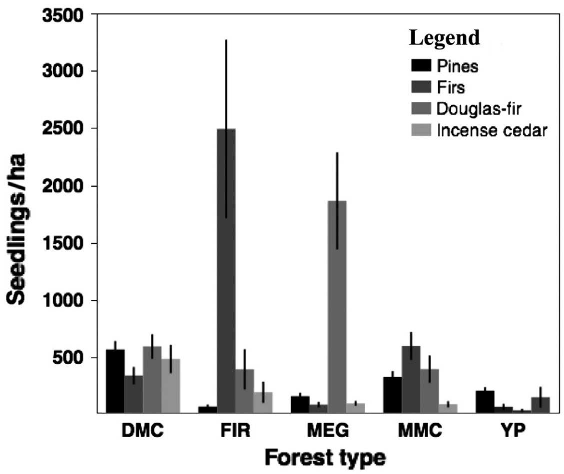

Fig. 5. Mean regenerating conifer densities by forest type. Mean densities of regenerating seedlings and saplings of the four species groups across five forest types are displayed. Median values were zero for all conifer groups in all forest types with the exception of firs in fir forest type, which had a median value of 186 seedlings and saplings/ha. See Table 4 for species composition of each forest type. See Table 1 for number of plots in each forest type.

at low-moderate and high-moderate fire severities, lowest at high fire severity, and intermediate in the unburned controls and low severity (Fig. 6; $F = 11.2$, $P < 0.001$). Median densities generally dropped along the gradient from no fire to high severity fire, and the median density in high severity fire plots was zero (Fig. 6). The highest spatial heterogeneity in conifer regeneration occurred in areas burned at low-moderate and high-moderate fire severities, where the differences between mean and median density are very large (mean densities much higher than median densities mean that there are scattered areas of very high density on the landscape). The lowest spatial variability in seedling densities was in the high severity class, followed by the unburned controls.

Although fire severity is a strong predictor of conifer regeneration, the effects of severity are more completely explained by the indirect effects of severity on increasing distance to potential seed sources and increasing shrub response and competition with seedlings. Distance to the nearest surviving seed trees increased by factor of 1.5–2.5× from unburned controls to areas of low and moderate severity fire, followed by a 4.5× increase as fire severity moved from high-moderate to high (Fig. 7; $F = 101.56$, $P < 0.001$). Conifer seeds had the farthest distance to travel in high severity plots with a mean distance to seed tree of 75.5 m (±2.4 SE). Note that the mean distances in the high severity group are underestimates of the true distances, as 19% of high severity plots had no visible seed tree and were thus entered as 200 m, the limit of our laser rangefinder. There was no difference in regeneration success whether the closest potential seed tree was upslope or downslope of plot center for all four conifer groups.

Fire severity was significantly related to patterns of bare ground, litter cover, shrub and herb cover, and live tree canopy (Fig. 8). Bare mineral soil increased from a mean of 5% cover in unburned plots to 13% in high severity plots ($F = 11.84$, $P < 0.001$). Five to 11 yr after fire, three percentage of high severity plots still had >60% bare mineral soil, an important threshold for erosion under heavy rain events (Page-Dumroese et al. 2000). Fire severity had a significant negative effect on percentage litter cover

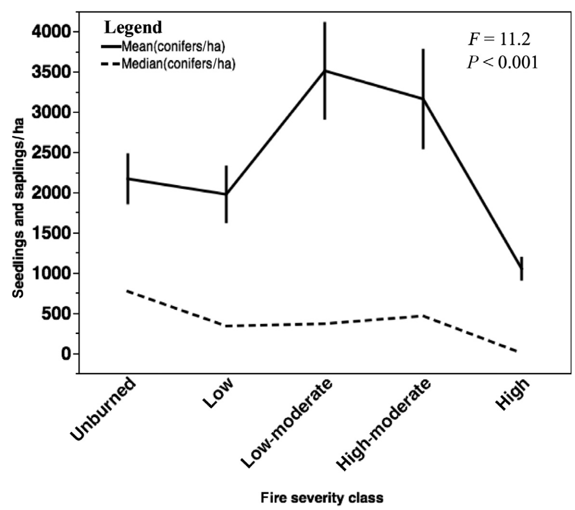

Fig. 6. Mean and median total conifer seedling densities across all fires. Mean and median values of total regenerating conifer seedlings and saplings. Mean values are often driven by a relatively small number of plots that have high regeneration rates. Median values are more representative of the spatial distribution of regenerating seedlings across the landscape. Error bars are based on ±1 SE.

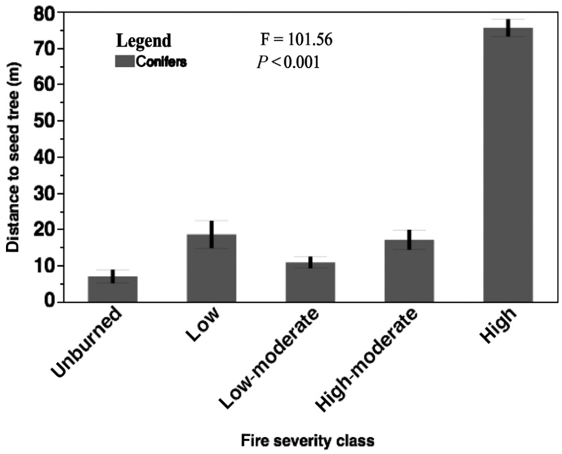

Fig. 7. Mean distance to live seed tree by fire severity class. Field crews measured the distance to the closest potential seed tree for each conifer species seedling that was found in the plot. When no regeneration was found in the plot, the closest conifer regardless of species was measured. Over 21% of the high severity plots had no visible conifer seed sources and were excluded from the means; thus, the actual mean distance to a viable seed tree is underestimated for high severity plots. Fire severity is an ordered categorical variable with five levels. Error bars are based on ±1 SE.

