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The role of disturbance in vegetation distribution, composition and structure at the landscape scale for two western US ecosystems

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Abstract

The role of disturbance in vegetation distribution, composition and structure at the landscape scale for two western US ecosystems

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Disturbance plays a key role in determining the structure, composition and function of ecosystems. Understanding disturbance regimes and their impacts on ecosystems is critical to understanding and managing these systems. This research examines how disturbance structures ecosystems at the landscape scale and how different disturbance agents interact. It is focused on two western US ecosystems: scrub and mixed evergreen forests of coastal northern California, USA and conifer forests of the western slope of the Cascade Mountains, Oregon, USA.

Disturbance has been variously defined, but here I follow the definition of Pickett and White (1985), "any relatively discrete event that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment." Disturbances can be biotic or abiotic and are distinct from perturbations which are departures from normal conditions but are not necessarily caused by a distinct event (Pickett and White 1985, White and Jentsch 2001). Both climate change and fire suppression would be considered perturbations but not disturbances as I am defining those terms here.

Fire is one of the most important disturbances in western US ecosystems (Sugihara et al. 2006). Variations in the frequency, intensity 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). However, because of the unpredictable nature of fire events, fire-vegetation dynamics are not well understood in some ecosystems. For example, the impacts of fire on landscape scale vegetation patterns in coastal northern California have previously not been documented. The first chapter documents landscape scale changes in vegetation communities at Point Reyes National Seashore following the 1995 Vision Fire. Following fire, I found substantial areas had transitioned from coastal scrub to ceanothus scrub (*Ceanothus thyrsiflorus* Eschsch.) or bishop pine (*Pinus muricata* D. Don) forest. 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.

Fire also has the potential to interact with other disturbance agents. In the Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) and redwood (*Sequoia sempervirens* (D.Don) Endl.) forests of Point Reyes National Seashore, introduction of the non-native pathogen *Phytophthora ramorum* (S. Werres, A.W.A.M. de Cock), which causes the disease Sudden Oak Death (SOD), has led to landscape scale mortality of tanoaks (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S.H. Oh). As tanoaks die and fall to the forest floor, they not only change forest structure and composition, but also change fuel loads and potentially fire behavior. The second chapter documents increases in fuel loads over time in long term monitoring plots in Sudden Oak Death infested forests. Throughout the study, I observed a significant positive relationship between dead tanoak basal area and surface fuels. I used the fire behavior modeling program BehavePlus to compare potential fire behavior between diseased and healthy stands. Model outputs indicated the potential for longer flame lengths, higher rates of spread and more intense surface fire in diseased stands. Analysis of the relationship between dead tanoak basal area and understory composition indicated that non-native forb cover is increasing in response to increasing SOD-mortality.

The third chapter focuses on the role of fire at the landscape scale in the conifer forests of the western Cascades at Crater Lake National Park, Oregon, USA. The west side forests of Crater Lake National Park are unique in that they represent one of the few places in the Cascade Range where an elevational gradient from low-elevation mixed conifer to high-elevation mountain hemlock forests remains intact and has never been logged. This presents a unique opportunity to study fire ecology in a place where fire can still function at the landscape scale. I examined stand structure, demography and reconstructed fire history using tree cores and fire scar data across an approximately 7000 hectare study area. Our plots were located in mountain hemlock (*Tsuga mertensiana* (Bong.) Carr), red fir (*Abies magnifica* A. Murr.), lodgepole pine (*Pinus contorta* Loudon) and mixed conifer forest types. Stand demography data from high elevation mountain hemlock forests showed continuous regeneration since the early 1600's with no fire scars present which is characteristic of very infrequent and/or low severity fire. Red fir forests showed a combination of both continuous and episodic regeneration over the past several centuries providing evidence for a mixed severity fire regime. Lodgepole pine stands were even-aged with no fire scar evidence and likely established following high severity fire events. Mixed-conifer forests were uneven-aged with the majority of trees established between 1880 and 1920. The median point fire return intervals for red fir and mixed conifer forests was 37.5 years.

Taken collectively, these chapters illustrate the important role of disturbance, and specifically of fire, in shaping the two ecosystems studied here. This work also demonstrates the potential for other disturbance agents, in this case a non-native pathogen, to impact fire behavior and fire effects. Understanding the ecological role of disturbance is critical to land management and conservation, particularly in the context of climate change (Turner 2010). As land managers move from concepts of "historic range of variability" (Landres et al. 1999) to more sophisticated guiding principles, such as resilience (Hobbs et al. 2009), a strong mechanistic understanding of ecosystem function, including disturbance ecology, will be more critical than ever.

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CHAPTER 1

Landscape-scale vegetation change following fire in Point Reyes, California

INTRODUCTION

Fire is one of the primary processes shaping landscape scale vegetation patterns in western North America. Variations in the frequency, intensity 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). The role of fire in creating landscape scale heterogeneity has been well documented in certain ecosystems such as the lodgepole pine forests of the Rocky Mountains (Schoennagel *et al.* 2008) and pine and mixed conifer forests of the Southwest and Sierra Nevada (Fule *et al*. 2002, Stephens *et al*. 2008, Collins and Stephens 2010). However, the impacts of fire on landscape scale vegetation patterns in coastal northern California have not been documented.

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 disturbances such as grazing and fire and to biotic interactions via processes such as succession (McBride and Heady 1968, McBride 1974, Callaway and Davis 1993, Keeley 2005). We use the term ‘disturbance’ to describe any “relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment (Pickett and White 1985)” and would like to emphasize that fire, along with many other disturbance agents, is an integral ecological process (Sugihara *et al.* 2006).

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 patterns in vegetation diversity.

As a result of the high diversity of this system, the response of plant communities to fire may be more complex than the heterogeneity that 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 northern California ecosystems documents shifts from woody to herbaceous vegetation following fire and is based on studies carried out at relatively small spatial scales (W.K. Cornwell, University of California, Berkeley, unpublished data). 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.

