Fire Ecology Volume 7, Issue 2, 2011
doi: 10.4996/fireecology.0702114

RESEARCH ARTICLE

LANDSCAPE-SCALE VEGETATION CHANGE FOLLOWING FIRE IN POINT REYES, CALIFORNIA, USA

Alison B. Forrestel[1, 2*], Max A. Moritz[1], and Scott L. Stephens[1]

[1]Ecosystem Sciences Division, Department of Environmental Science, Policy, and Management,
University of California, 137 Mulford Hall, Berkeley, California 94720-3114, USA

[2]Point Reyes National Seashore,
1 Bear Valley Road, Point Reyes Station, California 94956, USA

*Corresponding author: Tel.: 001-415-464-5200; e-mail: alison_forrestel@nps.gov

ABSTRACT

Fire is an important factor in determining plant community composition and distribution. This study quantifies landscape-scale vegetation change following a large fire at Point Reyes National Seashore, California, USA. Vegetation in the Point Reyes region is characterized by a complex mosaic of grassland, shrub, and forest plant communities, and by high levels of plant diversity. Although large fires are relatively rare on the coast of California north of San Francisco Bay, they are important in determining the distributions of plant communities at the landscape scale. We mapped vegetation communities throughout the study area using aerial imagery and analyzed how vegetation shifted following fire. We found substantial areas had transitioned from coastal scrub to ceanothus scrub (*Ceanothus thyrsiflorus* Eschsch.) or Bishop pine (*Pinus muricata* D. Don) forest following fire. Transitions from shrub to tree vegetation following fire have rarely been documented in this region. Logistic regression analysis was used to examine the factors influencing the post-fire distribution of Bishop pine and ceanothus scrub. Proximity to pre-fire Bishop pine stands and pre-fire vegetation type were the most important predictors of post-fire Bishop pine regeneration. Pre-fire vegetation type, burn severity, and topography were the most important predictors of post-fire ceanothus scrub distribution. This study demonstrates the capacity of these ecosystems for substantial change over short time periods in response to fire, and identifies some of the factors driving this change.

Keywords: *Ceanothus thyrsiflorus*, coastal California plant communities, fire effects, landscape ecology, multiple successional pathways, *Pinus muricata*, vegetation dynamics

Citation: Forrestel, A.B., M.A. Moritz, and S.L. Stephens. 2011. Landscape-scale vegetation change following fire in Point Reyes, California, USA. Fire Ecology 7(2): 114-128. doi: 10.4996/fireecology.0702114

INTRODUCTION

Fire is one of the primary processes shaping landscape-scale vegetation patterns in western North America. Variations in the frequency, intensity, seasonality, and spatial scale of fire strongly influence patterns of plant community regeneration (Turner *et al.* 1997, Agee

1998, Romme *et al.* 1998, Rundel *et al.* 1998, Brown *et al.* 1999, Sugihara *et al.* 2006, Potts *et al.* 2010). The role of fire in creating landscape-scale heterogeneity has been well documented in certain ecosystems such as the lodgepole pine (*Pinus contorta* Douglas ex Louden) forests of the Rocky Mountains (Schoennagel *et al.* 2008) and pine and mixed conifer forests of the southwest US, Sierra Nevada, and northwestern Mexico (Fulé *et al*. 2002, Stephens *et al*. 2008, Collins and Stephens 2010). At the landscape scale, plant communities in this region shift both spatially and temporally in response to processes such as a fire, grazing and succession.

The ecosystems of coastal northern California have high levels of both alpha and beta diversity (Whittaker 1972, Barbour *et al*. 2007, Thorne *et al.* 2009, Kraft *et al.* 2010). Many of the plant species and communities in this region are rare, due to the unique environment and biogeographic history and to human impacts such as urbanization and invasive species (Axelrod 1958, Davis and Borchert 2006, Seabloom *et al.* 2006). Some of these species and communities depend upon fire in order to persist. At the landscape scale, plant communities in this region shift both spatially and temporally in response to fire and disturbances such as grazing and to biotic interactions via processes such as succession (McBride and Heady 1968, McBride 1974, Callaway and Davis 1993, Keeley 2005).

The fire ecology of this region is complex. Plant communities are comprised of a mix of fire dependent and fire neutral species (Stuart and Stephens 2006). The fire history of coastal northern California has varied over time with periods of high fire frequency during the Native American and early rancher eras, and lower fire frequency prior to Native American management and again in recent times (Menzies 1793, Greenlee and Langenheim 1990, Brown *et al.* 1999, Keeley 2002, Anderson 2005, Keeley 2005, Stephens *et al.* 2007). Given its high alpha and beta diversity, wide range of adaptations to fire, and historical shifts in fire frequency, this region provides a rich opportunity for exploring the role of fire in driving landscape-scale vegetation patterns.

As a result of the high diversity of this system, the response of plant communities to fire may be more complex than what has been documented in other vegetation types (e.g., Turner *et al*. 1994, Collins and Stephens 2010). Further, because fire is less frequent in northern coastal California than in many other areas of the western US, opportunities to observe the impacts of fire on landscape-scale heterogeneity in this region are rare. The majority of published literature on vegetation transitions associated with fire in coastal California ecosystems documents shifts from woody to herbaceous vegetation following fire, and is based on studies carried out at relatively small spatial scales (e.g., Zedler *et al*. 1983, Callaway and Davis 1993, Keeley 2005, Talluto and Suding 2008; W.K. Cornwell, University of California, Berkeley, unpublished review). One landscape-scale study from the central coast region of California found higher transition rates from scrub to grassland in areas that had burned, and shifts from grassland to scrub in unburned areas (Callaway and Davis 1993). There is a paucity of information in the literature documenting other types of transitions such as grassland to forest, grassland to shrub, or shrub to forest following fire (but see Davis *et al.* 2010).