(F = 55.55, P < 0.001) and, especially and not surprisingly, live tree canopy (F = 313.31, P < 0.001). As fire severity increased, litter cover dropped from almost 80% in unburned plots to less than 50% in severely burned plots (Fig. 8). Along the same fire severity gradient, mean live tree cover decreased from a mean of 57% in unburned plots to 3% in high severity plots. Shrub cover 5–11 yr after fire was positively related to fire severity (F = 50.96, P < 0.001), although low and moderate plots were not significantly different. The mean shrub cover averaged across all fires was 11% in unburned plots and 35% in high severity plots. Herb cover was significantly increased by the presence of fire, but there was no statistical difference among the severity classes (F = 10.52, P < 0.001). The mean herb cover averaged across all fires increased from 8% in unburned plots to 20% in severely burned plots.

Postfire regeneration models

We developed two models that link conifer regeneration to biotic and abiotic variables.

The overall model (Tables 8 and 9) was calibrated by all 1490 plots across 14 fires and includes forest type as a five-level categorical variable. The second model was developed to link the explanatory variables to conifer regeneration specifically in YPMC forest types.

Our model output had a zero-inflation parameter of 1×10^{-6}, meaning that the seedling density for any given plot will be zero with probability P. In this case, logit(P) = 0 or the log (P/1 − P) = 0. Solving for P gives a value of 0.5, or 50% chance that the plot will have no regeneration. Over 43% of our plots had no regeneration, and the model captures this with an unbiased binomial probability. Our overall model predicts that conifer regeneration is negatively impacted by high severity fire, increased slope, greater distance to seed trees, increased shrub cover, and more southern aspects, while an increase in annual precipitation and forest stand live basal area generally augment conifer regeneration.

Relationships between biotic and abiotic variables and conifer regeneration

There were strong relationships between postfire regeneration and a number of the biotic and abiotic variables we measured (Tables 8 and 9 for model output; Appendix S1: Fig. S3 for univariate scatterplots; Appendix S1: Table S6 for seed tree distance class by fire severity class). Nine statistically significant explanatory variables were included in our final overall (e.g., including all forest types) predictive model (AIC = 7337.6, 8 points better than the second best model): distance to potential seed tree, slope, abs-aspect, annual precipitation, litter cover, shrub cover, live basal area, forest type, and fire severity (Tables 8 and 9; Appendix S1: Tables S3 and S4). Elevation, live overhead canopy cover, time since last fire, and the season of the fire were not statistically significant and were dropped from the model.

In our overall model, when accounting for the effects of the included predictor variables, only mixed evergreen forest showed a significant difference in seedling densities from the reference dry mixed conifer forest type, providing further support for our a priori decision to group the mixed conifer and yellow pine types. Distance to seed tree, shrub cover, and slope had the strongest negative relationships with conifer

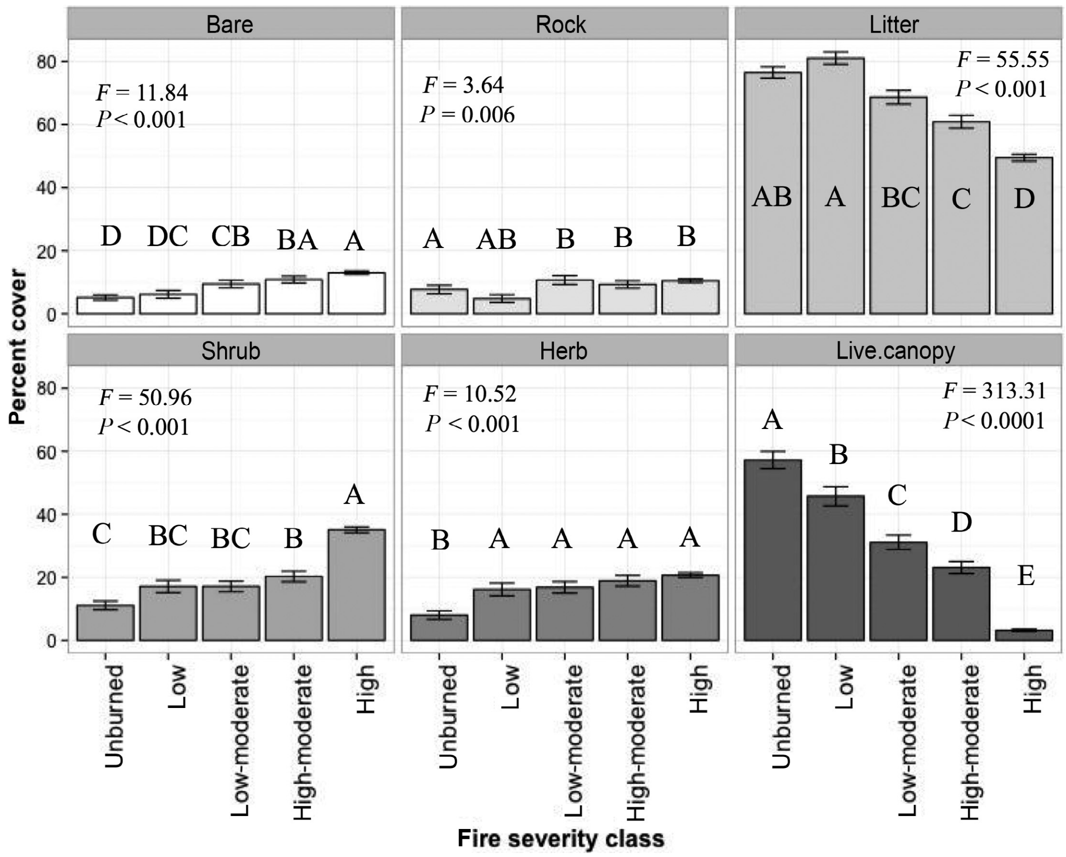

Fig. 8. Mean cover estimates by fire severity class. Error bars are based on ±1 SE. Levels not connected by the same letter are significantly different.

Table 8. Akaike's information criterion (AIC) score and random effects for generalized linear mixed model.