The 1995 Vision Fire at Point Reyes National Seashore (PRNS) 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 October 3 through October 8th, 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 central California coast due to fire suppression. 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 65 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). Elevation ranges from sea level to 429 m. 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. Summer precipitation is low, averaging less than 0.5 cm per month. Approximately eighty percent of the precipitation in the area occurs between November and March. 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). 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, CA) found summer fog drip provided an additional 22 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 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. In particular, this analysis will focus 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 are bishop pine forest, Douglas-fir forest, hardwood forest, riparian forest and shrubland, coastal scrub, blue blossom ceanothus, grassland, and herbaceous wetland.

Vegetation Mapping and Accuracy Assessment

We mapped vegetation after the Vision Fire using color digital orthophoto quarter quadrangles (1 m resolution), which were captured in March and April of 2004 (County of Marin 2010). This was supplemented by the National Agricultural Imagery Program aerial photography (1-2 m resolution) from August of 2005 (USDA Forest Service 2009). Polygons were mapped to the community types listed above based 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 was one hectare (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 these data were collected five to six years before 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 disturbance.

The accuracy assessment uses both the widely accepted confusion matrix and kappa coefficient approaches (Congalton *et al*. 1983, Congalton 1991, Foody 2002). The confusion matrix approach depicts 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 is listed in the appropriate row. From this ‘producer’s accuracy,’ or percentage of a particular vegetation class that has been correctly mapped as that vegetation class, and ‘user’s accuracy,’ or the percentage of a mapped class that is mapped correctly, were both calculated (Congalton 1991). The kappa statistic is also calculated as an indicator of accuracy, which accounts for any correct classification that is due to chance (Lillesand *et al*. 2004).

Vegetation Change

Vegetation change 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 was constructed using both raw area measurements and percent of total area (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 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 DEM 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) is calculated from Landsat bands 4 and 7 and the differenced NBR (dNBR) is 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 analysis used ArcGIS version 9.3 with standard extensions.

The initial data set included all pixels in the study area for a total of 51101 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. 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 % 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 the fire returned to bishop pine after the Vision Fire. Much of the bishop pine present post-fire is 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 patch 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 patch 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, slope and elevation (Figure 4). Again, the saturated model did not provide a better fit than the final model ($p = 0.380$).

DISCUSSION AND CONCLUSIONS

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 mapped as bishop pine. Informal examination of these areas revealed that they were coastal scrub with a low density bishop pine component (15-20% bishop pine cover). Since 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 community. 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). Since 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 drops off dramatically beyond distances of one kilometer from pre-fire bishop pine stands. Bishop pine seedlings predominantly established in areas 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 primarily 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 was likely left by a previous post-fire population of ceanothus which had senesced prior to the initial vegetation mapping effort.

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. The competitive disadvantage of coyote brush following fire may be due to coyote brush sprouts or seedlings being out-competed by the very dense seedling recruitment of bishop pine and ceanothus or due to limited sprouting and seeding of coyote brush in areas that burned with high intensity.

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 forests. However, studies in chaparral have found that burn severity is relatively unimportant in determining post-fire vegetation recovery, especially over the longer term (Keeley *et al.* 2005, Keeley *et al.* 2008).

Conclusions

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, Native American burning, herbivory and ranching (Anderson 2005). The Vision Fire is an example of an ecological event that caused major changes in landscape scale patterns of vegetation communities. This study provides direct evidence for how these changes 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 in the literature for this region, this study also demonstrates that multiple successional pathways occur in these systems following fire. Many studies have found evidence for multiple successional pathways following disturbance, 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 plastic vegetation type: transitions to grassland, ceanothus scrub and bishop pine as well as self-replacement all occurred following fire. 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 transitions and 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 disturbance and in the spatial variability of the vegetation composition over relatively short time frames. For managers, it is important to understand how disturbances such as fire can dramatically shift the distribution of different vegetation types along with the suite of wildlife species that those vegetation communities support.

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TABLES

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	Grass-land	Hard-wood	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/ Shrubland	343	298	-45	-13

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	Cean-othus	Coastal scrub	Douglas-fir	Grass-land	Hard-wood	Herbaceous wetland	Ripar-ian	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.

	Estimate	Std 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

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.