The 1995 Vision Fire at Point Reyes National Seashore (PRNS), California, USA, provided a unique opportunity to examine landscape-scale shifts in vegetation in coastal ecosystems. This fire was the largest, by several orders of magnitude, at PRNS since it was established in 1962. It burned 5000 ha from 3 October through 8 October 1995. Approximately 4690 ha of the burn were within the boundaries of PRNS, which is more than 15% of the total park area (Figure 1). Fires as large as the Vision Fire are rare in the highly urbanized areas of the northern California coast in

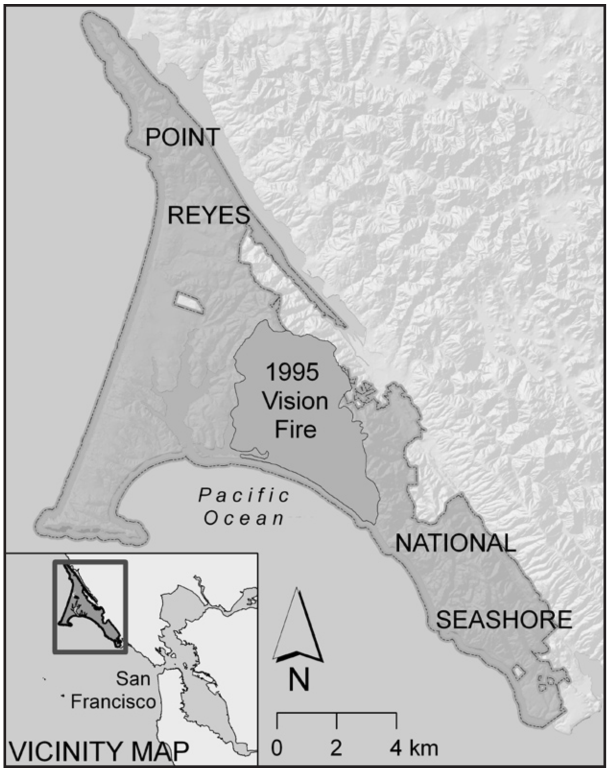

Figure 1. Map of Point Reyes National Seashore, California, USA, showing the perimeter of the 1995 Vision Fire.

the vicinity of PRNS. In addition, detailed vegetation maps were available from immediately prior to the burn. This study documents changes in post-fire vegetation in the Vision Fire burn area and examines how patterns of vegetation change are related to burn severity, topography, soils, and pre-fire vegetation.

METHODS

Study Area

Point Reyes National Seashore is located in coastal Marin County, California, USA, approximately 45 km north of San Francisco. It is a 28 751 ha peninsula, which is bounded on the northeast by the San Andreas Fault (Figure 1). The climate in the study area is Mediterranean with wet winters and cool, dry summers. Temperatures range from lows of 6 °C to 9 °C and highs of 18 °C to 24 °C during the summer months, to lows of 2 °C to 4 °C and highs of 15 °C to 17 °C during winter. Average annual precipitation ranges from 50 cm near the coast to as much as 100 cm near the Bear Valley visitor center (Bear Valley Weather Station 1964-2010). Approximately eighty percent of the precipitation in the area occurs between November and March. Summer precipitation is low, averaging less than 0.5 cm per month. Summer months are characterized by coastal fog. Precipitation from fog drip has not been quantified for PRNS, but one study further north on the California coast (Requa, California) found summer fog drip provided an additional 22 cm to 45 cm of water annually (Dawson 1998). The most extreme fire weather generally occurs in October and November when high pressure systems over the Great Basin result in dry, hot Diablo winds blowing out of the east or northeast. The Vision Fire was started by a campfire on 3 October 1995 and, during the period of active fire growth, relative humidity dropped to 9 %, winds reached 35 km hr^{-1}, and temperatures reached 28 °C (Marin County Fire Department, unpublished data).

The dominant plant communities in the study area are Bishop pine (*Pinus muricata* D. Don) forest, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) forest, northern coastal scrub (dominated by coyote brush, *Baccharis pilularis* DC), blue blossom ceanothus (*Ceanothus thyrsiflorus* Eschsch.) scrub, and northern coastal prairie (dominated by a mix of native and non-native, annual and perennial, grass species). Bishop pine forest and ceanothus scrub both depend on fire in order to persist. The dominant species of Douglas-fir forest, northern coastal scrub, and northern coastal prairie are all able to tolerate fire but do require fire to reproduce. This analysis focused on post-fire change in the distribution of Bishop pine and blue blossom ceanothus, because these two species changed in distribution and extent most dramatically following the fire.

In 2003, a detailed vegetation map was finalized for PRNS following both the California Manual of Vegetation and the National Vegetation Classification systems (Sawyer and Keeler-Wolf 1995, Grossman *et al*. 1998, Schirokauer *et al*. 2003). This vegetation map was based on 1994 imagery and therefore reflects the vegetation communities present prior to the 1995 Vision Fire. The results presented here use vegetation classified to the "vegetation management community" as defined in the PRNS Plant Community Classification and Mapping Project Final Report (Schirokauer *et al*. 2003). The vegetation management communities present in the study area were Bishop pine forest, Douglas-fir forest, hardwood forest, riparian forest and shrubland, coastal scrub, blue blossom ceanothus scrub, grassland, and herbaceous wetland.

Vegetation Mapping and Accuracy Assessment

We mapped vegetation after the Vision Fire using color digital orthophoto quarter quadrangle images (1 m resolution), which were collected in March and April 2004 (County of Marin 2010). These images were supplemented by the National Agricultural Imagery Program aerial photography (1 m to 2 m resolution) from August 2005 (USDA Forest Service 2009). Polygons were mapped to the same vegetation management community types on field reconnaissance data and expert knowledge of PRNS vegetation communities. A "heads-up digitizing" approach was used based on the recommendation of the California Department of Fish and Game Vegetation Classification and Mapping Program (Keeler-Wolf 2007). To maximize consistency with the existing vegetation map, the minimum mapping unit used was 0.5 ha (Schirokauer *et al*. 2003).

Accuracy assessment of the hand-digitized polygons was conducted using 206 accuracy assessment plots, which were installed in 1998 and 1999, after the Vision Fire, inside the fire perimeter. Plots were randomly located and were 0.5 ha in size. At each plot, percent cover was determined for each species with >1% cover, and height class and percent cover were estimated by life form (Schirokauer *et al*. 2003). Although the plot data were collected five to six years before the date of the imagery used for vegetation mapping, changes over this period were likely limited to changes in vegetation stature, minor shifts in species composition, or successional changes over small areas. The broad vegetation community classes used for this analysis are relatively stable over short time frames in the absence of large scale fire and disturbance (Point Reyes National Seashore, Fire Effects Monitoring Program, unpublished data).