Model	All forest types	Mixed conifer forests
AIC	7337.6	4947.2
Random effects		
Fire	0.64 SD	0.72 SD
Cluster within fire	0.72 SD	0.81 SD
Dispersion parameter	0.40	0.40

Notes: Model is total conifers/plot = fire severity + distance to seed tree + shrub cover + litter cover + live basal area + slope + abs-aspect + annual precipitation + forest type + (1|Fire/cluster). See Appendix S1: Table S1 for a complete list of variables and their origins.

regeneration. In our model, distance to potential seed tree had a negative effect on conifer seedling density (Coeff. = −0.977, SE = 0.16, $P < 0.001$). As distance to potential seed tree increased, there was a consistent decrease in regenerating conifers. Increasing distance to seed tree by one distance category (e.g., from the 0–30 m level to the >30–60 m level) resulted in 62% less regenerating conifers (95% confidence interval 49–72%). Shrub cover also had a negative effect on regenerating conifers (Table 9, Coeff. = −0.011, SE = 0.002, $P < 0.001$): A 10% increase in shrub cover reduced the conifer seedling count by an average of 10% (95% confidence interval 6–15%). Slope had a negative effect on conifer seedling densities (Coeff. = −0.012, SE = 0.003, $P < 0.001$): With each 5 percentage increase in slope, regenerating conifers were reduced on average by 6% (95% CI: 3–10%).

On the other hand, live tree basal area, abs-aspect, and average annual precipitation had significant positive effects on conifer regeneration (Table 9). In our model, for every additional square meter of live basal area in the nearby

Table 9. Output for generalized linear mixed model with random effects.

Model	All forest types			Mixed conifer forests		
	Coefficients	SE	P	Coefficients	SE	P
Categorical variables						
Fire severity						
Linear	0.590	0.174	<0.001***	0.440	0.223	0.048*
Quadratic	−0.460	0.151	<0.001***	−0.441	0.187	0.019*
Forest type						
Mixed evergreen	−0.855	0.204	<0.001***			
Dry mixed conifer	reference					
Moist mixed conifer	0.156	0.185	0.398			
Yellow pine	−0.401	0.217	0.064			
Fir	0.035	0.310	0.909			
Biotic variables						
Distance to seed tree						
Linear	−0.977	0.158	<0.001***	−0.865	0.205	<0.001***
Shrub cover	−0.011	0.002	<0.001***	−0.009	0.003	<0.001***
Litter cover	0.010	0.002	<0.001***	0.011	0.003	<0.001***
Live basal area (m)	0.018	0.004	<0.001***	0.021	0.006	<0.001***
Abiotic variables						
Slope	0.012	0.003	<0.001***	−0.009	0.004	0.031*
Abs-aspect	0.005	0.001	<0.001***	0.008	0.001	<0.001***
Annual precipitation	0.003	0.001	<0.001***	0.003	0.001	<0.001***

Notes: Model is total conifers/plot = fire severity + distance to seed tree + shrub cover + litter cover + live basal area + slope + abs-aspect + annual precipitation + forest type + (1| Fire/cluster). See Appendix S1: Table S1 for a complete list of variables and their origins. Fire identity is specified as a random effect. Cluster (a grouping of spatially close plots) is nested within fire to account for variation at the local scale. Conifer stem count data are analyzed with a zero-inflated generalized linear mixed model, specifying a negative binomial distribution with a log link to account for strong overdispersion in the data. We chose dry mixed conifer forest type as the reference system in Model 1 because regeneration was more evenly distributed among the conifer groups, yellow pines had the highest densities compared to other forest types, and the sample size was the largest. All coefficients are on the log-scale.

*$P<0.05$; ***$P<0.001$.

stand, there is a 2% increase in conifer seedling density (Coeff. = 0.018, SE = 0.004, $P < 0.001$ [95% confidence interval 1–3%]), reflecting the presence of nearby potential seed trees. Abs-aspect, defined here as the absolute value of 180 minus plot aspect, had a significant effect on conifer regeneration ($P < 0.001$). Our model indicated that for every 10° increase in abs-aspect (a 10° shift to the North), there were 5% more seedlings (95% CI: 3–7%). For each increase of 10 mm of annual precipitation, our model also predicted a 3% (95% CI: 1–4%) increase in the number of seedlings.

Model validation for YPMC high severity plots

Reforestation efforts in burned areas in Forest Service Region 5 are currently focused on areas with more than 50% basal area mortality. However, data from the 14 fires we analyzed suggest that postfire regeneration in the high-moderate fire severity class (50–75% basal area mortality) is usually sufficient to meet current stocking guidelines. Thus, in our validation efforts, we focused on the high fire severity class (≥75% basal area mortality). We obtained independent tree regeneration data from four fires in YPMC forest that burned with high severity in our study region: the Angora Fire (2007) in the Lake Tahoe Basin (n = 72; H. D. Safford, *personal data*), the American River Fire (2008) on the Tahoe National Forest (n = 28; K.R. Welch, University of California, Davis), the BTU Lightning Fire (2008) on the Lassen and Plumas National Forests (n = 50; K. R. Welch, University of California, Davis), and the Rich Fire (2008) in the Feather River Canyon (n = 19; data from M. DeSiervo, Humboldt State Univ.). Data were sampled 5 yr after fires, except for the Rich that were collected 3 and 4 yr after fire.

Overall, our model overpredicted seedling densities when observed values were <1000 seedlings/ha, and underpredicted when observed densities

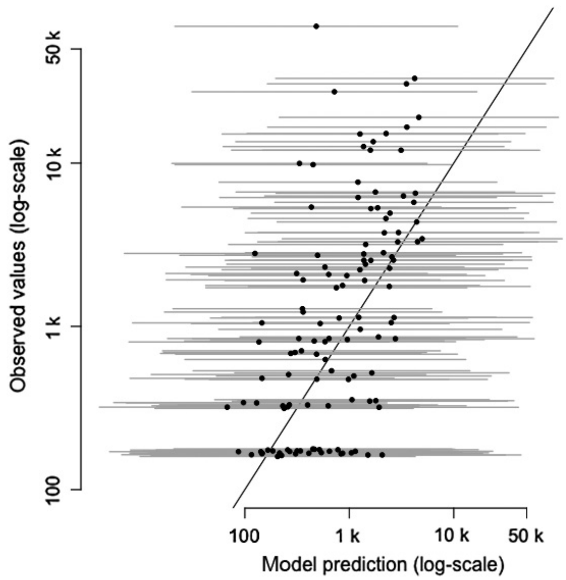

Fig. 9. Predicted seedling densities plotted against actual seedling densities (seedlings/ha) in high severity plots. 96% of the predicted counts are located within the confidence intervals generated by the mixed conifer forest regeneration model. The predicted counts are contingent on there being at least one seedling in the plot ($y > 0$); seedlings/ha.

