Divergent successional pathways of stand development following fire in a California closed-cone pine forest

Brian J. Harvey & Barbara A. Holzman

Harvey, B. J. (corresponding author, bjharvey@wisc.edu, present address: Ecosystem and Landscape Ecology Lab, Department of Zoology, University of Wisconsin, Madison, WI, 53706, USA)
& Holzman, B. A. (bholzman@sfsu.edu): Department of Geography, San Francisco State University, San Francisco, CA, 94312, USA

Abstract

Questions: What are the major trends in vegetation community structure and forest stand structure over a 14-yr post-fire period in a California closed-cone pine forest? Which biotic and abiotic factors best explain variation in stand structure at different stages of post-fire succession, and does the relative importance of these factors remain constant? Is there evidence of multiple successional pathways of forest stand development?

Location: Post-fire *Pinus muricata* (bishop pine) forests at Point Reyes National Seashore, CA, USA.

Methods: We quantified post-fire vegetation change from field data collected 1, 2, 6 and 14 yr following stand-replacing wildfire that occurred in 1995. General linear models were used to assess trends in composition (plant functional groups and species diversity) and generalized linear models were used to assess trends in stand structure (post-fire *P. muricata* density) and determine the relative importance of abiotic and biotic factors on stand structure in different early-successional post-fire years.

Results: Species richness and diversity peaked in the first 2 yr following fire, and then declined through year 14. Initial post-fire *P. muricata* tree regeneration was high (mean 249 750 stems·ha^{-1} in year 1) and remained well above pre-fire stand density levels by year 14 (mean 15 179 stems·ha^{-1}). Post-fire *P. muricata* seedling density was associated with topographic factors in years 1 and 2, negatively associated with cover of a non-native herb in year 2, and negatively associated with cover of an early/mid-successional shrub and positively associated with slope in years 6 and 14. Two alternative pathways of post-fire stand development have emerged by year 14. A high-density, closed-canopy pathway (mean 40 875 stems·ha^{-1}) with early intra-specific thinning resulted on steep slopes and ridges with low shrub cover. In contrast, a low-density, open-canopy pathway (mean 1250 stems·ha^{-1}) resulted on gentle slopes and where shrub cover was high.

Conclusions: This study provides evidence of divergent successional pathways and illustrates the importance of early-successional species interactions and topography on longer-term stand development trajectories in serotinous conifer forests. Early heterogeneity in vegetation establishment set the course for variability in stand structure in mid-seral stages and may persist into later stages.

Introduction

Severe, stand-replacing disturbances modify the composition and structure of forest ecosystems, initiating secondary succession and setting the long-term trajectory for forest development. While general post-fire successional trends have been characterized for many fire-prone forests, multiple pathways often occur within systems, and

the factors that drive these variations are less understood. Stand development pathways may differ with the interval between successive disturbances (Paine et al. 1998; Schoennagel et al. 2003; Johnstone & Chapin 2006; Donato et al. 2009), disturbance severity (Turner et al. 1999; Johnstone et al. 2010; Barrett et al. 2011), residual biotic legacies (Tinker et al. 1994; Franklin et al. 2000), topographic/landscape context (Fastie 1995; Kurkowski et al. 2008) or post-disturbance species interactions (Stuart et al. 1993; Franklin & Bergman 2011). Initial post-fire forest stand structure can vary widely and persist for centuries (Kashian et al. 2004, 2005), driving variability in many ecosystem functions, such as terrestrial carbon and nutrient flux (Turner et al. 2004; Smithwick et al. 2005). Understanding the drivers of alternative successional pathways and their consequences for stand development is therefore critical to forecasting future trajectories of ecosystem function in forested landscapes.

Classical stand development models characterize post-fire succession as establishment by many species immediately following a fire, and a shift in dominance from annual and perennial herbs to shrubs and eventually trees in later stages (e.g. Oliver 1980). Stand development may follow alternative successional pathways from early- to late-seral stages (Cattelino et al. 1979), which can result from probabilistic processes or stochastic events at different points in time during or following disturbance (Abrams et al. 1985). Early-successional forest ecosystems can be characterized by high compositional and structural diversity when herbs, shrubs and trees are all present (Swanson et al. 2011). However, little is known about how early heterogeneity in structural complexity can persist to later old-growth stages of forest stand development (but see Johnstone et al. 2004). While some forests are characterized by early heterogeneity that can later converge toward more uniform stand structure (Kashian et al. 2005), other young stands may exhibit 'precocious' structural characteristics that persist through later successional stages (Donato et al. 2012) and are important for functions such as wildlife habitat (e.g. Fontaine et al. 2009). Structural complexity is typically associated with older forests and is often a management target, making the characterization and tracking of pathways of structural heterogeneity in early stands important.

The California closed-cone pine ecosystem dominated by *Pinus muricata* (bishop pine) is characterized by a relatively short fire cycle for forests, making it a good system for studying successional processes. *Pinus muricata* is fast growing, highly serotinous and characterized by a stand-replacing fire regime with a fire-return interval of ca. 40–70 yr (Sugnet 1985). These attributes present an opportunity to quantify vegetation change and detect potential multiple pathways of forest stand development

over years to decades, rather than decades to centuries – yielding information that can usually only be inferred through chronosequence or retrospective studies (e.g. Johnstone et al. 2004).

The 5000 ha Vision Fire in October 1995 burned over 400 ha of *P. muricata* forest in Point Reyes National Seashore, serving as a natural experiment to study post-fire succession. This was the first large fire (>100 ha) since the park was established in 1962, and the most recent in the *P. muricata* forest since 1927 (Sugnet 1985). The initial post-fire vegetation community was characterized by high species richness, which included dense but variable *P. muricata* tree regeneration and dominance of many early-successional herbaceous and shrub species (Folger 1998). Early-successional trends revealed moderate negative relationships between non-native annuals and post-fire *P. muricata* seedling density, but little effect of native shrubs on successional trajectories (Pribor 2002; Holzman & Folger 2005). Less known, however, is whether these effects are maintained such that early-seral structural and compositional patterns will persist through successional time. Further, pathways of stand development in California closed-cone pine forests are poorly understood.