The accuracy assessment used both the widely accepted confusion matrix and kappa coefficient approaches (Congalton *et al*. 1983, Congalton 1991, Foody 2002). The confusion matrix approach depicted the mapped vegetation communities in each row and the field-observed vegetation communities from the accuracy assessment plots in each column. The mapped vegetation type of each accuracy assessment plot was listed in the appropriate row. From this "producer's accuracy," or percentage of a particular vegetation class that had been correctly mapped as that vegetation class, and "user's accuracy," or the percentage of a mapped class that was mapped correctly, were both calculated (Congalton 1991). The kappa statistic was also calculated as an indicator of accuracy, which accounted for any correct classification that was due to chance (Lillesand *et al*. 2004).

Vegetation Change

Vegetation change between the 1994 and 2004 images was quantified by calculating the percentage change in area from pre- to post-fire in each vegetation class. Additionally, spatially explicit vegetation change was calculated and a transition matrix and diagram were constructed using raw area measurements (Mouillot *et al*. 2005).

Logistic regression analysis was used to examine the patterns driving vegetation change following fire. Specifically, analysis focused on post-fire presence or absence of Bishop pine and ceanothus scrub as response variables because those vegetation types experienced the greatest change following fire. In building logistic regression models, we considered the following predictor variables: slope, aspect, elevation, soil type, pre-fire vegetation type, burn severity, and, for analyses of Bishop pine, distance from pre-fire Bishop pine stands. Slope, aspect, and elevation were all based on digital elevation model data, which were resampled to 30 m × 30 m pixels. Soil type data came from the Marin County Soil Survey (USDA 1985). Pre-fire vegetation data came from the PRNS vegetation map described above (Schirokauer *et al*. 2003). Landsat-based differenced normalized burn ratio data were used as the metric of burn severity. The normalized burn ratio (NBR) was calculated from Landsat bands 4 and 7, and the differenced NBR (dNBR) was the post-fire NBR subtracted from the pre-fire NBR (Key and Benson 2006). The dNBR data for the Vision Fire were obtained through the Monitoring Trends in Burn Severity program, which provides burn severity data using dNBR methodology for all large fires in the United States dating back to 1984 (Eidenshink *et al*. 2007). Soils and vegetation layers were converted from vector to 30 m × 30 m raster format. All GIS analyses used ArcGIS version 9.3 (Environmental Research Institute, Redlands, California, USA) with standard extensions.

The initial data set included all pixels in the study area for a total of 51 101 observations. Semivariograms were constructed to explore patterns of spatial autocorrelation in the data (Rossi *et al*. 1992, O'Sullivan and Unwin 2002). Based on the semivariograms, which showed spatial autocorrelation up to 200 m, the data were randomly subsampled so that all data points were a minimum of 200 m apart. This resulted in a dataset of 346 observations, which was used for all subsequent analyses. Data were analyzed using logistic regression, and all parameters were tested for normality and heteroscedasticity. Models initially included all variables, and those with significant effects ($P < 0.05$) in the initial model were selected for inclusion in the final model. Likelihood-ratio tests were used to compare the full versus reduced models. All statistical analyses were completed using the R statistical software version 2.11.1 (R Development Core Team 2009).

RESULTS

Accuracy Assessment

The accuracy assessment is summarized in Table 1; overall mapping accuracy was 79%. The producer accuracy, or percentage of field plots that were mapped correctly, ranged from a high of 91% for the Bishop pine community type to a low of 56% for the hardwood community type. The producer accuracy for Bishop pine, blue blossom ceanothus, and coastal scrub, which collectively comprise 75% of the study area, ranged from 83% to 91%. User accuracy, or percentage of the mapped areas that corresponded with field plots of the same vegetation type, ranged from 90% for herbaceous wetland to 70% for grassland. For Bishop pine, blue blossom ceanothus, and coastal scrub, the user accuracy ranged from 72% to 87%. The kappa coefficient for the overall classification was 0.75.

Vegetation Change

Changes in vegetation are summarized in Table 2. The largest change was in ceanothus, which increased by 844 ha, or more than 4000%. Bishop pine increased by 360 ha, or 85%. The largest decreases were in coastal scrub, which was reduced by 672 ha, or 27%,

Table 1. Accuracy assessment of vegetation classification using field-based plot data. Areas where the mapped community matched the field-assessed community are highlighted in gray. Producer accuracy, or the percentage of field plots that were mapped correctly, is shown for each vegetation class in the bottom row. User accuracy, or the percentage of mapped polygons that corresponded with field plots of the same vegetation type, is shown in the far right column.

	Field assessed community									
Mapped community	**Bishop pine**	**Ceanothus**	**Coastal scrub**	**Douglas-fir**	**Grassland**	**Hardwood**	**Herbaceous wetland**	**Riparian**	**Total**	**% user accuracy**
Bishop pine	31	1	10	1					43	72
Ceanothus	2	17	2	1		1			23	74
Coastal scrub		1	76		3	2	4	1	87	87
Douglas-fir	1			7					8	88
Grassland			3		7				10	70
Hardwood		1				5			6	83
Herbaceous wetland							9	1	10	90
Riparian			1			1		15	17	88
Total	34	20	92	9	11	9	14	17	206	
% producer accuracy	91	85	83	78	64	56	64	88		79

Table 2. Pre-fire to post-fire vegetation change by community type. The total mapped area of each vegetation type is shown before and after fire as well as the change expressed both in hectares and as a percent of the pre-fire area for each vegetation class.

Community	Pre-fire (ha)	Post-fire (ha)	Change (ha)	Change (%)
Bishop pine	423	782	360	85
Ceanothus	18	862	844	4642
Coastal scrub	2476	1804	-672	-27
Douglas-fir	833	447	-386	-46
Grassland	344	242	-102	-30
Hardwood forest	89	101	12	13
Herbaceous wetlands	80	86	6	7
Other	16	6	-10	-62
Riparian forest or shrubland	343	298	-45	-13

and Douglas-fir, which decreased by 386 ha, or 46 %.