were >1000 seedlings/ha, with the magnitude of the underprediction increasing with observed density (Fig. 9). When parsed by fire, the model underpredicted mean seedling densities and variation among plots on all four fires (Table 10), ranging from predicting 53% of observed mean densities on the BTU Fire, to only 9% on the Rich Fire (which included many plots that were more than three standard deviations from the mean). The model was somewhat better at predicting median densities, with an accurate prediction for the Angora Fire, an overprediction for the BTU Fire, and underpredicted median densities for the other two fires (Table 10).

Given high stochasticity and local idiosyncracies in the factors that drive actual seedling densities, managers may be more interested in knowing whether a site is likely to meet some predetermined measure of regeneration success. For the purposes of determining how accurately our model can predict whether a location is likely to support regeneration that is above or below a given stocking standard ±5 yr after fire, we measured agreement between the model and field data from the four independent fires using a confusion matrix, basing our comparison on the Region 5 stocking standard for YPMC forest (494 seedlings/ha).

Overall classification accuracy among the four fires averaged 74%, ranging from 62% on the BTU Lightning Fire to 82% on the American River Fire (Table 11). We also assessed “producer’s” and “user’s” accuracies, where producer’s accuracy refers to the probability that a plot that is above or below the threshold is actually classified as such by the model, while user’s accuracy measures the probability that a plot classified as above or below the threshold by the model is actually in that class on the ground. For the individual classes (>494 seedlings/ha and <494 seedlings/ha), overall producer’s accuracies were 58% and 64%, respectively, and overall user’s accuracies were 92% and 28%, respectively (summed from Table 11).

Field tool

To develop a useful tool for forest managers working in California YPMC forests in the first years following a fire, we used the model to create a set of graphics that identifies the predicted number of regenerating conifers 5–7 yr after high severity fire across a set of environmental conditions (Fig. 10 is in metric units, and Fig. 11 is in English units). We also developed a set of graphics to be used for areas that burned with high-moderate severity (Appendix S1: Figs. S1, S2), as USFS forest managers working in Region 5 also assess those areas for regeneration success. Using basic forestry tools such as a clinometer, a laser rangefinder, a basal area gauge, and a compass, a forest manager can use a simple sampling protocol (an example is given in Appendix S1) and paper copies of Figs. 10 or 11 to predict with approximately 70–80% accuracy whether conifer regeneration 5 yr after fire will be above or below a predetermined stocking threshold. The number of regenerating conifers 5 yr after fire can also be predicted from the figures, but obviously with much lower accuracy. Note that these predictions only apply where at least one seedling is found in the sample field plot, as in plots with no seedlings, there is an approximately 50% chance that no regeneration will occur before 5 yr. The example sampling protocol we described in Appendix S1 accounts for this.

Table 10. Predicted and actual seedling densities in high severity plots in YPMC forests.

Fire	YPMC	Predicted seedlings/ha			Actual seedlings/ha		
		Mean	Median	SD	Mean	Median	SD
Angora	Dry	211	175	91	538	167	1370
American River	Moist	1033	1038	467	4849	2171	7588
BTU Lightning	Moist	876	850	406	1647	418	2991
Rich	Moist	963	900	395	10,697	2839	16,772

Note: YPMC, yellow pine and mixed conifer.

Discussion

We found that (1) regeneration after fire in the central NAMCZ is highly heterogeneous; (2) most burned forest areas in the study area are not regenerating sufficiently to meet current Forest Service desired stocking levels; (3) the regeneration that is occurring is heavily dominated by shade-tolerant, fire-intolerant species; (4) fire severity is unimodally related to conifer regeneration, with the lowest regeneration rates occurring in high severity areas; and (5) levels of postfire conifer regeneration 5–7 yr after fire can be roughly predicted in the field using a handful of easily acquired variables.

Our data show that "seedling" (seedling plus sapling) densities after fire in our study area are highly heterogeneous on the landscape, with a small number of regeneration "jackpots" driving apparently high mean values. Various other studies of regeneration in the NAMCZ show similarly high spatial variability in regeneration (Stephens and Fry 2005, Shatford et al. 2007, Collins and Roller 2013, Crotteau et al. 2013). This high spatial variability leads us to question the usefulness of using mean seedling densities to quantify postfire (or any) regeneration. Median densities give a much better idea of the spatial coverage of regeneration (and this fact is represented in Forest Service stocking guidelines, which are based on medians), and they show that more than 40% of our sampled landscape does not support regeneration 5–7 yr after fire. Most of our plots lacking conifer regeneration were found in areas of high severity fire and in the drier forest types, and our data support growing concern that the well-documented trend toward larger and more severe fires is a major

Table 11. Confusion matrices based on YPMC model and high severity plots.

Predicted	Actual: Above 494 seedlings/ha	Actual: Below 494 seedlings/ha	User's accuracy (%)
(A) Angora fire (dry mixed conifer)			
Above 494 seedlings/ha	1	0	100
Below 494 seedlings/ha	16	55	77
Producer's accuracy (%)	6	100	Overall accuracy: 78
(B) American River fire (moist mixed conifer)			
Above 494 seedlings/ha	20	1	95
Below 494 seedlings/ha	4	3	4
Producer's accuracy (%)	83	75	Overall accuracy: 82
(C) BTU Lightning fire (moist mixed conifer)			
Above 494 seedlings/ha	23	2	92
Below 494 seedlings/ha	17	8	32
Producer's accuracy (%)	58	80	Overall accuracy: 62
(D) Rich fire (moist mixed conifer)			
Above 494 seedlings/ha	14	3	82
Below 494 seedlings/ha	2	0	0
Producer's accuracy (%)	86	0	Overall accuracy: 74

Note: YPMC, yellow pine and mixed conifer.