By combining data collected in 2009 (14 yr post-fire) with data collected 1, 2 and 6 yr post-fire, we addressed several questions about post-fire vegetation dynamics in serotinous conifers. First, what are the general trends in vegetation community structure (relative abundance of plant functional groups and species diversity) and forest stand structure (post-fire *P. muricata* density) over a 14-yr period following a stand-replacing fire? Second, which biotic (species interactions, potential seed source) and abiotic (disturbance severity, topography) factors best explain variation in stand structural development at different stages of post-fire succession – and are these factors stable through time or do they shift in importance? Finally, what evidence of alternative successional pathways of forest stand development exists following stand-replacing fire in this system?

Many adaptations to fire (e.g. serotiny, resprouting, soil seed-banking, thick bark) exist among species in this ecosystem; therefore species diversity was expected to be high immediately following fire. Early post-fire species were expected to have a dominant effect on subsequent succession, supporting the initial floristics model (Egler 1954). Biotic interactions were expected to be important drivers of variability in stand structure, as they were in early post-fire years and as has been found in other Pacific coast (US) coniferous systems (e.g. Stuart et al. 1993). Because *P. muricata* grows in a topographically complex region, topography may affect species interactions, and therefore successional pathways and outcomes (e.g. Kurkowski et al. 2008).

Methods

Study area

Point Reyes National Seashore is located along the Pacific Coast of northern California (38.05°N, 127.85°W; Fig. 1). The park is characterized by a mediterranean climate with warm dry summers and cool moist winters. Heavy maritime fog mitigates warm and dry summer conditions that otherwise persist further inland in northern California. Average annual precipitation is 91 cm, minimum temperature is 8.4 °C (January), and maximum temperature is 14.5 °C (September; National Park Service 2012). The park contains over 28 000 ha of coastal serotinous conifer forest, mixed evergreen forest, coastal scrub, coastal grassland and dune/salt marsh vegetation communities.

The study area is located in pre-fire continuous *P. muricata* forest occurring primarily on granitic quartz-diorite soils ranging in elevation from 210 to 330 m along the northern portion of Inverness Ridge on the Point Reyes Peninsula. Prior to the 1995 Vision Fire, the study area was a mature, even-aged forest dominated by *P. muricata* (85% of trees), and scattered individuals of *Quercus agrifolia* (coast live oak), *Lithocarpus densiflorus* (tan oak), *Umbellularia californica* (California bay/laurel) and *Arbutus menziesii* (Pacific madrone; Ornduff & Norris 1997). Pre-fire stand density (trees ≥ 2.5 cm DBH) was variable (mean 766 stems·ha^{-1}, range = 220–1860 stems·ha^{-1}; author, unpubl. data). The forest understorey consisted primarily of *Vaccinium ovatum* (evergreen huckleberry), with scat-

tered individuals of other shrubs: *Rhamnus californica* (California coffeeberry), *Gaultheria shallon* (salal), *Manzanita* spp. (manzanita species), *Myrica californica* (wax myrtle), *Rubus parviflorus* (thimbleberry) and *Chrysolepis chrysophylla* (golden chinquapin). *Polystichum munitum* (western sword fern) and *Pteridium aquilinum* (western bracken fern) were also present. Herbaceous cover was very low. *Ceanothus thyrsiflorus* (blue blossom ceanothus) was present, but rare (Ornduff & Norris 1997). The most recent fire in the study area prior to the Vision Fire occurred in 1927 (Sugnet 1985); however the perimeter of this fire was never mapped. Therefore, forest stands in the study area likely originated at some point prior to 1928 and experienced a minimum fire-free interval of 68 yr at the time of the Vision Fire.

Data collection

Thirty post-fire monitoring plots were established in 1996 (1 yr following the Vision Fire) in pre-fire closed-canopy *P. muricata* forest that experienced stand-replacing (high severity) fire, as evidenced by complete mortality of pre-fire vegetation and consumption of litter and duff layers down to mineral soil (Holzman & Folger 2005; Fig. 1). Plots were distributed within areas that met these criteria and were accessible by trail. At minimum intervals of 30 m along trails, plots were located at randomly determined distances (>20 m away from trail) and side (left–right) from the trail. Plots were within pre-fire *P. muricata* plant
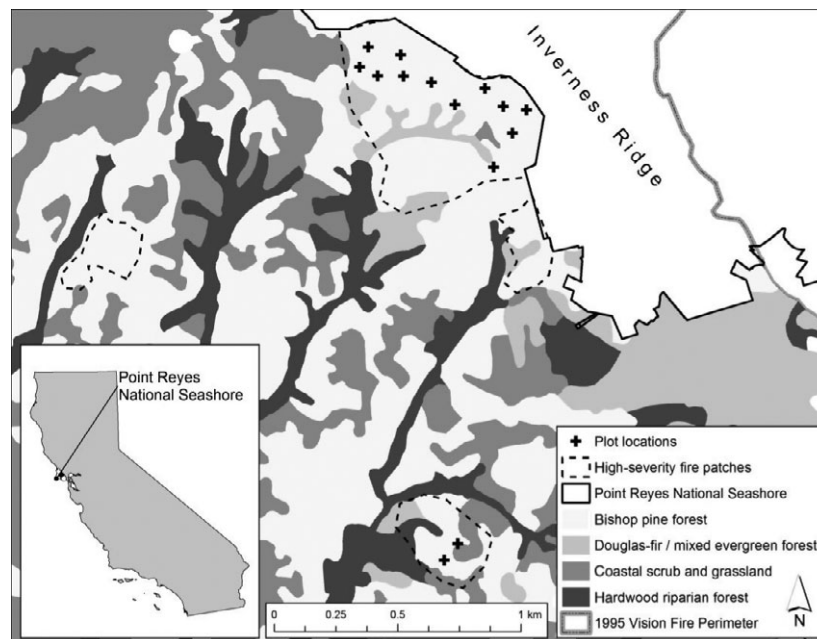