Vegetation changes were examined more closely by looking at spatially explicit shifts in vegetation community (Figure 2). Figure 3 shows a transition diagram of major vegetation types from pre-fire vegetation to post-fire vegetation. Table 3 depicts transitions among all vegetation types. There were substantial shifts not only in the overall area of each vegetation community, but also in the distribution of these communities across the landscape. In the case of Bishop pine, only 240 ha, or approximately 60 %, of the area of Bishop pine present before

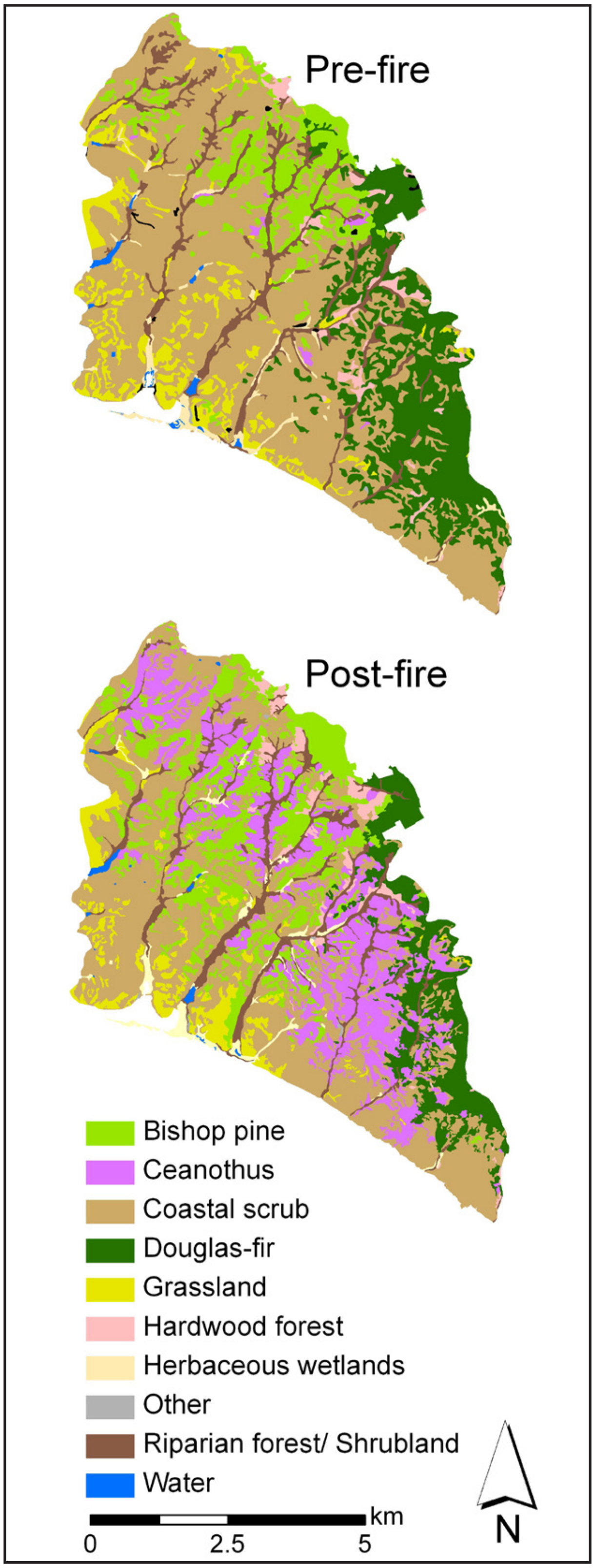

Figure 2. Vegetation communities at Point Reyes National Seashore, California, USA, before and following the 1995 Vision Fire.

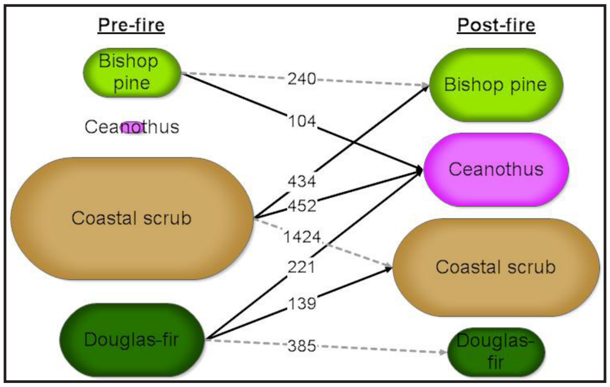

Figure 3. Transitions among major vegetation types following the 1995 Vision Fire. The size of each ellipse is proportional to the extent of that community within the study area. Solid arrows indicate transitions between vegetation communities, and dashed gray arrows indicate areas where the vegetation type remained the same following fire. Arrows are labeled with the number of hectares that either transitioned or stayed the same. A minimum 100 ha threshold was used for inclusion in the diagram.

the fire returned to Bishop pine after the Vision Fire. Much of the Bishop pine present post-fire was growing in areas that were formerly coastal scrub. Blue blossom ceanothus also made significant incursions into areas of former coastal scrub and Bishop pine forest.

Based on logistic regression models, distance from pre-fire Bishop pine stand and pre-fire vegetation type were significant predictors of Bishop pine presence or absence (Table 4). The probability of Bishop pine occurrence decreased with increasing distance from pre-fire Bishop pine stands (Figure 4). The saturated model for Bishop pine did not provide a better fit than the final model, which included only distance from pre-fire Bishop pine stand and pre-fire vegetation type ($P = 0.315$). For blue blossom ceanothus distribution, pre-fire vegetation type, burn severity, slope, and elevation were all significant predictors in the final model (Table 5). The probability of ceanothus occurrence increased with increasing burn severity and slope, and decreased with increasing elevation (Figure 4). Again, the saturated model did not provide a better fit than the final model ($P = 0.380$).

Table 3. Transitions among vegetation types following the 1995 Vision Fire. Pre-fire vegetation classes are listed in the row headers, and post-fire vegetation classes are listed in the column headers. Areas of no change are depicted in the diagonal. All units are hectares.

	Post-fire vegetation								
Pre-fire vegetation	**Bishop pine**	**Ceanothus**	**Coastal scrub**	**Douglas-fir**	**Grassland**	**Hardwood**	**Herbaceous wetland**	**Riparian**	**Pre-fire total**
Bishop pine	240	104	33	5	4	22	1	12	423
Ceanothus	4	10	4	0	0	0	0	1	18
Coastal scrub	434	452	1424	32	66	19	10	36	2476
Douglas-fir	42	221	139	385	1	27	0	18	833
Grassland	38	0	124	3	168	0	7	4	344
Hardwood	9	27	5	12	0	26	0	10	89
Herbaceous wetland	1	1	10	4	1	0	53	9	80
Riparian	11	45	59	5	1	6	8	206	343
Post-fire total	782	862	1804	447	242	101	86	298	4645

Table 4. Logistic regression results of factors that influenced the presence of Bishop pine following the 1995 Vision Fire at Point Reyes National Seashore, California, USA.