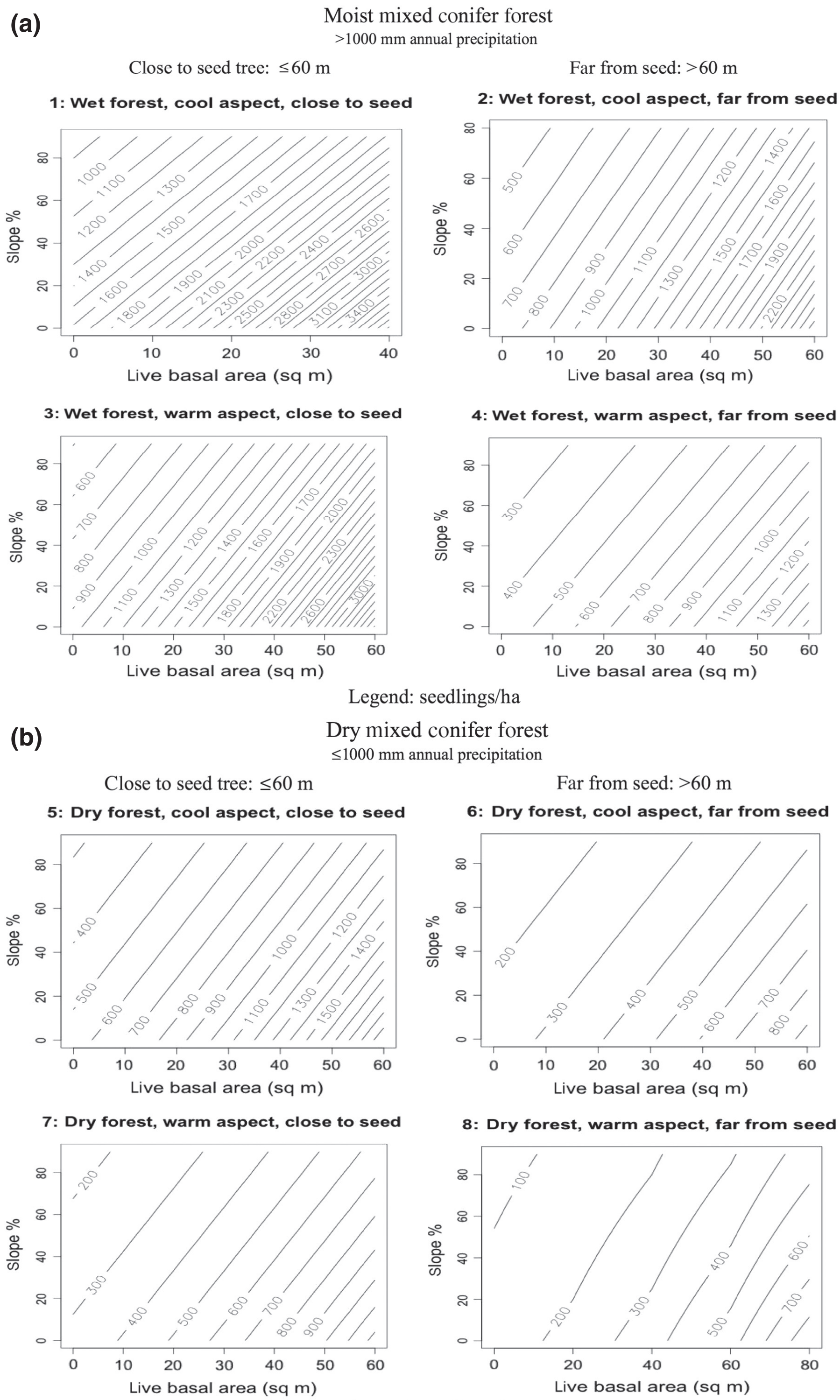

Fig. 10. Predicting conifer regeneration (seedlings/ha) in yellow pine and mixed conifer forests 5 yr after high severity fire using basal area gauge (sq meters) and clinometer.