	Estimate	Std 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

FIGURES

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

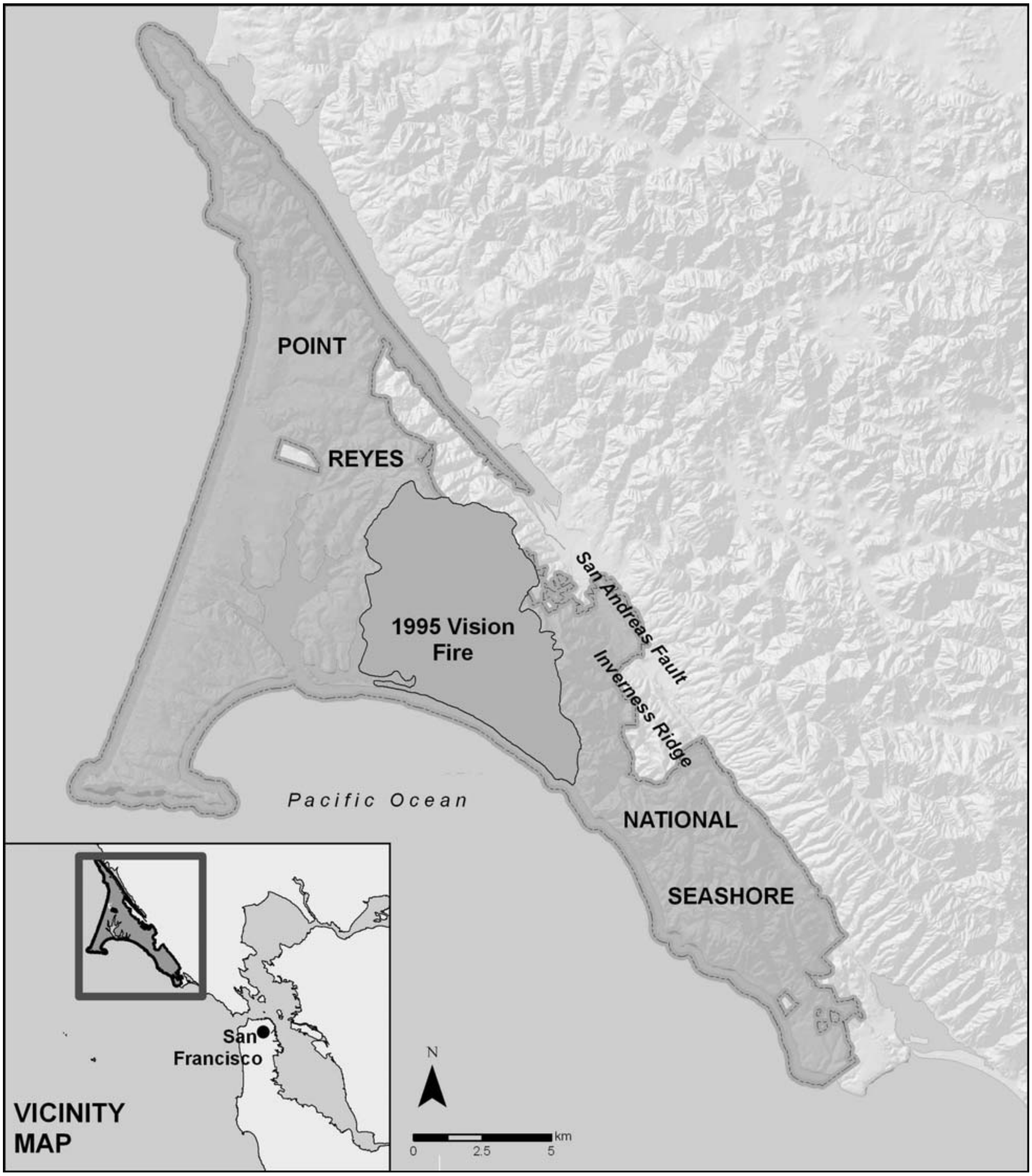


Figure 2. Vegetation communities at Point Reyes National Seashore, California before and following the 1995 Vision Fire

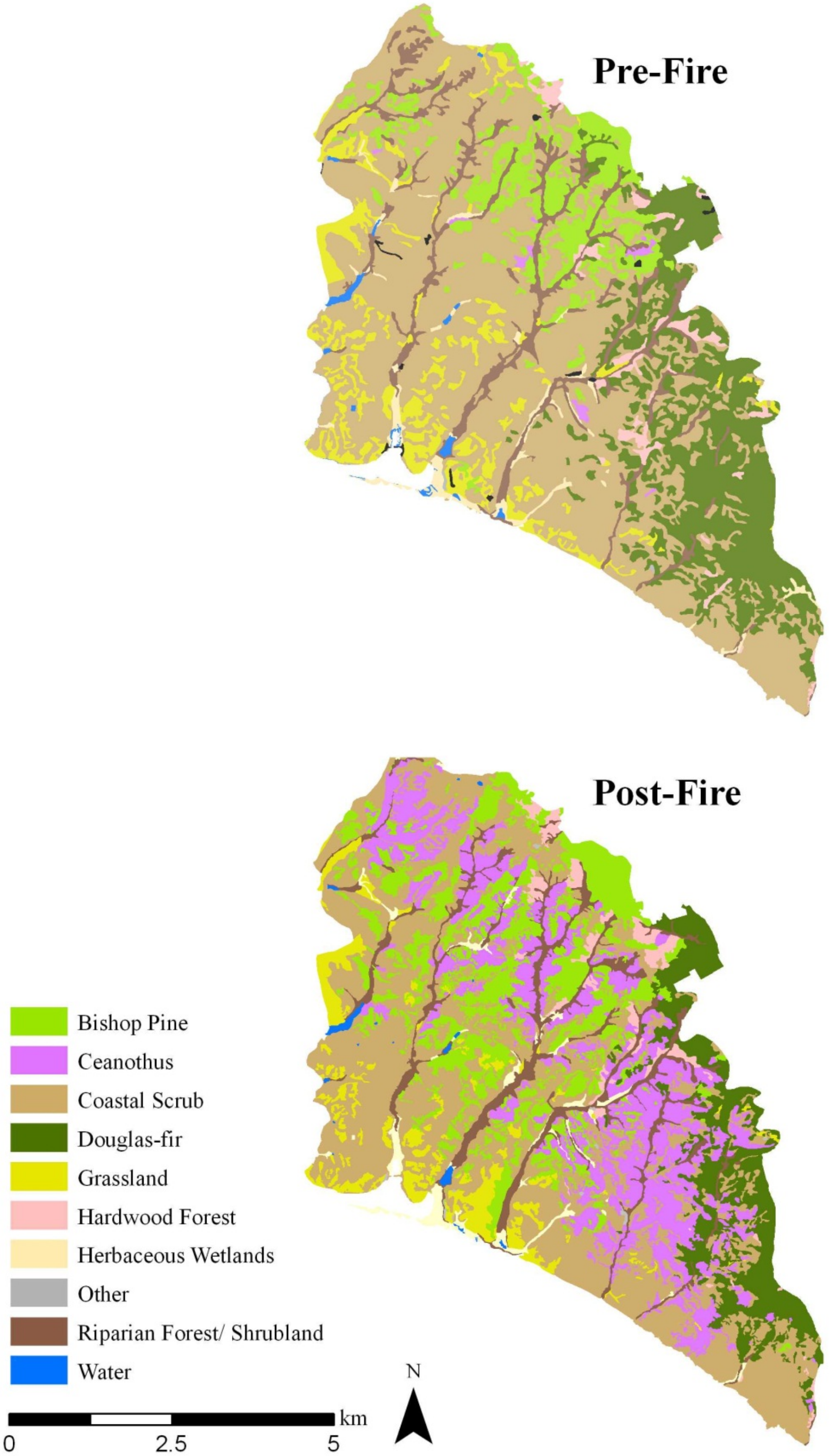


Figure 3. Transitions among major vegetation types following the 1995 Vision Fire. The size of each ellipse is proportional to the extent of that community within the study area. Solid arrows indicate transitions between vegetation communities and dashed arrows indicate areas where the vegetation type 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.