	Estimate	**Standard error**	***Z* value**	***P* value**
Intercept	-1.40	0.38	−3.706	0.00021
Distance to pre-fire Bishop pine	−2.89E-03	1.15E-03	−2.512	0.012017
Pre-fire Bishop pine	1.23	0.51	2.421	0.015495
Null deviance: 208.71 on 345 degrees of freedom				
Residual deviance: 133.84 on 345 degrees of freedom				
AIC: 151.84				

DISCUSSION

Mapping and Accuracy Assessment

Overall map accuracy was good and was comparable to that of the original mapping effort. Over 5 % of the overall mapping error resulted from areas classified based on the field data as coastal scrub that were subsequently mapped as Bishop pine. Informal examination of these areas revealed that they were coastal scrub with a low density Bishop pine component (15 % to 20 % Bishop pine cover). Because these trees will undoubtedly increase in ecological importance as they grow and expand their canopies, it is preferable to consider areas of open growing Bishop pine as Bishop pine rather than coastal scrub.

Vegetation Change

Bishop pine forest changed both in extent and distribution following the Vision Fire. Not only did Bishop pine extent nearly double, but the distribution of Bishop pine forest shifted from being restricted to ridge tops pre-fire to extending from the ridges all the way down to the Pacific coast post-fire. It should be noted that there were isolated individual Bishop pine trees present in areas closer to the Pacific coast prior to the fire; the change we describe refers to the distribution of the Bishop pine commu-

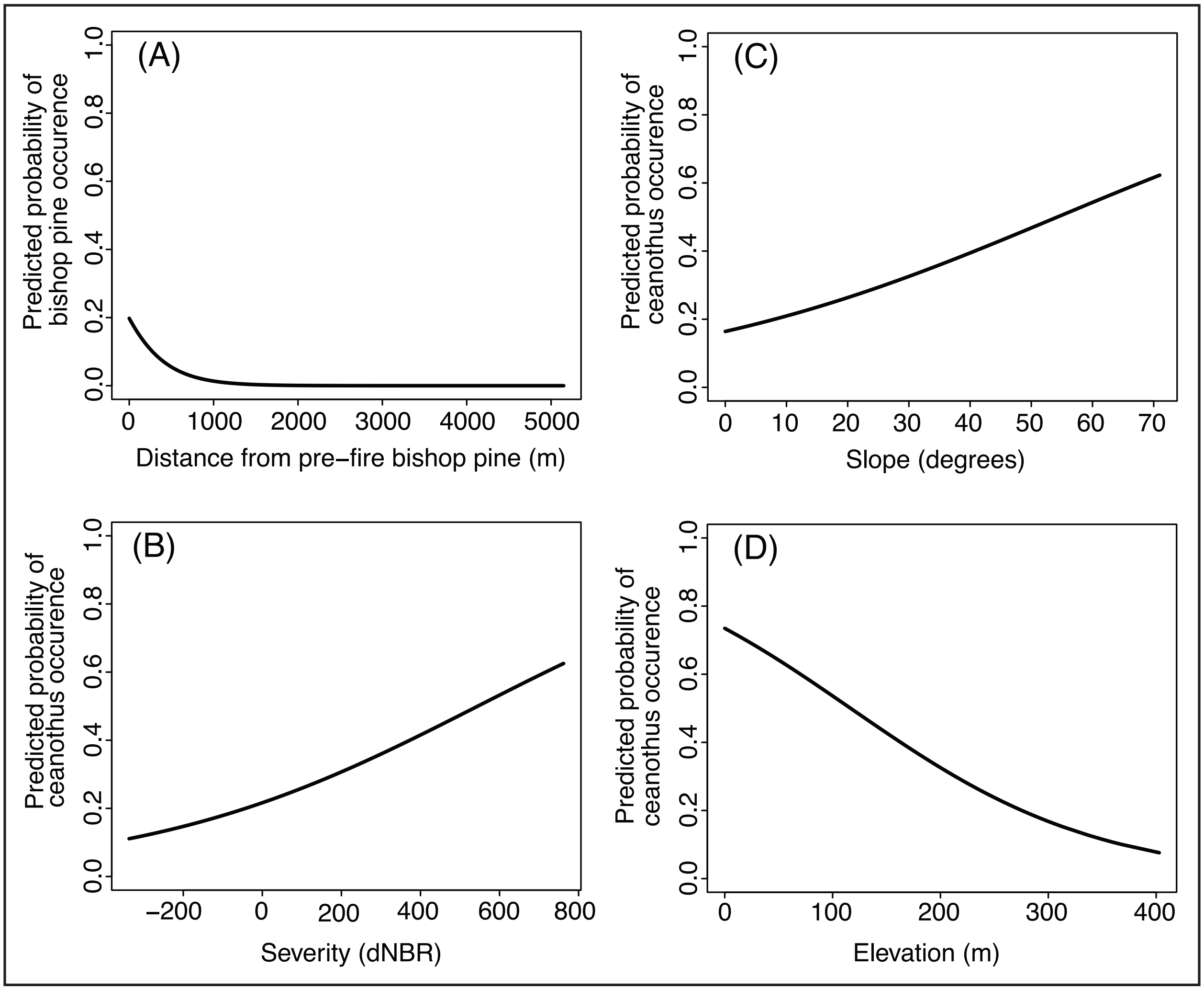

Figure 4. (A) Effect of distance from pre-fire Bishop pine on the predicted probability of Bishop pine occurrence following fire based on logistic regression models. Predicted probabilities assume that the site was not Bishop pine prior to fire. (B) Effect of burn severity on the predicted probability of ceanothus occurrence following fire based on logistic regression models. Predicted probabilities assume that the site was coastal scrub prior to fire; the slope is 35°, and the elevation is 200 m. (C) Effect of slope on the predicted probability of ceanothus occurrence following fire based on logistic regression models. Predicted probabilities assume that the site was coastal scrub prior to fire; the dNBR is 300, and the elevation is 200 m. (D) Effect of elevation on the predicted probability of ceanothus occurrence following fire based on logistic regression models. Predicted probabilities assume that the site was coastal scrub prior to fire; the dNBR is 300, and the slope is 35°.

nity. Bishop pine expansion following fire is not surprising given the autecology of this species. Bishop pine is serotinous and is adapted to high severity stand replacement fires (Sugnet and Martin 1984, Stuart and Stephens 2006). Because the Vision Fire burned through pre-fire Bishop pine forest with high intensity, we are confident that the vast majority of areas mapped as Bishop pine following the fire regenerated from seed post-fire.