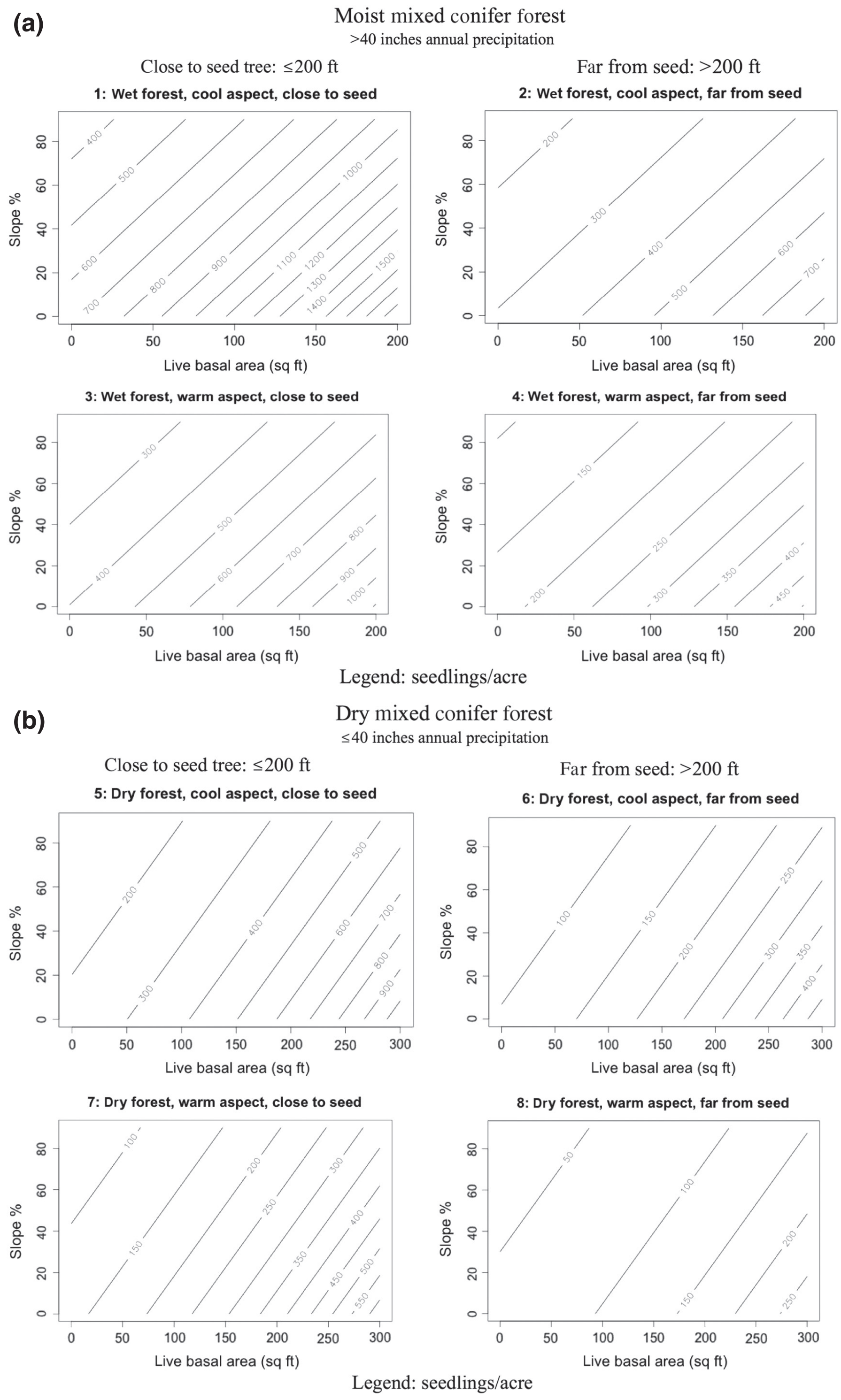

Fig. 11. Predicting conifer regeneration (seedlings/acre) in yellow pine and mixed conifer forests 5 yr after high severity fire using basal area gauge (sq feet) and clinometer. This graphic is intended for forest management agencies and professionals that use English units in the field. See Appendix S1 for sampling protocol and explanation of the seedling density prediction tool.

threat to conifer forest sustainability in our study region (Lenihan et al. 2008, Miller and Safford 2012, Mallek et al. 2013).

Our data also show that 5–7 yr after fire, most burned areas did not meet Forest Service Region 5 stocking rate guidelines for conifer regeneration. For mixed conifer forests, desired stocking rates were only met on average in four of the fires we studied, and in these fires (Showers, Sims, Bassetts, and Ralston), regeneration was very unevenly distributed across the landscape. Stocking thresholds were achieved in only two of the five fires (Freds and Power) that burned through fir forests, again with high intrafire variability. We stress that the fact that conifer regeneration in these fires met a desired median threshold does not mean that reforestation was/is not necessary in some parts of these burned landscapes. This is because stocking sufficiency is determined at the spatial scale of the forest stand and not on a fire-wide basis.

Forest Service desired stocking levels were developed to meet requirements of the National Forest Management Act of 1976 for productive forestlands and are aimed principally at guaranteeing timber resources. These stocking levels also implicitly assume that standard plantation management practices will be followed, most importantly that postplanting forest management will periodically thin forest stands. Today, the Forest Service in our study area is a relatively minor player in the timber production industry (Morgan et al. 2012), and many forest plantations have gone years to decades without postplanting management. As such, it may be that current stocking guidelines are unnecessarily high, at least for areas where forest regeneration after fire does not have a timber focus and where plantation stand manipulation is unlikely. A formal reconsideration of these guidelines has not been made, but the Forest Service is beginning to make some informal adjustments to these stocking guidelines. For example, our field plots were about 1/70 of an acre in area by design, as the Pacific Southwest Region Regional Silviculturist at that time felt that 70 mature trees/acre (about 175/ha) were sufficient stocking in most YPMC forests (M. Landram, USFS Region 5, *personal communication*). Not all foresters in California agree with this assessment, and there is a ongoing debate as to how postfire plantations should be planted and managed (Allen et al. 2002, Beschta et al. 2004, Zhang et al. 2008). Whatever the case, lower desired stocking levels would mean that more of the burned area we sampled would meet the standard, although it would not change the fact that 43% of the plots we sampled supported no regeneration at all.

In yellow pine and mixed conifer post-fire forests, species composition of the seedling and sapling populations was heavily dominated by shade-tolerant firs, Douglas-fir, and incense cedar. We found that shade-tolerant species outnumbered pines on eight of the 14 fires and that pines were regenerating well (i.e., meeting the stocking threshold in 50% or more plots) only on the Showers Fire. Although many studies in YPMC forests have noted increases in white fir and Douglas-fir densities over the last century (Gray et al. 2005, Webster and Halpern 2010; Safford and Stevens, 2016), our results indicate that incense cedar is also regenerating well across the study region. Dolanc et al. (2014) also noted a very strong increase in the density of small and medium-sized incense cedar in the Sierra Nevada between the 1930s and 2000s. This is due in part to incense cedar's ability to grow in full shade conditions coupled with the high density of incense cedar in the pre-fire forest community acting as remnant seed trees. Historically, cedars were not valued as much as other conifers and were often ignored during harvest operations, a practice which artificially increased their relative density (Leiberg 1902). Today, incense cedar is one of the conifers least subject to insect- and disease-driven mortality (Savage 1994, Smith et al. 2005) and many stands that have lost pines and firs to beetle kill support an enhanced component of incense cedar.