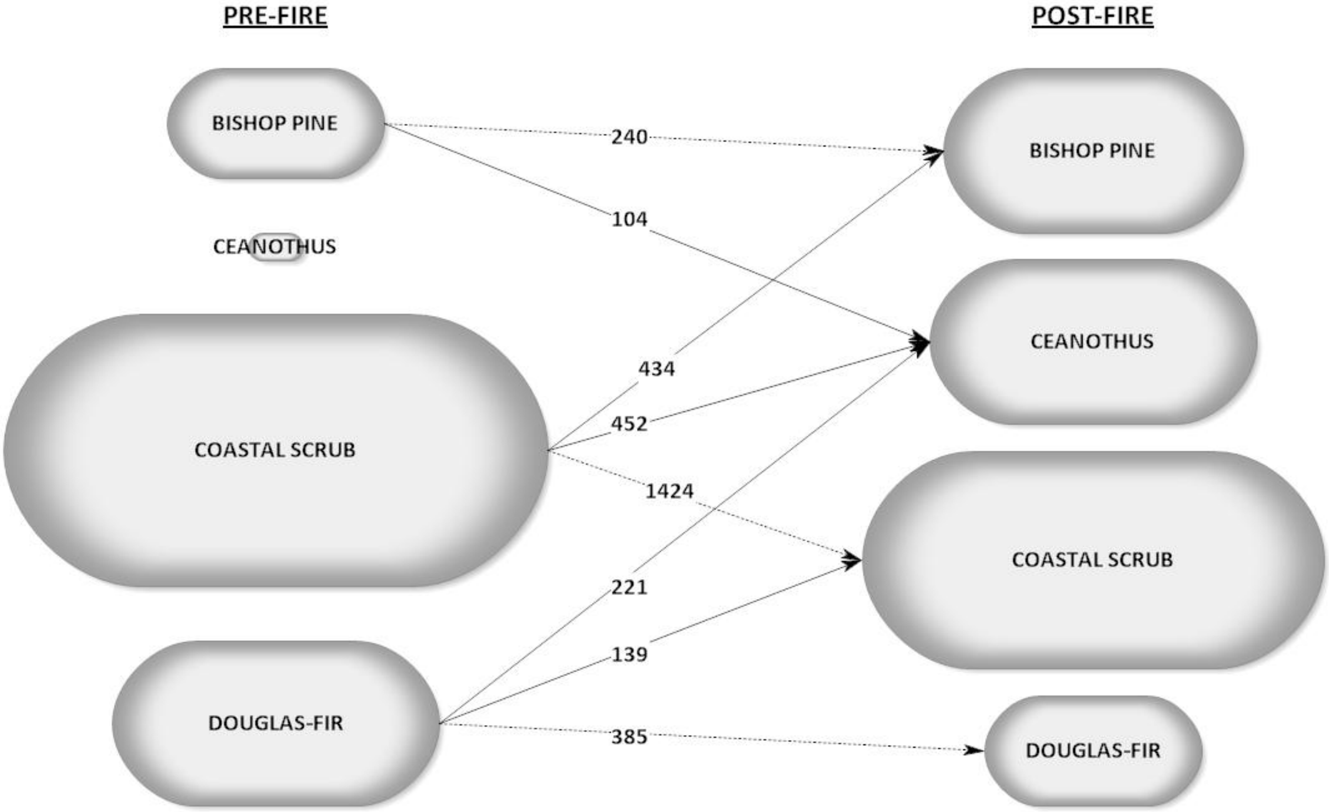
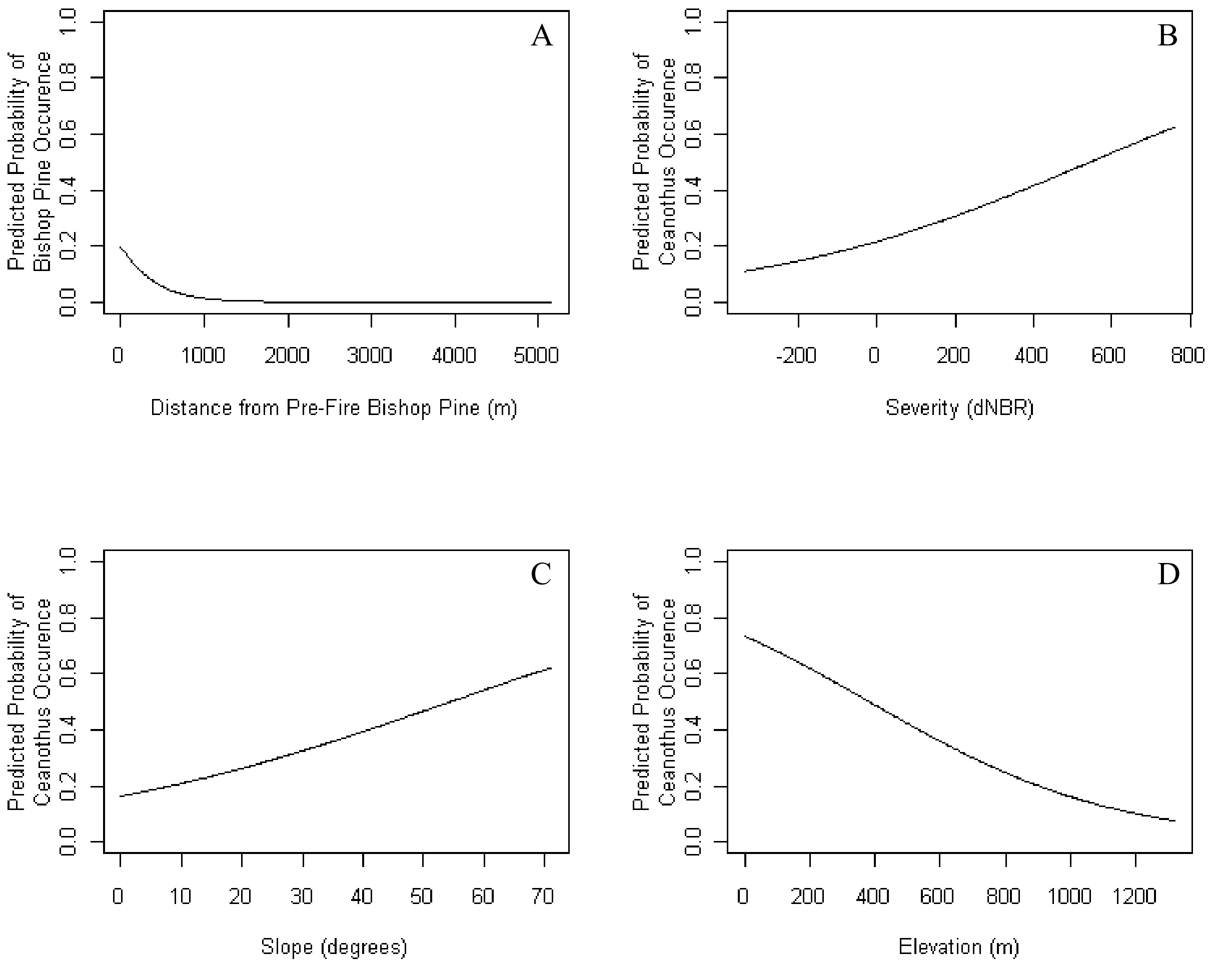