Logistic regression models revealed that the best predictors for post-fire Bishop pine regeneration were whether the pre-fire vegetation was dominated by Bishop pine and proximity to pre-fire stands of Bishop pine. The occurrence of post-fire Bishop pine stands

Table 5. Logistic regression results of factors that influenced the presence of ceanothus scrub following the 1995 Vision Fire at Point Reyes National Seashore, California, USA.

	Estimate	Standard error	*Z* value	*P* value
Intercept	–1.96	0.86	–2.27	0.998
Pre-fire coastal scrub	1.22	0.46	2.68	0.007
dNBR	2.36E-03	1.11E-03	2.134	0.033
Slope	0.03	0.01	3.058	0.002
Elevation	–2.66E-03	7.60E-04	–3.495	≤0.001

Null deviance: 331.36 on 345 degrees of freedom

Residual deviance: 224.42 on 345 degrees of freedom

AIC: 274.42

drops off dramatically beyond distances of 1 km from pre-fire Bishop pine stands. Bishop pine seedlings predominantly established in areas that were dominated by Bishop pine and coastal scrub pre-fire. Some areas of pre-fire grassland were converted to Bishop pine post-fire. Seed dispersal, which is mainly wind driven, was likely the primary factor determining where Bishop pine regeneration occurred. Dispersal by small mammals may also occur, but the impacts of small mammals on Bishop pine distribution are not clear. The presence of suitable mycorrhizal symbionts may also be an important factor in post-fire Bishop pine establishment (Baar *et al.* 1999). Similar expansion of closed cone pine species following fire has been observed in other parts of California (S. Fritzke, National Park Service, personal communication).

Blue blossom ceanothus also changed drastically in its extent following the Vision Fire. Although scattered individuals were present pre-fire, the sort of dense, expansive stands described in this study were absent before the fire. Species in the genus *Ceanothus* exhibit a wide array of life history strategies, including sprouting or reproducing only from seed following fire (Keeley and Zedler 1978). At PRNS, blue blossom ceanothus exhibits an obligate seeding strategy, but there is evidence that other populations of this species may produce basal sprouts following fire (Fross and Wilken 2006; T. Parker, San Francisco State University, personal communication). The buried seed bank that germinated following the Vision Fire had likely been left by a previous post-fire population of ceanothus that had senesced prior to the initial vegetation mapping effort due to age-dependent mortality.

Based on logistic regression models, blue blossom ceanothus established in lower elevation, high burn severity areas with steep slopes. Similar to Bishop pine, most of this expansion was into areas that had been previously dominated by coastal scrub. Coyote brush may be less likely to follow high intensity fire due to limited sprouting and seedling establishment.

There is mixed evidence regarding the impact of burn severity on vegetation recovery following fire. The importance of burn severity varies with vegetation type and the aspect of post-fire vegetation being studied (e.g. Turner *et al.* 1999, Keeley *et al.* 2005, Franklin *et al.* 2006, Keeley *et al.* 2008). Our study found a significant positive relationship between burn severity and post-fire ceanothus distribution, which is consistent with other studies (Moreno and Oechel 1994, Keeley *et al.* 2005). The lack of evidence for the importance of burn severity in determining Bishop pine distribution is inconsistent with the findings of Turner *et al.* (1999) in lodgepole pine forests. However, studies in chaparral have found that burn severity is relatively unimportant in determining post-fire vegetation recovery, especially over the longer term, as long as fire intervals are long enough for seedbank accumulation (Keeley *et al.* 2005, Keeley *et al.* 2008).

The mosaic of plant communities at Point Reyes National Seashore has undoubtedly been shifting over time and space for thousands of years due to climate, successional processes, lightning fires, burning by Native Americans, herbivory, and ranching (Anderson 2005). The Vision Fire is an example of an ecological event that caused major changes in the landscape-scale patterns of PRNS vegetation communities. This study provides direct quantitative evidence for the changes that can occur following fire, and provides a unique example of post-fire vegetation transitions from grassland to forest, and from shrub to forest.

In addition to providing evidence for vegetation transitions that have not commonly been observed and documented in the literature for this region, this study also demonstrates that multiple successional pathways are possible following fire in this ecosystem (i.e., a given pre-fire vegetation type has the potential to shift to any number of vegetation types following fire). Many studies have found evidence for multiple successional pathways following fire, although, to our knowledge, few of these studies have focused on the ecosystems of northern coastal California (for an example from the central coast of California, see Callaway and Davis 1993). In our study, coastal scrub was probably the most dynamic vegetation type: transitions to grassland, ceanothus scrub, and Bishop pine, as well as self-replacement, all occurred following fire. Some of the changes we documented, such as the shift from Douglas-fir forest to blue blossom ceanothus, will not persist over the long term. These areas will likely shift back to their pre-fire state in the absence of another fire. Other changes, such as the transition from coastal scrub to Bishop pine forest, are more likely to persist over long time periods and represent fire-meditated shifts to alternative states. Many possible causes for multiple successional pathways have been proposed, including disturbance history, vegetation composition at the time of disturbance, topography, burn intensity, buried and aerial seed sources, soils, and stochastic factors (Abrams *et al.* 1985, Fastie 1995). Vegetation composition prior to fire, topography, burn intensity, and seed source availability, as well as stochastic factors, were likely the most important determinants of successional pathways following the Vision Fire.

Understanding these landscape-scale vegetation dynamics is interesting from a theoretical perspective and important for management. Few ecosystems are so plastic in their response to fire and in the spatial variability of the vegetation composition over relatively short time frames. For managers, it is important to understand how processes such as fire can dramatically shift the distribution of different vegetation types along with the suite of wildlife species that those vegetation communities support.