Fig. 1. Study area and plot locations. High-severity fire patches were manually digitized from burn severity data available from the Monitoring Trends in Burn Severity website (mtbs.gov). Vegetation polygons are digitized from pre-fire (1994) aerial imagery (Shirokauer 2004).

community polygons in a 1994 (pre-fire) GIS vegetation map of the park (Shirokauer 2004), were dominated by *P. muricata* (>50% of pre-fire basal area was *P. muricata*) and contained between 140 and 1140 pre-fire *P. muricata* stems·ha^{-1} (mean 602 stems·ha^{-1}). Semivariograms indicated that original plot locations were correlated at distances up to ~80 m; therefore only plots separated by >80 m were used in all analyses ($n = 14$ plots; Fig. 1).

Plots were sampled in Jul/Aug 1996 (year 1) and 1997 (year 2). Although original plots were marked with steel rebar stakes in 1996, exact plot positions could not be relocated in 2001 due to dense regrowth of trees and shrubs. In Jul/Aug 2001 (year 6) and 2009 (year 14), plots were located in the same stands as years 1 and 2 using GPS coordinates; however exact plot centre and orientation were randomized to avoid bias in plot placement.

The same sampling protocol was followed in each sampling year. Plots were configured around a 50-m transect oriented in a randomly assigned azimuth. Pre-fire stand structure was characterized by recording the number of pre-fire trees (all killed by fire) in each of five diameter size classes (2.5–10.0 cm; 10–30 cm; 30–60 cm; 60–90 cm; and >90 cm at DBH) for tree species along a 10 × 50 m (0.05 ha) belt transect centred on the main plot transect. Post-fire seedling/tree density (live trees established post-fire) was recorded in 20 1-m^2 quadrats placed every 2.5 m along the centre transect in each post-fire sample year. Dead saplings/trees established post-fire were also recorded in year 14 only. Ground cover was recorded using the point intercept method at every meter along the centre transect, recording multiple hits when overlapping layers of vegetation existed. Cover measurements were made below the transect tape (ca. 1.3 m above the ground) by lowering a thin (<1-mm diameter) metal pointer at each point and recording the species of any vegetation (or litter/bare ground) with which the pointer came into contact. When vegetation projected above the transect tape, a canopy densitometer (optical crosswire sighting tube) was used to obtain vertical hits as an overhead extension of the point intercept method. Bare ground or litter was recorded if no vegetative cover was present in the vertical dimension of the point above and below the transect tape. Plot locations were recorded at transect endpoints using a Trimble GeoExplorer II (years 1, 2, 6) or Trimble Juno (year 14) GPS. At the time of sampling in 2009 (year 14), sample stands were located in areas unaffected by pine pitch canker disease (a non-native fungal pathogen currently spreading through the *P. muricata* forest at Point Reyes; Crowley et al. 2009). Therefore, density-dependent thinning was characterized as dead *P. muricata* trees that established post-fire with no evidence of mechanical wounds, disease, insect infestation or other tree death obviously not related to competition (Harvey et al. 2011).

Pre-fire stand density was calculated for each plot by summing the number of pre-fire stems across size classes in the belt transect and converting to trees per ha. Post-fire *P. muricata* tree density was calculated for each plot by averaging the values for the 20 1-m^2 quadrats. Relative percentage cover values for each plant species or ground cover class were calculated for each plot by dividing the total number of hits for each species by the total number of hits for a plot (summing to 100% total cover). Species richness and diversity were quantified for each plot using the number of species and the Shannon–Wiener index (H'), respectively. Richness and diversity were calculated for each plot and averaged across plots for each year. Plots categorized as stand replacing (or crown fire) can vary considerably in continuous metrics of fire severity. To test for finer resolution effects of fire severity within stand-replacing fire, burn severity data were downloaded from the Monitoring Trends in Burn Severity website (mtbs.gov), and fire severity was quantified for each plot by extracting the relative differenced normalized burn ratio (RdNBR; Miller & Thode 2007) for each plot. Topographic variables (elevation, aspect, slope, curvature, topographic position index) were generated in ARCGIS (v. 9.3; Environmental Systems Resource Institute, Redlands, CA, US) from a 10-m resolution digital elevation model. Topographic and fire severity variables were extracted for each plot by calculating the length-weighted mean values (Beyer 2004) for segments of the transect that were in each 10-m cell (for topographic variables) or 30-m cell (for fire severity).

Data analysis

To examine general successional trends, relative species cover proportions were grouped into plant functional group (trees, shrubs, ferns, herbs, bare ground and litter) and compared across the four sampling periods. All percentage cover estimates were transformed using the arcsine square root transformation prior to analysis. Repeated-measures ANOVA with post-hoc Tukey's HSD tests were used to evaluate the effect of time since fire (year) on species richness, diversity and plant functional group cover (after transformation). Because tree density (count data) often violates the assumptions of linear statistical models, we used generalized linear models (GLMs) with a negative binomial error structure and a log-link function for all models where post-fire *P. muricata* tree density was the response variable. Repeated-measures models were used for any model that included multiple years of post-fire *P. muricata* density. In addition to mean values, variability can be an important response metric of system properties following disturbance (Fraterrigo & Rusak 2008). Therefore, we compared the coefficient of variation (CV) of post-fire *P. muricata* tree density within plots across years to

assess trends in stand-level forest structural heterogeneity, and compared the CV of post-fire *P. muricata* tree density among plots across years to assess trends in landscape-level forest structure heterogeneity using repeated-measures ANOVA with post-hoc Tukey's HSD tests.