The yellow pine species are regenerating at very low rates in the YPMC forests of our study area. This is partly a result of the lower density of pine seed trees in contemporary forests, and partly due to the current environmental conditions in YPMC forests, which negatively impact seed survival. Yellow pine densities are currently low primarily due to two factors: preferential timber harvest and fire suppression policies. Yellow pines are valuable economically and were favored for harvest (along with sugar pine) after the arrival of Euro-Americans in the study area (Leiberg 1902). Fire exclusion, which began in the early 20th century, has removed the factor that most reliably thinned competing fire-intolerant species and prepared the mineral soil seed beds that are necessary for yellow pine seedling survival (Safford and Stevens, 2016). In sum, logging and fire suppression have promoted the heavy infill of more fire-intolerant species of fir, incense cedar, and Douglas-fir and reduced the availability of bare mineral soil due to heavy surface litter retention. They have also removed the selective pressure of low and moderate severity fire that is necessary to promote genetic fire resistance (Keeley et al. 2011).

Yellow pine species are important components of YPMC forests in the NAMCZ. Indeed, Barbour and Minnich (1999) called them "the biological thread that holds the forest together." The yellow pines are more resistant to fire and drought mortality than their shade-tolerant competitors (they are thus more "resilient" to forest disturbances that are linked to climate warming), and they have generally greater value as wildlife habitat and food sources (Brown et al. 2004; Safford and Stevens, 2016). Even as early as the beginning of the 20th century, foresters noted inadequate pine regeneration across parts of the western United States (Helms and Tappeiner 1996). Extensive research on ponderosa pine regeneration (reviewed in Savage et al. 1996) suggests that stand conditions, precipitation events, and seasonal temperature changes critically influence the success of seedling establishment and survival. Seeds typically germinate in the growing season following cone maturation, and once established, seedlings are highly susceptible to desiccation and their roots must reach sufficient depth in time to acquire soil moisture as surface layers dry out throughout the Mediterranean summer (Gray et al. 2005, Zald et al. 2008). The deep litter layer and shady understory that characterizes much of the modern YPMC belt in the NAMCZ are highly inimical to yellow pine recruitment.

Our study targeted fires that had burned 5–7 yr prior to data collection, a phase when tree survival and growth are most sensitive to microsite environment and resource availability (Zald et al. 2008). Seedling establishment and mortality are thought to stabilize during these first 5 yr, and this snapshot provides an idea of the likely postfire successional patterns. We also included an 11-year-old fire (Pendola), which gives us insight later in the first decade of forest recovery. The NAMCZ experiences the highest interannual variability in precipitation in the United States (Cayan et al. 1998), and all the conifers we sampled mast, producing large numbers of viable seeds only every 3–7 years (Burns and Honkala 1990). Studies only taking into account immediate postfire seedlings (1–3 yr) may therefore be difficult to interpret and may not provide a realistic view of actual patterns in forest regeneration.

Conifer regeneration showed a unimodal response to fire severity with a peak in moderate and low fire severities. High severity fires consistently had the least number of regenerating conifers, followed by intermediate levels of regeneration in unburned controls. This pattern suggests that conifers may benefit from intermediate fire disturbance by freeing resources and releasing competition for space, light, and water. While high severity fires are detrimental to regeneration of all of the conifer species we sampled (they are not generally detrimental to serotinous species like *Pinus attenuata*), moderately burned areas may preferentially benefit fire-resistant pines that can survive moderate burns which often kill fire-intolerant firs.

Our analysis of the data is also revealing species-specific responses to the fire severity gradient, and we will report on these in a subsequent study.

Yellow pine and mixed conifer forests in the NAMCZ historically experienced frequent low and moderate severity fires. However, with a projected increase in frequency of high severity fires in the region (Lenihan et al. 2008, Miller et al. 2009, Westerling et al. 2011, Miller and Safford 2012, Safford et al. 2012), forest managers need to better understand the impact of high severity fires on successional pathways and future forest composition. High severity fires have been shown to stimulate a greater hardwood response through postfire sprouting (Cocking et al. 2014), while also removing competing conifer seed trees. We also found that high severity fires lead to a stronger shrub response than low severity fires, primarily through fire-stimulated seed germination (*Ceanothus*, *Arctostaphylos*) and sprouting. Together, the increased presence of hardwoods and shrubs in high severity areas leads to greater competition with emerging conifer seedlings in the postfire environment.

Mechanisms of regeneration failure following high severity fire

The incorporation of biotic and abiotic variables in this study allows us to better understand the mechanisms driving conifer recruitment after fire. The strong negative relationship between high severity fire and conifer regeneration was due mostly to two factors: More severely burned plots are further from seed trees, and they are higher in competing shrub cover. Propagule arrival is the primary factor that determines potential regeneration in a postfire environment (Bonnet et al. 2005, Donato et al. 2009), and its importance is captured in our regeneration model. There was a significant increase in distance to seed tree for all species between moderate and high severity fires, as the canopy cover and potential seed trees were severely reduced. Viable conifer seeds had (much) further to travel to repopulate high severity areas.

We found that plots with complete regeneration failure were generally located in the interior of severely burned areas, farther from potential seed trees, in areas with less living tree basal area, and in drier landscapes. During the first 5 yr, these areas also tended to be dominated by a greater shrub presence. Regeneration failure is also more likely to occur when the fire burns before seeds reach maturity and are not yet viable. Conifer seed banks are short-lived in these systems. Thus, regeneration is first dependent on remnant trees in the landscape providing seed sources and, second, on the microclimatic conditions favorable to seed germination and establishment (i.e., precipitation in the years immediately following a fire, and adequate light resources to stimulate growth). The combination of lack of seed sources and harsh microclimatic conditions may have contributed to regeneration failure in these severely burned areas.

Previous studies in the NAMCZ have demonstrated that 30–60+ years is often required for conifers to get established after a high severity fire (Helms and Tappeiner 1996, Russell et al. 1998) due to rapid establishment and expansion of shrubs that sprout from surviving root crowns or arise from persistent soil seed banks that for some species are stimulated to germinate by fire-related cues. Light competition and soil moisture may be the most important limiting factors to conifer seedling survival in the NAMCZ (Gray et al. 2005, Balandier et al. 2006, Oakley et al. 2006, Irvine et al. 2009), and rapidly growing shrubs compete with conifer seedlings for these resources in the years following a fire (Gordon and Rice 1993, Knapp et al. 2012). Extensive research (reviewed in Helms and Tappeiner 1996) has shown that reducing shrub canopy cover to 30% or below helps to minimize competition and promote conifer regeneration. However, shrubs can also have facilitative effects on seedling establishment by offering protection against high radiation, extreme temperatures, and desiccating winds (Castro et al. 2002, Gomez-Aparicio et al. 2004, Rolo et al. 2013). Our study did not find support for the facilitating effects of shrub cover, as shrubs consistently had a negative effect on conifer regeneration in our data 5–7(11) yr after fire. However, facilitative ("nurse plant") effects are more likely in the very low cover conditions that characterize the immediate postfire environment, so we cannot properly evaluate this phenomenon.