ACKNOWLEDGMENTS

We would like to thank the Point Reyes National Seashore natural resource and fire management staff for support in making this project happen. In addition, we would like to thank K. Peay for initial inspiration and M. Lahiff and K. Peay for assistance with statistical analyses.

LITERATURE CITED

Abrams, M.D., D.G. Sprugel, and D.I. Dickmann. 1985. Multiple successional pathways on recently disturbed jack pine sites in Michigan. Forest Ecology and Management 10: 31-48. doi: 10.1016/0378-1127(85)90012-X

Agee, J.K. 1998. The landscape ecology of Western forest fire regimes. Northwest Science 72: 24-34.

Anderson, R.S. 2005. Contrasting vegetation and fire histories on the Point Reyes Peninsula during the pre-settlement and settlement periods. Northern Arizona University, Flagstaff, USA.

Axelrod, D.I. 1958. Evolution of the Madro-Tertiary geoflora. The Botanical Review 24: 433-509. doi: 10.1007/BF02872570

Baar, J., T. Horton, A. Kretzer, and T. Bruns. 1999. Mycorrhizal recolonization of *Pinus muricata* from resistant propagules after a stand-replacing wildfire. New Phytologist 143: 409-418. doi: 10.1046/j.1469-8137.1999.00452.x

Barbour, M., T. Keeler-Wolf, and A.A. Schoenherr. 2007. Terrestrial vegetation of California, third edition. University of California Press, Berkeley, USA.

Brown, P.M., M.R. Kaufmann, and W.D. Shepperd. 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. Landscape Ecology 14: 513-532. doi: 10.1023/A:1008137005355

Brown, P.M., M.W. Kaye, and D. Buckley. 1999*a*. Fire history in Douglas-fir and coast redwood forests at Point Reyes National Seashore, CA. Northwest Science 73(3): 205-216.

Callaway, R.M., and F.W. Davis. 1993. Vegetation dynamics, fire, and the physical environment in coastal central California. Ecology 74: 1567-1578. doi: 10.2307/1940084

Collins, B.M., and S.L. Stephens. 2010. Stand-replacing patches within a ‘mixed severity’ fire regime: quantitative characterization using recent fires in a long-established natural fire area. Landscape Ecology 25: 927-939. doi: 10.1007/s10980-010-9470-5

Congalton, R. 1991. A review of assessing the accuracy of classifications of remotely sensed data. Remote Sensing of Environment: 35-46. doi: 10.1016/0034-4257(91)90048-B

Congalton, R., R. Oderwald, and R. Mead. 1983. Assessing Landsat classification accuracy using discrete multivariate analysis statistical techniques. Photogrammetric Engineering and Remote Sensing 49: 1671-1678.

County of Marin. 2010. Marin map. <http://mmgis.marinmap.org/PublicRecords/Default.asp>. Accessed 1 September 2010.

Davis, F.W., and M. Borchert. 2006. Central Coast bioregion. Pages 321-349 in: N.G. Sugihara, J.W. van Wagtendonk, K.E. Shaffer, J. Fites-Kaufman, and A.E. Thode, editors. Fire in California’s ecosystems. University of California Press, Berkeley, USA.

Davis, F.W., M. Borchert, R.K. Meentemeyer, A. Flint, and D.M. Rizzo. 2010. Pre-impact forest composition and ongoing tree mortality associated with sudden oak death in the Big Sur region, California. Forest Ecology and Management 259: 2342-2354. doi: 10.1016/j.foreco.2010.03.007

Dawson, T. 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117: 476-485. doi: 10.1007/s004420050683

Eidenshink, J., B. Schwind, K. Brewer, Z. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. Fire Ecology 3(1): 3-21. doi: 10.4996/fireecology.0301003

Fastie, C.L. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. Ecology 76: 1899-1916. doi: 10.2307/1940722

Foody, G.M. 2002. Status of land cover classification accuracy assessment. Remote Sensing of Environment 80: 185-201. doi: 10.1016/S0034-4257(01)00295-4

Franklin, J., L. Spears-Lebrun, D. Deutschman, and K. Marsden. 2006. Impact of a high-intensity fire on mixed evergreen and mixed conifer forests in the Peninsular Ranges of southern California, USA. Forest Ecology and Management 235: 18-29. doi: 10.1016/j.foreco.2006.07.023

Fross, D., and D. Wilken. 2006. Ceanothus. Timber Press, Portland, Oregon, USA.

Fulé, P.Z., W.W. Covington, M.M. Moore, T.A. Heinlein, and A.E.M. Waltz. 2002. Natural variability in forests of the Grand Canyon, USA. Journal of Biogeography 29: 31-47. doi: 10.1046/j.1365-2699.2002.00655.x

Greenlee, J., and J. Langenheim. 1990. Historic fire regime and their relation to vegetation patterns in the Monterey Bay area of California. American Midland Naturalist 124: 239-253. doi: 10.2307/2426173

Grossman, D., K. Goodin, M. Anderson, P. Bourgeron, M. Bryer, R. Crawford, and L. Engelking. 1998. International classification of ecological communities: terrestrial vegetation of the United States. The Nature Conservancy, Washington, D.C., USA.

Keeler-Wolf, T. 2007. The history of vegetation classification and mapping in California. Pages 1-42 in: M. Barbour, T. Keeler-Wolf, and A. Schoenher, editors. Terrestrial vegetation of California. University of California Press, Berkeley, USA.

Keeley, J.E. 2002. Native American impacts on fire regimes of the California coastal ranges. Journal of Biogeography 29: 303-320. doi: 10.1046/j.1365-2699.2002.00676.x

Keeley, J.E. 2005. Fire history of the San Francisco East Bay region and implications for landscape patterns. International Journal of Wildland Fire 14: 285-296. doi: 10.1071/WF05003

Keeley, J.E., and P.H. Zedler. 1978. Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. American Midland Naturalist 99: 142-161. doi: 10.2307/2424939

Keeley, J.E., C.J. Fotheringham, and M. Baer-Keeley. 2005. Determinants of postfire recovery and succession in Mediterranean-climate shrublands of California. Ecological Applications 15: 1515-1534. doi: 10.1890/04-1005

Keeley, J.E., T. Brennan, and A.H. Pfaff. 2008. Fire severity and ecosystem responses following crown fires in California shrublands. Ecological Applications 18: 1530-1546. doi: 10.1890/07-0836.1

Key, C., and N. Benson. 2006. Landscape assessment: sampling and analysis methods. Pages LA-1-LA-51 in: D. Lutes, R. Keane, J. Caratti, C. Key, N. Benson, S. Sutherland, and L. Gangi. FIREMON: Fire effects monitoring and inventory system. USDA Forest Service RMRS-GTR-164-CD. Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Kraft, N.J.B., B.G. Baldwin, and D.D. Ackerly. 2010. Range size, taxon age and hotspots of neoendemism in the California flora. Diversity and Distributions 16: 403-413. doi: 10.1111/j.1472-4642.2010.00640.x

Lillesand, T., R. Kiefer, and J. Chipman. 2004. Remote sensing and image interpretation. Fifth edition. John Wiley and Sons, New York, New York, USA.