Step-wise model selection among competing GLMs was performed separately for each post-fire sampling year to determine the relative importance of abiotic and biotic variables in explaining variability in post-fire stand structure (post-fire *P. muricata* tree density) across time. Potential candidate variables consisted of 31 variables in the following categories: disturbance severity, potential seed source, species interactions and topography (Appendix S1). Variables with a significant Spearman's rho correlation ($P \leq 0.05$ for two-tailed test) were added as candidate variables to the full regression model for each year. The Bayesian information criterion (BIC) was used to conservatively select the best model for each year with the fewest explanatory terms. Top models among years were compared qualitatively to assess relative (e.g. effect size) or absolute (e.g. significance) changes in explanatory variables with increasing time since fire.

Two further analyses were conducted to assess alternative stand development pathways and test for differences among them. To detect changes in the relative dominance of stands by either *P. muricata* or *C. thyrsiflorus* (the dominant post-fire shrub) over time since fire, we calculated the difference in relative cover of *P. muricata* and *C. thyrsiflorus* for each plot in year 1 and year 14 (plots with no difference in relative cover = 0, plots dominated by *P. muricata* = 1.0, plots dominated by *C. thyrsiflorus* = −1.0). Histograms of these values in year 1 and year 14 were generated to illustrate where stands existed along this gradient of dominance by either species at different points in time following fire. For stands in the highest and lowest quartiles for *P. muricata* density in year 14 (hereafter referred to as the closed-canopy [*n* = 4] and open-canopy [*n* = 4] pathways, respectively), we tested for differences in stand density at 1, 2 and 6 yr post-fire to compare rates of self thinning and stand development trajectories. Further, we compared differences between the open- and closed-canopy pathways in years 1 and 14 for the following variables: stand structure variability (CV of post-fire *P. muricata* density), species richness, species diversity and relative dominance of *P. muricata* or *C. thyrsiflorus*. Comparisons between pathways were conducted using Welch's *t*-test (conservatively assuming unequal variances) and relative percentage cover values were arcsine square root transformed prior to analysis.

For all models, $P \leq 0.05$ was considered strong support for significant differences/effects and $P \leq 0.10$ to be moderate support for significant differences/effects to avoid missing ecologically meaningful relationships due to modest sample size (i.e. Type II error). Regression models were assessed for heterogeneity of residuals, normality of errors, multicolinearity among explanatory variables and overly influential data points (Cook's distance value >0.5). Model residuals were tested for spatial autocorrelation using semivariograms. Statistical analyses were performed in the R statistical software (v. 2.12; R Foundation for Statistical Computing, Vienna, AT). Results in text and tables are presented as means ± 1 SE unless otherwise noted.

Results

Vegetation community structure and forest stand structure

Fourteen years following fire, the forest has generally transitioned from an early-seral stage dominated by herbs and shrubs to a mid-seral stage dominated by shrubs and trees; however all functional groups were present immediately following the fire in year 1 (Fig. 2, Appendix S2). Although shrub cover (composed of 78% *C. thyrsiflorus* in year 14) decreased between year 6 and year 14, shrubs continued to dominate, with 46 ± 5% relative cover in year 14. Relative cover of trees (composed of 91% *P. muricata* in year 14) increased between each post-fire sampling year to 38 ± 5% in year 14. Relative cover of ferns decreased steadily after year 1, while herb cover was initially high but nearly non-existent after year 2 (Fig. 2, Appendix S2). Bare ground and litter cover decreased to near zero in year 2 after most growing space became occupied by vegetation. Species richness peaked 2 yr post-fire, at 9.9 ± 0.7 species per plot, and thereafter declined in
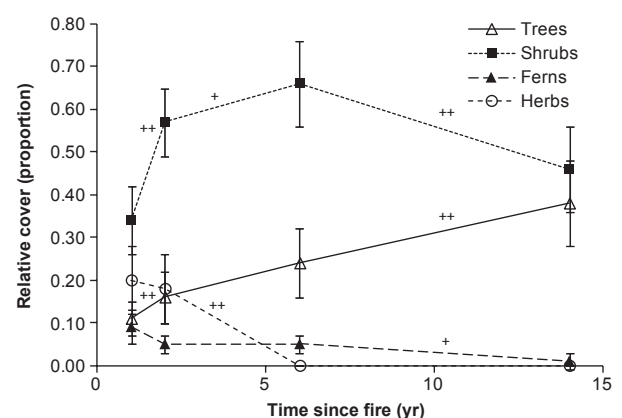

Fig. 2. Mean relative cover of trees, shrubs, ferns and herbs, between 1 and 14 yr post-fire. Error bars represent ± 2 SE. Significant difference between successive sample events (years) using repeated-measures ANOVA and Tukey's HSD test denoted with $^+P \leq 0.10$, $^{++}P \leq 0.05$. Statistical tests were conducted on arcsine square root transformed values for percentage cover data.
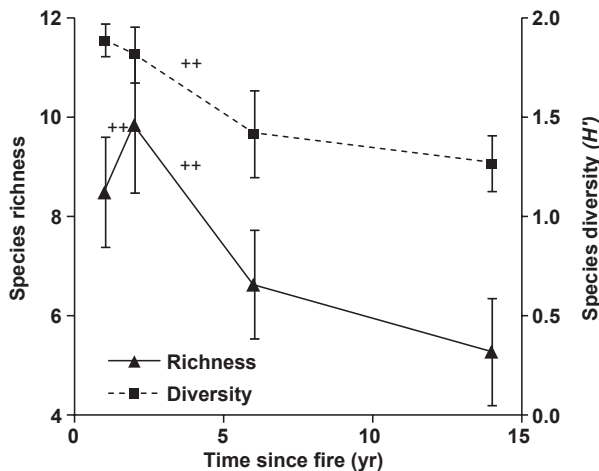
Fig. 3. Mean species richness and Shannon diversity (H') between 1 and 14 yr post-fire. Error bars represent $\pm$ 2 SE. Significant difference between successive sample events (years) using repeated-measures ANOVA and Tukey's HSD test denoted with $^{++}P \leq 0.05$.