Figure 4. (A) Effect of distance from pre-fire bishop pine on the predicted probability of bishop pine occurrence following fire based on logistic regression models. Predicted probabilities assume the site was not bishop pine prior to fire. (B) Effect of burn severity on the predicted probability of ceanothus occurrence following fire based on logistic regression models. Predicted probabilities assume the site was coastal scrub prior to fire, the slope is 35°, and the elevation is 600m. (C) Effect of slope on the predicted probability of ceanothus occurrence following fire based on logistic regression models. Predicted probabilities assume the site was coastal scrub prior to fire, the dNBR is 300, and the elevation is 600m. (D) Effect of elevation on the predicted probability of ceanothus occurrence following fire based on logistic regression models. Predicted probabilities assume the site was coastal scrub prior to fire, the dNBR is 300, and the slope is 35°.



CHAPTER 2

Fire and Disease in two Coastal California Forest Types: Sudden Oak Death Impacts on Fuels and Potential Fire Behavior

INTRODUCTION

Invasive fungal pathogens have serious impacts worldwide (Loo 2009). Pathogens such as the Irish potato blight (*Phytophthora infestans* (Mont.) de Bary) have devastated food supplies and human societies. Wildlife populations have been impacted by species such as the chytrid fungus (*Batrachochytrium dendrobatidis*) which is contributing to a global decline in amphibians (Berger et al. 1998). Other fungal diseases, including chestnut blight (*Cryphonectria parasitica* (Murrill) M.E. Barr), have drastically altered ecosystems by effectively eliminating foundation species such as the American chestnut (*Castanea dentate* (Marshall) Borkh.) (Ellison et al. 2005). In North American forests today more than twenty invasive fungal pathogens are known to cause significant mortality of woody species (Liebhold et al. 1995). Notable examples include white pine blister rust (*Cronartium ribicola* A. Dietr.) which is having devastating impacts on five needle pines, beech bark disease (caused by a beetle and fungal complex) which is killing the American beech (*Fagus grandifolia* Ehrh.) and Sudden Oak Death (SOD; caused by the fungus-like pathogen *Phytophthora ramorum* (S. Werres, A.W.A.M. de Cock) which impacts both tanoaks (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S.H. Oh) and true oaks (*Quercus* sp.).

Loss of or dramatic declines of species, populations, or age classes due to invasive pathogens can have major impacts on ecosystems. These impacts include changes in ecosystem structure, decreased biodiversity, changes in hydrology and nutrient cycling, and cascading impacts throughout the food web (Ellison et al. 2005, Loo 2009). The potential for invasive pathogens to interact with other ecological perturbations and yield unexpected or nonlinear responses is of particular concern (Paine et al. 1998, Turner 2010).

Invasive fungal pathogens or insect pests have the potential to interact with wildfire by changing fuel loads and thereby fire behavior (Dale et al. 2001, Lundquist 2007, Simard et al. 2011). Increased fuel loads from disease or pest-related mortality may lead to increased fire intensity and fire effects (Lynch et al. 2006, Metz et al. 2011). Changes in fire intensity can in turn shift the trajectory of post-fire succession and potentially create opportunities for invasion by non-native plants following fire (Sugihara et al. 2006). However, the relationship between pests, pathogens and fire behavior is complex, varying with the pest or pathogen in question, the ecosystem that is impacted, and local fire regimes and climate (Parker et al. 2006, Jenkins et al. 2008). In some cases, forest pests or pathogens may actually dampen the potential effects of wildfire by thinning canopy fuels as trees die (e.g. Simard et al. 2011). This study examines potential interactions between Sudden Oak Death and wildfire in a coastal California ecosystem.