McBride, J. 1974. Plant succession in the Berkeley Hills. Madroño 22: 317-380.

McBride, J., and H. Heady. 1968. Invasion of grassland by *Baccharis pilularis* DC. Journal of Range Management 21: 106-108. doi: 10.2307/3896366

Menzies, A. 1793. California journal excerpts published in 1924. California Historical Society Quarterly 2: 302.

Moreno, J., and W. Oechel. 1994. Fire intensity as a determinant factor of postfire plant recovery in southern California chaparral. Pages 26-45 in: J. Moreno and W. Oechel, editors. The role of fire in Mediterranean-type ecosystems. Springer-Verlag, New York, New York, USA.

Mouillot, F., J.P. Ratte, R. Joffre, D. Mouillot, and S. Rambal. 2005. Long-term forest dynamic after land abandonment in a fire prone Mediterranean landscape (central Corsica, France). Landscape Ecology 20: 101-112. doi: 10.1007/s10980-004-1297-5

O'Sullivan, D., and D. Unwin. 2002. Geographic information analysis. Wiley, Hoboken, New Jersey, USA.

Pickett, S.T.A., and P.S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, San Diego, California, USA.

Potts, J.B., E. Marino, and S.L. Stephens. 2010. Chaparral shrub recovery after fuel reduction: a comparison of prescribed fire and mastication techniques. Plant Ecology 210: 303-315. doi: 10.1007/s11258-010-9758-1

R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Romme, W.H., E.H. Everham, L.E. Frelich, M.A. Moritz, and R.E. Sparks. 1998. Are large, infrequent disturbances qualitatively different from small, frequent disturbances? Ecosystems 1: 524-534. doi: 10.1007/s100219900048

Rossi, R., D. Mulla, A. Journel, and E. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecological Monographs 62: 277-314. doi: 10.2307/2937096

Rundel, P., G. Montenegro, and F. Jaksic. 1998. Landscape disturbance and biodiversity in Mediterranean-type ecosystems. Springer-Verlag, New York, New York, USA.

Sawyer, J., and T. Keeler-Wolf. 1995. A manual of California vegetation. California Native Plant Society, Sacramento, California, USA.

Schirokauer, D., T. Keeler-Wolf, J. Menke, and P. van der Leeden. 2003. Point Reyes National Seashore, Golden Gate National Recreation Area, and surrounding wildlands plant community classification and mapping project final report. National Park Service, Point Reyes Station, California, USA.

Schoennagel, T., E.A.H. Smithwick, and M.G. Turner. 2008. Landscape heterogeneity following large fires: insights from Yellowstone National Park, USA. International Journal of Wildland Fire 17: 742-753. doi: 10.1071/WF07146

Seabloom, E., J. Williams, D. Slayback, D.M. Stoms, J.H. Viers, and A. Dobson. 2006. Human impacts, plant invasion, and imperiled plant species in California. Ecological Applications 16: 1338-1350. doi: 10.1890/1051-0761(2006)016[1338:HIPIAI]2.0.CO;2

Stephens, S.L., D.L. Fry, and E. Franco-Vizcaino. 2008. Wildfire and spatial patterns in forests in northwestern Mexico: the United States wishes it had similar fire problems. Ecology and Society 13(2): 10.

Stephens, S.L., R.E. Martin, and N.E. Clinton. 2007. Prehistoric fire area and emissions from California's forests, woodlands, shrublands, and grasslands. Forest Ecology and Management 251: 205-216. doi: 10.1016/j.foreco.2007.06.005

Stuart, J., and S. Stephens. 2006. North Coast bioregion. Pages 147-170 in: N.G. Sugihara, J.W. Van Wagtendonk, K.E. Shaffer, J. Fites-Kaufman, and A.E. Thode, editors. Fire in California's Ecosystems. University of California Press, Berkeley, USA.

Sugihara, N.G., J.W. van Wagtendonk, K.E. Shaffer, J. Fites-Kaufman, and A.E. Thode. 2006. Fire in California's ecosystems. University of California Press, Berkeley, USA.

Sugnet, P., and R. Martin. 1984. Fire history and post-fire stand dynamics of the Inverness Bishop pine at Point Reyes National Seashore. Thesis, University of California, Berkeley, USA.

Talluto, M.V., and K.N. Suding. 2008. Historical change in coastal sage scrub in southern California, USA, in relation to fire frequency and air pollution. Landscape Ecology 23: 803-815. doi: 10.1007/s10980-008-9238-3

Thorne, J.H., J.H. Viers, J. Price, and D.M. Stoms. 2009. Spatial patterns of endemic plants in California. Natural Areas Journal 29: 344-366. doi: 10.3375/043.029.0402

Turner, M.G., W.W. Hargrove, R.H. Gardner, and W.H. Romme. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. Journal of Vegetation Science 5: 731-742. doi: 10.2307/3235886

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

Turner, M.G., W.H. Romme, and R.H. Gardner. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. International Journal of Wildland Fire 9: 21-36. doi: 10.1071/WF99003

USDA. 1985. Soil survey of Marin County, California. Soil Conservation Service, Washington, D.C., USA.

USDA Forest Service. 2009. National Agricultural Imagery Program (NAIP). <http://www.fsa.usda.gov/FSA/apfoapp?area=home&subject=prog&topic=nai>. Accessed 1 September 2010.

Whittaker, R. 1972. Evolution and measurement of species diversity. Taxon 21: 213-251. doi: 10.2307/1218190

Zedler, P.H., C.R. Gautier, and G.S. McMaster. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. Ecology 64: 809-818. doi: 10.2307/1937204