Many conifer seeds are preyed upon by rodents and avifauna, thereby reducing the pool of potential regenerating trees (Whelan 1986). Although both fir and pine species have several important animal seed-predators, pine seeds are favored by rodents, which may consume up to 99% of the seed crop (Fowells and Schubert 1956, Whelan 1986). We were not able to account for rodent herbivory or caching in our model, but we recognize that seed predation likely further erodes the regeneration success of pine species. Yellow and sugar pine seeds are also considerably heavier than the firs, Douglas-fir, and incense cedar (Table 4). In combination, the increase in distance to seed tree, heavy seed size, and preferential seed-predation challenge these pine species to become established after high severity fires. On the other hand, rodents and birds also disperse pine seeds via caching for winter food source. Some of these caches are forgotten and often germinate the following spring. Thus, rodents and birds can have both a positive and negative effect on regenerating pines. Our study did not directly evaluate these dynamics, although the net effect is of course included in our regeneration data.

Model application

Nearly 86,000 ha of National Forest lands was burned in the 14 fires of this study. While forest restoration will certainly be an important component of postfire management plans, understanding natural regeneration dynamics forms the foundation of a restoration strategy. Our model is one of the first to quantify biotic and abiotic variables that contribute to conifer regeneration success and/or failure and should be a useful tool for forest managers who are struggling with budget limitations and large tracts of deforested lands. Many of the variables in our model can be collected relatively easily from remotely sensed LANDSAT data (fire severity), Digital Elevation Models (slope, aspect), vegetation mapping (forest type), and climate data sources such as PRISM (annual precipitation; Epting and Verbyla 2005).

Our study draws from sites in central and northern California, but our results and predictive model should be generally applicable to the NAMCZ and neighboring areas with similar species assemblages and climate. The results of this study help to identify where on the landscape conifer regeneration is most likely to fail and where supplemental planting is most justified, improving restoration efficiency. Based on our model, we developed a graphic to assist forest managers to gauge the potential for natural regeneration to meet stocking objectives in YPMC forests approximately 5 yr after a high severity fire (Figs. 10, 11). We have also included restocking figures and model validation tables for high-moderate severity plots (Appendix S1: Table S4, Figs. S1, S2) for forest managers in Region 5, an area of concern for the US Forest Service. Using simple forestry tools, a manager can enter the forest in the years following a fire, take a few measurements, and reference the figures to roughly predict regeneration success. A description of the suggested protocol is provided in Appendix S1.

Like all models, the model behind Figs. 10 and 11 does not produce perfect fits. The model predictions are conditional on $y > 0$, and there is approximately a 50% chance that $y = 0$. Even so, our model showed overall accuracies averaging 74% when the management question was "will this site support regeneration that meets my desired stocking level." These are respectable numbers for a process driven by so many stochastic factors. With respect to the components of that accuracy however, there was not much concordance among the different fires and the wet and dry YPMC submodels (Table 11). This is likely due to general stochasticity, as well as the all-important influence of precipitation in the years after fire. The year after the Rich Fire (2009) included a very wet growing period (May–August), and 2010 was much wetter than average, so conditions for seedling germination and survival were better than average. This explains the much higher mean densities that were sampled on the ground. The Angora Fire (2007) occurred during the driest year in 29 yr and was followed by the third driest year in the same period; both years experienced almost no growing season precipitation. The fire also occurred in June, when conifer seeds were not yet mature. This may have contributed to 47% of plots supporting no regeneration 5 yr after fire, but some plots supported much higher seedling densities than our model predicted (the "jackpots" that drive up mean densities in all fires). We are satisfied that the overall accuracy of our model will make it a useful tool for resource managers, but further data collection and statistical refinement will permit the development of an even more robust model in the future. Whatever the case, field users should take into account factors like postfire growing season precipitation and fire date (in relation to typical timing of seed maturity) as they determine how meticulously model predictions will be followed in making planting or other management decisions.

Future refinements to the model include adding species-specific modules, and a spatial component to capture large contiguous high severity areas, where seed trees may be unevenly distributed across the landscape. As conifers do not exist in isolation, it is important to also understand the impact of hardwood competition via seeding and resprouting in those sites where both functional types co-exist. Together, these further expansions of the model will add levels of detail that further aid restoration activities and help forest managers to influence successional pathways toward a future species composition that is more resilient to future fire disturbance.

There has been concern about low rates of tree regeneration in the postfire environment (Donato et al. 2009, Crotteau et al. 2014), and it has been suggested that active restoration practices may be necessary to promote healthy forests with increased resilience to disturbances like wildfire and insect outbreaks, a clearly stated objective of the Ecological Restoration Implementation Plan for US Forest Service Region 5 (California; USDA 2011). Artificial regeneration and supplemental planting are valid options, but these practices often need to be supported by other management activities such as site preparation, brush thinning, and invasive species treatments (Hobbs et al. 1992, Helms and Tappeiner 1996, Brown et al. 2004, Bohlman et al. 2016). Forest managers are also beginning to consider using seedling stock with greater genetic heterogeneity to increase the probability of capturing traits adapted to changed climates in the future (J. Sherlock, USFS, *personal communication*). Use of our model can help forest managers in their planning and implementation of efficient, cost-effective, and ecological defensible tree planting, but ultimate success in restoring forests after severe fire will rest just as much on the qualities of the planting stock and the doggedness with which forest managers maintain optimal and fire-safe growing conditions on the ground.

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