each subsequent sample year to 5.3 $\pm$ 0.5 species per plot in year 14 (Fig. 3, Appendix S2). Species diversity (H') was highest in post-fire years 1 and 2, when most species were present and within-plot evenness was high, and has consistently declined since post-fire year 2.

After high initial post-fire *P. muricata* regeneration in most plots (minimum seedling density was 46 500 stems·ha^{-1} in year 1), the magnitude of structural variability among stands continually increased over 14 yr, and remained well above pre-fire levels. Post-fire *P. muricata* tree density decreased by >50% between each successive sampling year, from 249 750 $\pm$ 50 075 stems·ha^{-1} in year 1 to 15 179 $\pm$ 5418 stems·ha^{-1} in year 14 (Fig. 4a, Appendix S2). While mean density decreased over 14 yr,

the variability in stems per hectare demonstrated increasing heterogeneity at two spatial scales (Fig. 4b). Within-plot (stand-level) heterogeneity in post-fire *P. muricata* tree density (measured as the mean of within-plot CVs for each year) increased from 62 $\pm$ 7% 1 yr post-fire to 170 $\pm$ 29% 6 yr post-fire, thereafter remaining high through year 14. Among-plot (landscape-level) heterogeneity increased modestly between 1 and 6 yr post-fire (CV ~ 80%), but thereafter nearly doubled by 14 yr post-fire (CV = 134%). Mean post-fire stem density and among-plot variability in stand structure remain far above pre-fire levels (766 stems·ha^{-1}, CV = 40%). While density decreased in all stands across years, the rate of decline varied substantially among stands.

Biotic and abiotic factors associated with successional pathways of stand development

The significance and importance of different covariates with post-fire *P. muricata* tree density shifted with increasing time since fire (Table 1). First year post-fire *P. muricata* seedling density was best explained by aspect. Higher initial post-fire seedling density was associated with south-west-facing aspects, which are relatively warm and dry. However, seedling establishment was prolific throughout the study area, as minimum seedling density was 46 500 seedlings·ha^{-1} in year 1. Second year post-fire *P. muricata* seedling density was also associated with south-west aspects and was negatively associated with relative cover of *Erechtites minima* (Australian fireweed) a non-native herb that can germinate from long-lived soil seed banks (Table 1). *In situ* seed source (pre-fire *P. muricata* stem density) was not a significant covariate with post-fire *P. muricata* seedling density in year 1 (Spearman's rho = 0.24, $P > 0.10$), or year 2 (Spearman's rho = 0.36,
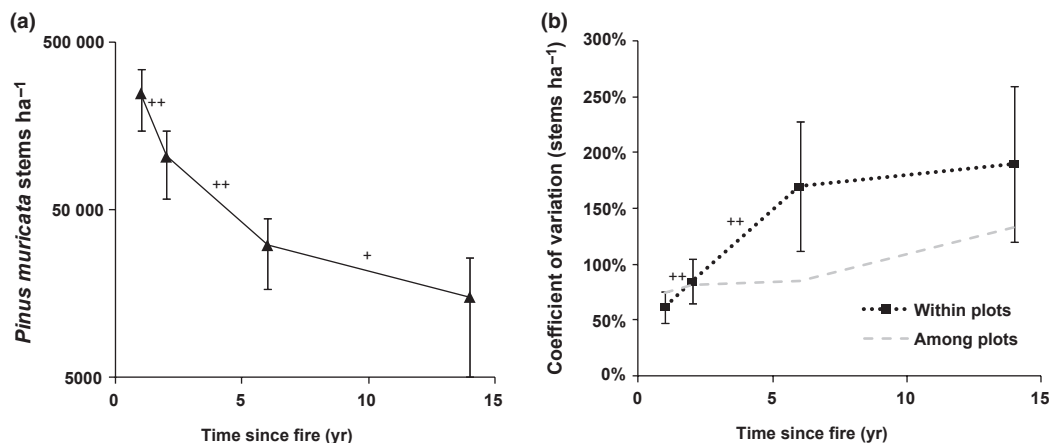

Fig. 4. (**a**) Mean post-fire *Pinus muricata* tree density (stems per ha) and (**b**) within-plot and among-plot coefficient of variation (CV) between 1 and 14 yr post-fire. Error bars represent $\pm$ 2 SE. Significant difference between successive sample events (years) denoted with $^{+}P \leq 0.10$, $^{++}P \leq 0.05$.

Table 1. Final regression models for *Pinus muricata* density (live stems ha^{-1}) in each year of postfire sampling. All models were generated using stepwise selection using the Bayesian information criterion (BIC) score from generalized linear models with a negative binomial error family and a log link.

Years After Fire	Covariate	Abiotic/Biotic	β	Standard Error	Z	P	Effect
1	NE index	Abiotic	−1.457	0.561	−2.596	0.009	(−)
2	NE index	Abiotic	−1.732	0.386	−4.490	<0.001	(−)
	ERMI	Biotic	−6.966	1.963	−3.548	<0.001	(−)
6	CETH	Biotic	−2.793	0.951	−2.938	0.003	(−)
14	CETH	Biotic	−4.788	0.824	−5.809	<0.001	(−)
	SLOPE	Abiotic	0.115	0.027	4.204	<0.001	(+)

CETH, *Ceanothus thyrsiflorus* relative cover; ERMI, *Erechtites minima* relative cover; SLOPE, slope (degrees), and NE index, transformed aspect: 45° = 2 and 225° = 0 (Beers et al. 1966).