Landscape scale mortality of true oaks in the black oak group and tanoaks, referred to as Sudden Oak Death, is caused by the pathogen, *Phytophthora ramorum.* This pathogen is likely non-native and introduced from Asia via the nursery trade; symptoms were first observed in Marin County, California in the mid-1990's (Rizzo and Garbelotto 2003, Mascheretti et al. 2009). *P. ramorum* causes lethal bole cankers in oaks in the black oak group and tanoaks. Dozens of other species act as foliar hosts. *P. ramorum* sporulates on these species but has little or no effect on their health. Coast live oak (*Quercus agrifolia* Née), the most impacted true oak species in Marin County, has some natural resistance, with 30% mortality observed over one 8-year study (McPherson et al. 2010). Tanoak mortality was reported at 50% in the same long term study (McPherson et al. 2010) and others have documented tanoak mortality close to 100% (Davis et al. 2010, Ramage et al. 2011b). Mortality rates are higher among tanoaks in part because they are the only species that supports both sporulation and bole canker formation (Rizzo and Garbelotto 2003, Rizzo et al. 2005). In addition, tanoaks have thus far shown very little resistance to *P. ramorum* and it is possible that they will be mostly or entirely extirpated from coastal forests as a result of this disease (Rizzo and Garbelotto 2003, Rizzo et al. 2005).

The direct impacts of SOD on coastal California forests, including mortality rates and changes in stand structure and regeneration, have been well documented (Waring and O'Hara 2008, McPherson et al. 2010, Ramage et al. 2011a, Ramage et al. 2011b). However, the potential interactions between SOD and other disturbance agents such as wildfire are less well studied. There has been some evidence that SOD infection rates are lower in areas that have recently burned (Moritz and Odion 2005). A few studies have attempted to quantify the impacts of SOD on wildfire. Metz et al (2011) took a retrospective approach to investigate the relationship between SOD severity and fire effects in the 2008 Basin Fire in Big Sur, California. The authors found that an overall comparison of healthy versus diseased plots in the Basin Fire showed no differences in burn severity. However, plots with recent SOD infections, where infected tanoaks were still standing with dead leaves, showed higher burn severity than both healthy plots and plots with older infection (Metz et al. 2011). However, this study did not incorporate factors such as weather and topography that would have impacted fire severity and potentially confounded their results. Valachovic et al. (2011) measured fuel loads in healthy and diseased stands as well as stands where tanoak had been killed with herbicide (a standard forestry practice which was used in this study as a proxy for older SOD-infestations) and did prospective modeling of the potential impacts of SOD on fire behavior. They did not find a significant difference between the fuel loads of diseased versus healthy stands, but they did find differences between herbicide-treated and healthy stands. Another study looked at potential changes in crown fire ignition of tanoaks killed by *P. ramorum* (Kuljian and Varner 2010). This study found that foliar moisture content, which is an important predictor of the ability for a surface fire to transition to crown fire, decreased from 82% in healthy tanoaks to 78% in diseased tanoaks. Dead tanoak foliage had a foliar moisture content of 12% (Kuljian and Varner 2010).

This is the first study to directly measure changes in surface fuels over time associated with Sudden Oak Death and to use those data to model potential changes in fire behavior. We combined direct field observations with fire behavior modeling to assess the impacts of SOD on potential fire behavior of Douglas-fir (*Pseudotsuga menziesii*) and redwood (*Sequoia sempervirens*) forests in Point Reyes National Seashore, California, USA. We tracked surface fuels over a four year period in a network of plots and used those data to populate fire behavior models. Additionally, because little is known about whether this disease could facilitate the establishment of invasive species in the understory, we also measured changes in species composition amongst the herbaceous species in each plot. Our study addresses the following hypotheses: 1. Surface fuels initially increase and then level off over time in SOD-infested Douglas-fir and redwood forests; 2. Increased surface fuels lead to increased predicted fire intensity and 3. Non-native herbaceous species are more prevalent in SOD-infested forests.

METHODS

Study area and plot selection

Fieldwork was conducted in Point Reyes National Seashore and in areas of Golden Gate National Recreation Area, which are managed by Point Reyes National Seashore (referred to collectively here as PRNS). The combined area managed by PRNS is approximately 36,000 hectares and is located in Marin County, California, about 45 km northwest of San Francisco. The climate of PRNS is Mediterranean with wet winters and cool, dry summers. Based on local weather station data from 1964-2012, the average minimum and maximum monthly temperatures during summer months ranged from lows of 6°C to 9°C to highs of 18°C to 24°C. Average winter minimum and maximum temperatures were similar with lows ranging from 2°C to 4°C and highs of 15°C to 17°C. Average annual precipitation in the study area over this same time period was 100 cm per year (Bear Valley Weather Station 1964-2012). A large majority of the precipitation occurs between October and March although the summer drought is attenuated by coastal fog which can provide substantial moisture inputs to ecosystems when intercepted by plant canopies. Vegetation at PRNS is characterized by coastal grassland and scrub closer to the Pacific Ocean and Douglas-fir, mixed evergreen and redwood forest along ridge lines further inland. Plots were located in both redwood/tanoak and Douglas-fir forest types as defined in the PRNS vegetation classification (Schirokauer et al. 2003). Figure 1 shows the study area and plot locations. Redwood and Douglas-fir forests in PRNS are second-growth stands and were logged in the late 19th and early 20th centuries. SOD was first documented in PRNS in 2004. Portions of the study area directly abut the Marin Municipal Water District, which was the likely the location of SOD introduction in Marin in the mid-1990s (Rizzo et al. 2002, Mascheretti et al. 2009, McPherson et al. 2010).

Plot selection followed a stratified random split-plot sampling design. Paired plots, one healthy and one diseased, were established at the beginning of the study period. Random points were generated in GIS in both Douglas-fir and redwood vegetation types using the PRNS vegetation GIS layer (Schirokauer et al. 2003). In the field, an expanding radius search starting from these random points was used to locate diseased-healthy plot pairs that met our selection criteria. Selection criteria included a minimum threshold for both canopy cover (≥25%) and basal area (≥ 0.46 m^2) of the dominant species (redwood or Douglas-fir), slopes less than 60%, and a minimum basal area of tanoak of 0.93 m^2 (10 ft^2). In a few cases, a healthy or diseased plot was established without a plot-pair if no pair could be found meeting the selection criteria. All plots were circular with a 12.62 m radius (0.05 ha). In total, 15 Douglas-fir (5 diseased, 10 healthy) and 14 redwood (7 diseased, 7 healthy) plots were established. Based on initial data analysis in 2007, one of the redwood diseased plots was identified as an outlier due to much higher stem densities and smaller trees than other plots and was removed from future field measurements and analysis. More details about plot selection are found in Ramage et al. (2011a).