$P > 0.10$), and was not retained as a term in the regression model for either year.

By 6 yr after the fire, most early-successional herbs and shrubs had decreased in cover (Fig. 2), and stands were becoming dominated by either *P. muricata* or *C. thyrsiflorus*, which collectively accounted for 70% of the relative cover. In year 6, post-fire, *P. muricata* tree density was negatively associated with relative cover of *C. thyrsiflorus* (Table 1). By year 14, *P. muricata* stem density was positively associated with slope, as thinning progressed at a faster rate on shallower slopes. Effects of *C. thyrsiflorus* increased in magnitude and remained important from year 6 to year 14, as stand structure continued to diverge (Table 1). Fire severity was not a predictor of post-fire *P. muricata* density in any post-fire year. None of the models in any year contained significant spatial autocorrelation in model residuals ($P > 0.10$).

One year following fire, most stands were relatively balanced between cover of *P. muricata* and the most prevalent shrub, *C. thyrsiflorus* (Fig. 5a); relative cover of these two species was unrelated (Spearman's rho = 0.13, $P > 0.10$). Small differences among stands in year 1 were later accentuated such that by year 14 divergence among stands was trending toward dominance of either *P. muricata* or *C. thyrsiflorus* (Fig. 5b). This is supported by the negative relationship 14 yr after fire between *C. thyrsiflorus* cover and dead *P. muricata* stem density (Spearman's rho = −0.51, $P < 0.10$).

Tracking the successional trajectory of stands that were in the closed-canopy pathway (upper quartile of *P. muricata* density in year 14) and the open-canopy pathway (lower quartile of *P. muricata* density in year 14) illustrates the divergence of stands with increasing time since fire (Fig. 6). Small differences between pathways were evident in year 1 (Table 2). By year 14, these differences between pathways became more pronounced and significant as the closed-canopy pathway remained with higher density and density differed by over one order of magnitude between pathways (Table 2, Fig. 6). In addition to *P. muricata* density, differences between pathways in stand structure variability (CV of *P. muricata* density), species richness and
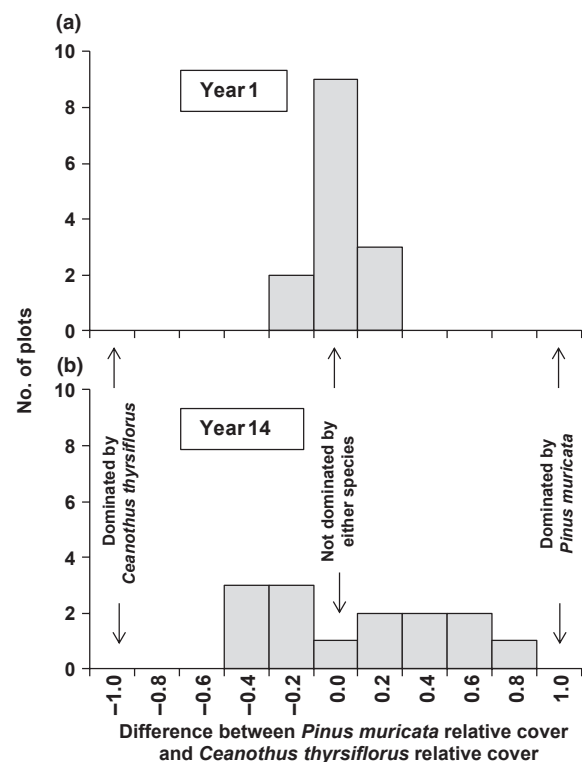

Fig. 5. Frequency histogram of difference between relative cover for *Pinus muricata* and *Ceanothus thyrsiflorus* in post-fire year 1 (**a**) and post-fire year 14 (**b**) for each plot, illustrating divergence in stand structure through time. Values on *x*-axis are generated by subtracting the relative percentage cover of *C. thyrsiflorus* from the relative percentage cover of *P. muricata*, where −1.0 = plot dominated by *C. thyrsiflorus*; 0.0 = plot equally occupied by both species; 1.0 = plot dominated by *P. muricata*.

relative dominance of *P. muricata* or *C. thyrsiflorus* increased in magnitude between year 1 and year 14 (Table 2). Mean within-stand species diversity (H') was similar in year 1 and year 14 (Table 2). Topography was likely important in mediating pathways, as stands in the closed-canopy pathway were on steeper slopes (23.8°) than those in the open-canopy pathway (13.5°; $t = 4.45$, $P < 0.01$).
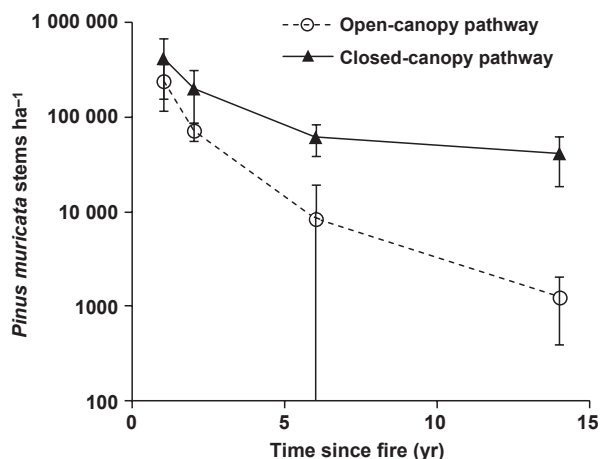
Fig. 6. Mean post-fire *Pinus muricata* density (stems per ha) in the two pathways of post-fire stand development. The closed-canopy pathway is in plots that were in the upper quartile of *P. muricata* density ($n = 4$) in year 14, while the open-canopy pathway is in plots that were in the lower quartile of *P. muricata* density ($n = 4$) in year 14. Error bars represent ± 2 SE.

Table 2. Stand structure (postfire for *Pinus muricata* density) and variability, relative cover of *P. muricata* and *Ceanothus thyrsiflorus*, and species diversity metrics in the two pathways of stand development in postfire year 1 and year 14. Values are means (1 SE).

Variable	Postfire Year	Open-Canopy Pathway	Closed-Canopy Pathway
P. muricata	1	237 375 (62 929)	410 250 (130 679)
Stems ha^{-1}	14	1250 (433)$^{++}$	40 875 (11 255)
CV of *P. muricata*	1	64 (7)$^{++}$	41 (5)
density (%)	14	364 (49)$^{++}$	65 (7)
P. muricata relative	1	9 (2)$^{+}$	19 (3)
cover (%)[a]	14	11 (3)$^{++}$	57 (6)
C. thyrsiflorus relative	1	25 (7)	12 (2)
cover (%)[a]	14	54 (6)$^{++}$	15 (7)
Species Richness	1	10.0 (1.1)$^{++}$	6.5 (0.9)
(no. of species)	14	6.5 (1.0)$^{+}$	3.5 (0.7)
Shannon diversity (*H'*)	1	1.91 (0.10)	1.78 (0.09)
	14	1.39 (0.12)	1.10 (0.16)

Significant difference between pathways (Welch's *t*-test) within a year are denoted with $^{+}(P \leq 0.10)$, $^{++}(P \leq 0.05)$. [a]Statistical tests on percent cover data were conducted on arcsine square root transformed values.

Discussion

Our study is the first to directly track post-fire succession for over a decade in a California closed-cone pine ecosystem, providing insight into post-disturbance pathways of stand development in serotinous coastal pine forests. Prior to fire, forest structure was relatively uniform and dominated by *P. muricata*. The divergent pathways we describe here provide evidence of early post-fire heterogeneity in

structure persisting into later seral stages of stand development, supporting the hypothesis of 'precocious complexity' (Donato et al. 2012). While *P. muricata* is an endemic species with a restricted native distribution, the patterns observed in our study may be applicable to other serotinous pines in mediterranean climates (e.g. *P. attenuata*, *P. halapensis*, *P. radiata*).

Consistent with the initial floristics model (Egler 1954) and findings in other coastal conifer forests in mediterranean climates (Capitanio & Carcaillet 2008; Franklin 2009), species diversity and richness peaked 1 and 2 yr following fire, respectively, due to the presence of early- and late-successional species. This peak in diversity and richness is largely due to the myriad adaptations to fire among species in this plant community. While *P. muricata* maintains a serotinous aerial seed bank, other less-dominant evergreen trees have thick insulating bark (e.g. *Q. agrifolia*) or can resprout from the root crown or the stem (*U. californica*). Many shrubs (e.g. *C. thyrsiflorus, Manzanita* spp.) can also resprout or maintain persistent soil seed banks that are stimulated by fire. Because sampling occurred in late summer during all post-fire years, our absolute species richness estimates are likely an underestimate because only woody perennials and late-season annuals would have been recorded during sampling in July and August. However, sampling periods were all during the same months, making relative comparisons valid.

Collectively, our results suggest two pathways of stand development, where small differences between early post-fire stands of relatively high tree density have increased in magnitude as stands diverged in structure and became more dissimilar with time since fire. Prior to the Vision Fire, stands in the Inverness Ridge *P. muricata* forest were dominated by *P. muricata* and characterized by relatively low variability in structure. While stands that proceeded along different pathways were characterized by small structural differences in early post-fire years, they later diverged substantially. By year 14, the closed-canopy pathway was characterized by lower species richness, dominance of conifers rather than shrubs, and post-fire *P. muricata* stand density over an order of magnitude higher and structural variability an order of magnitude lower than the open-canopy pathway (Table 2). As *P. muricata* establishment occurs in a short window (~1 yr) following fire, stands in the open-canopy pathway are expected to remain at low *P. muricata* stem density until the next stand-replacing fire. However, the relatively low pre-fire CV of density among stands suggests that there may be convergence in stand structure decades after fire, as *P. muricata* continues to self-thin in high-density stands and late-seral species (e.g. *Q. agrifolia, U. californica*) establish in gaps between forested patches.

Experimentally manipulated studies with conifers and *C. velutinus* (snowbrush ceanothus) lend insight to potential mechanisms behind the successional patterns in our study. Shade-intolerant conifers surrounded by *C. velutinus* that have their highest branches emerging above the *C. velutinus* canopy can be up to 70% taller than open-grown trees, whereas those with their tallest branches below the *C. velutinus* canopy can be up to 50% shorter than open-grown trees (Erickson & Harrington 2006). This suggests that early post-fire stands of mixed *C. thyrsiflorus* and *P. muricata* likely diverged based on which species outgrew the other in height initially. The positive relationship between *P. muricata* stand density and slope suggests that *P. muricata* was able to establish early dominance on steeper slopes with thinner soils, while *C. thyrsiflorus* was able to do so on gentler slopes with deeper soils. Similar outcomes between shrubs and conifers that are dependent on topographic context have been reported in northern California and southwest Oregon (Irvine et al. 2009). Because we did not measure tree heights, it is unknown if trees in the stands where *P. muricata* overtopped *C. thyrsiflorus* are taller from the facilitative effects of *C. thyrsiflorus*. Future experimental studies with *P. muricata* and *C. thyrsiflorus* could be conducted to test this hypothesis. While cover of *C. thyrsiflorus* and slope may act synergistically on driving *P. muricata* stand structure, our data suggest that their effects are largely complementary. *Ceanothus thyrsiflorus* cover and slope were statistically unrelated in all post-fire sampling years.