Data collection and sampling

Plots were initially established in the summer of 2007 and were remeasured during the summers of 2009 and 2011. Within each plot, each tree ≥3cm diameter at breast height (DBH) was mapped. The following characteristics for each tree were recorded in each sampling year: species, DBH, height, height-to-live crown and status (live versus dead). For SOD-susceptible species (tanoak and coast live oak), we also recorded detailed information on SOD symptoms (bleeding, bole cankers, Hypoxylon fungi, beetle holes and (or) frass, and canopy dieback;

Swiecki and Bernhardt 2006, McPherson et al. 2010). Post-mortality deterioration for these species was characterized using the percentage of dead leaves still clinging to dead trees as well as the height and stem diameter of bole breakage. Stems of species other than tanoak were not recorded if broken below breast height, but to ensure that we captured the majority of SOD-induced tanoak mortality, tanoak stems that were broken below breast height were recorded if the fallen bole wood was intact at the outset of the study. Multi-stemmed trees that were split below breast height were counted as separate trees.

Fuels data were collected using 12.6 m standard planar intercept transects (Brown et al. 1982). During the initial sampling effort, in 2007, two transects (at 0° and 180° azimuths from plot center) were measured. In 2009 and 2011, this was increased to four transects per plot, one in each cardinal direction. Along each transect, surface fuels were tallied in timelag-classes. The number of 1-hour fuels (< 0.64cm diameter) and 10-hour fuels (0.64 – 2.54cm diameter) that crossed the transect plane between 10.5 and 12.5 meters were counted, and the number of 100-hour fuels (2.54cm – 7.62cm diameter) that crossed the transect plane between 8.5 and 12.5 meters were counted. Diameter was recorded for each 1000-hour fuel (> 7.62cm diameter) that crossed the transect plane between 0 and 12.62m. If no 1000-hour fuels were encountered between 0 and 12.62m, transects were extended to 20m. In addition to overstory and fuels data, we also collected data on tree regeneration and understory response. Tree regeneration data are not summarized here (see Ramage et al. 2011a). Understory data were collected for the entire plot area by assigning modified Braun-Blanquet cover classes (Barbour et al. 1987) for each species present.

Data analysis

We analyzed changes in each fuel class over time using one-tailed t-tests to compare fuels at the beginning of our study period to fuels at the end of our study period. We used Bonferroni corrections to adjust for multiple comparisons. Fuel loads were calculated with the program FFI (Lutes et al. 2009) using standard fuel constants (Brown 1974). We tested the effects of tanoak mortality (basal area of dead tanoak) on total fuels in each sampling year using linear mixed effects models where each plot-pair was treated as a block. Because surface fuels tend to have high spatial variation and our sample size was relatively small, we combined our data across forest type and disease status for this analysis. Two healthy Douglas-fir plots were excluded from this analysis because they contained large, fallen Douglas-fir trees which overwhelmed the fuels signature of the plot. 2011 data were log-transformed to meet assumptions of normality and homoscedasticity. However, untransformed data are shown graphically to allow for visual comparison with 2007 and 2009 data (Figure 3).

The surface fire modeling program BehavePlus (Heinsch and Andrews 2010) was used to compare potential changes in fire behavior between diseased and healthy stands. BehavePlus provides information on modeled surface fire behavior at the stand level. BehavePlus inputs were based on a combination of field data and pre-existing datasets. We selected standard surface fuel models (Scott and Burgan 2005) based on the average fuel characteristics of healthy and diseased plots. In assigning fuel models, we used 2007 healthy plots as our reference for fuels in healthy forests and 2011 diseased plots as our references for fuels in diseased forests since these two time points represent each end of the healthy-diseased spectrum. Fine dead fuel moisture and wind data were calculated using 97th percentile weather from the Barnabe RAWS station (1995-2004), which is 2.5km north of the study area. The 97th percentile corresponds with weather during the 1995 Vision Fire which burned approximately 5,000 ha of PRNS northwest of the study area. Live woody fuel moisture was based on values measured by Marin County for peak fire season (October) (Marin County Fire Department 2012).

We analyzed the effects of SOD-mortality (basal area of dead tanoak) on understory response using 2011 data only with linear mixed effects models where each plot-pair was treated as a block. Only 2011 data were used because these data represent understory response to the most advanced stages of SOD and give the best picture of where these stands may be headed in the future. Understory response was examined for five functional groups: non-native forbs, native forbs, non-native grasses, native-grasses, and native shrubs (no non-native shrubs were encountered). For the non-native and native grass analyses, one outlier plot, with substantially higher grass cover than other plots, was removed. Removal of the outlier did not affect statistical results, but improved visual interpretation of scatter plots. Data for native forbs and shrubs were log-transformed to meet assumptions of normality and homoscedasticity. In addition to the five guilds mentioned above, we also examined the effect of tanoak mortality on tanoak regeneration, which was dominated by resprouts from dead or dying overstory trees. We used Bonferroni corrections to adjust for multiple comparisons. All statistical analyses used R Statistical Software (version 2.15.0, R Development Core Team, Vienna, Austria) with the nlme package (Pinheiro et al. 2009).

RESULTS

Tanoak Mortality and Fuel Loads

Tanoak mortality progressed over the study period across both forest types in healthy and diseased plots (Figure 2). Fuel loads increased over the same time period across forest type, fuel size and disease status categories (Figure 3). Changes in fuel loads are significant for 1-hour fuels across both forest types and disease statuses and for 10-hour fuels in Douglas-fir plots ($p<0.01$ with Bonferroni correction; Table 1). Changes in 100-hour fuels are significant only in redwood diseased plots. Total fuels (1- through 1000-hour fuels) changes are significant for diseased Douglas-fir and healthy redwood plots. Throughout the study, there was a significant relationship between fuel load and basal area of dead tanoaks (Figure 4).