Although dense stands of *C. thyrsiflorus* may have inhibited dominance of *P. muricata*, these early-seral shrub patches between closed-canopy forests likely set the template for long-term structural and compositional diversity in tree species. Plants in the *Ceanothus* genus increase available soil nitrogen through symbiotic fixation (Delwiche et al. 1965), which can lead to improved site fertility compared to nearby stands dominated by pines (Johnson 1995). Further, once established, *Ceanothus* shrubs can facilitate the establishment of shade-tolerant species while inhibiting shade-intolerant species (e.g. pine) – shifting forest composition in the absence of stand-replacing disturbance (Oakley et al. 2006). Long fire-free periods can drive transitions from shrubs to closed-canopy conifer forest when shade-tolerant conifers are present (Nagel & Taylor 2005; Odion et al. 2010). This outcome is possible if comparatively shade-tolerant *Pseudotsuga menziesii* (Douglas-fir) could disperse into *Ceanothus* stands from nearby forests in the study area; however *P. muricata* is relatively shade-intolerant and seeds are rarely released in the absence of fire.

Pinus muricata and *C. thyrsiflorus* dominated the early- to mid-seral stages in the first 1.5 decades following fire, however slower-growing, late-seral species in this system

(e.g. *Q. agrifolia, U. californica*) remained present at relatively low cover and stem density. Individuals of these species present in year 14 largely regenerated vegetatively rather than through seed, due to the rapid occupation of the growing space by seed-dispersed and faster-growing species. However, because *Q. agrifolia* and *U. californica* seedlings are shade-tolerant, animal-dispersed seeds may contribute to eventual establishment in areas currently dominated by the early/mid-seral stands of *C. thyrsiflorus*. Shrub cover can facilitate *Q. agrifolia* establishment by serving as a 'nurse plant' to ameliorate harsh conditions (Callaway & D'Antonio 1991) or by promoting seed dispersal from birds into patches of shrubs (Callaway & Davis 1998). While the specific relationship between *Q. agrifolia* and *C. thyrsiflorus* is unknown, sites currently dominated by *C. thyrsiflorus* should provide suitable germination sites for *Q. agrifolia* seedlings that require high soil moisture (Matsuda & McBride 1986). However, no post-fire seedlings of either of these late-seral trees or *P. menziesii* were found 14 yr after fire, as stem density and cover of *C. thyrsiflorus* remains high.

Our results show the continuation of some early trends noted in the initial two post-fire sampling years (Holzman & Folger 2005) and illustrate links between early heterogeneity and later divergence in stand development pathways. Specifically, qualitative observations of differences in *P. muricata* density and *C. thyrsiflorus* cover between topographic contexts in years 1, 2 and 6 (Holzman & Folger 2005) were quantified in the present study, and these differences became more pronounced through time, influencing stand structure through mid-seral stages (year 14). Co-occurrence of *C. thyrsiflorus* and *P. muricata* within forest stands was common 1 and 2 yr following fire, but has become increasingly rare as time since fire has increased. Negative relationships between invasive *E. minima* and post-fire *P. muricata* seedling density in year 2 were not hypothesized to be of long-term importance (Holzman & Folger 2005). It is impossible to know with certainty if legacy effects from early competition between *E. minima* and *P. muricata* seedlings remain, because of intense post-fire management of *E. minima* in the park and the lack of repeated measures at the same exact locations. However, at the highest level of relative cover for both *E. minima* and *L. arboreus* in year 2, *P. muricata* density was >45 000 stems·ha^{-1}, suggesting minimal effects. These results support findings of minimal long-term effects of early-seral invasive species in other stand-replacing fire regimes dominated by serotinous conifers (Wright & Tinker 2012).

Several important differences are apparent between post-fire succession in this previously forested area and other areas where *P. muricata* forest expanded following fire (Harvey et al. 2011). Seed source was not a significant

predictor of post-fire *P. muricata* seedling density in the present study, presumably because pre-fire seed availability was generally high throughout the area. However, distance to the nearest pre-fire stand edge and individual tree were the most important predictors of *P. muricata* forest presence and stand density in areas where the forest expanded following fire (Forrestel et al. 2011; Harvey et al. 2011). Nitrogen deposition from wind-blown ash and the presence of mycorrhizal associates may also be an important driver of where new post-fire stands develop, as *P. muricata* is an obligate ectomycorrhizal host (Horton et al. 1998; Grogan et al. 2000a,b).

Conclusion

Understanding alternative successional pathways in forest stand development following a major disturbance is important for predicting ecosystem response and forecasting long-term trajectories of compositional and structural diversity in fire-prone forests. Using the California closed-cone pine forest as a model system, we found evidence of two successional trajectories, whereby previously closed-canopy forest can follow alternative stand developmental pathways following a severe fire. While initial post-fire regeneration was high in most sites, stands quickly diverged in structure following either a high-density, closed-canopy pathway dominated by *P. muricata* or a low-density, open-canopy pathway dominated by *C. thyrsiflorus*. Topographic position was the most important abiotic driver of alternative outcomes, with steeper slopes dominated by *P. muricata* and shallower slopes dominated by *C. thyrsiflorus*. Early heterogeneity persisted into middle seral stages and is expected to remain into later seral stages in this forest, providing support for important 'precocious complexity' in stand structure that can be established in early-successional forests.

Acknowledgements

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. List of potential predictor variables for generalized linear models.
Appendix S2. Values for trends in species richness, relative cover, and post-fire *P. muricata* tree density.