Fire Behavior Modeling

Fuel model TL3 was selected to represent healthy plots because TL3 most closely matched field conditions, although it is a slight over-estimate of fuels and therefore the intensity of predicted fire behavior. For diseased plots, we selected fuel model TL5, which is a slight under-estimate of fuel conditions as measured in the field. Table 2 shows surface fuel characteristics for diseased and healthy plots compared to average values for fuel models TL3 and TL5 (Anderson 1982). Weather and fuel moisture values used as BehavePlus inputs are shown in Table 3 along with modeled outputs for healthy and diseased stands. Modeled fire behavior in diseased stands exhibits higher rate of spread, heat per unit area, fireline intensity and flame length than in healthy stands.

Understory response

The relationship of understory response to tanoak mortality by functional group is shown in Figure 5. Both non-native forbs and resprouting tanoak cover showed a significant positive relationship with dead tanoak basal area ($p<0.008$). Other functional groups had no significant relationship.

DISCUSSION AND CONCLUSIONS

Tanoak Mortality & Fuel Loads

Our results showed that tanoak mortality increased over the study period, particularly among plots that were healthy at the beginning of the study (Figure 2). A detailed analysis of disease progression on these plots from 2007 to 2009 can be found in Ramage et al. 2011a. The levels of mortality we observed are consistent with or higher than what has been observed in other research (McPherson et al. 2010, Ramage et al. 2011a). By the end of the study period, mortality appeared to be leveling off in diseased plots, but not healthy plots. This suggests that over some time period, greater than the 4-year period of this study, living tanoak basal area may stabilize at a level that is a small fraction of its initial basal area.

As tanoak mortality progressed in our study plots, surface fuels concurrently increased. The fuel loads we observed were similar to those reported for healthy Douglas-fir and redwood forests in other studies (National Park Service 1998, Dicus 2003, Fonda and Binney 2011). No one has previously quantified fuel loads in forests with well-established SOD infestations. Valachovic et al. (2011) attempted to quantify the effects of SOD on fuel loads in Douglas-fir forests using herbicide-treated stands as a proxy for heavy SOD infestation. The fuel loads we observed in diseased stands were higher than in healthy stands, but substantially lower than those found by Valachovic et al. (2011) in herbicide-treated forests. We detected significant changes in surface fuels among the smaller fuel classes. This is important because fine fuels (litter, 1-, 10- and 100-hour fuels) have the greatest impact on fire spread (Rothermel 1972). Intuitively, this is the response we would expect as tanoaks die and leaves, branches and eventually entire trees fall to the forest floor (see Figure 6). Fuels in the 100-hour size class also increased, but changes over time were not significant except in the case of diseased redwood plots. Surface fuels are often highly variable at small scales (Fry and Stephens 2010) and this variability may have been the reason we did not detect statistically significant changes in the 100-hour size class for the other plot types. We observed marginally significant increases for coarse woody debris in healthy plots but not diseased plots. This may be because there were already substantial amounts of 1000-hour fuels present on the forest floor of diseased plots at the outset of our study and suggests that fuels loads, like tanoak mortality, may level off over time. Large fuels are not the primary carriers of fire spread, but they can increase fire effects, particularly on soils. These fuels tend to smolder for long periods following the passage of the flaming front and have the potential to significantly alter soils, below-ground communities and the potential for regeneration (Neary et al. 1999). On the positive side, increases in large fuels could improve habitat and cover for ground-dwelling species such as the dusky-footed woodrat (Hamm 1995, Fehring 2003, Tempel and Tietje 2005).

Throughout the study period, there was a strong relationship between tanoak mortality and fuel loads at the plot level as shown in Figure 4. Over the course of the study period, total fuels increased across all plots and the distinction between diseased and healthy plots began to break down. There is some indication that fuels might be leveling off in the diseased plots by 2011. Among plots with high levels of mortality, total fuels may level off due to both decomposition and decreased additions of fuels as fewer tanoaks remain in the plots.

Fire Behavior Modeling

Fuel models TL3 and TL5 (Scott and Burgan 2005) were selected for healthy and diseased plots, respectively. Using these fuel models, BehavePlus model outputs for surface fire behavior predict higher spread rate, flame length, heat per unit area and fireline intensity for diseased versus healthy plots. With all other factors equal, higher flame lengths increase the probability that a surface fire will lead to torching or passive crown fire. For example, during two prescribed fires in mixed redwood/Douglas-fir forest at Muir Woods National Monument, when flame lengths increased from 0.5m to 1m, fire behavior became much more active and small trees began to torch (National Park Service 1998). These increases in surface fire intensity and the increased possibility of torching or crown fire could make fires in SOD-affected Douglas-fir and redwood forests harder to suppress than in healthy forests. This was qualitatively observed by fire fighters in the 2008 Basin Fire, who reported 25% increases in fire intensity in SOD-impacted forests (Lee et al. 2009). More intense fire behavior is likely to lead to more severe fire effects. If diseased forests burn more intensely, we might expect to see decreased seedling recruitment, different species recruiting post-fire, increased canopy mortality and the potential for increased impacts to soils and soil communities.

Although our results indicate the potential for increased fire intensity and probability of torching in SOD-impacted stands, these fire behavior modeling outputs should be interpreted cautiously. First, our results are largely dependent on the choice of surface fuel model which is, by definition, somewhat subjective (Collins et al. 2010). Second, model constants were derived for Rocky Mountain conifers, so quantitative model outputs should be interpreted cautiously. However, the overall pictures of substantial increases in fire intensity associated with increased fuels from SOD is compelling.

Understory response

Our results show increasing non-native forb cover associated with tanoak mortality. Although there is evidence of canopy gaps leading to increasing exotic species cover from similar forest types (Blair et al. 2010), to our knowledge, this has never been documented in association with SOD. This is a troubling indicator that over time, growing space made available due to SOD may be claimed by invasive plants. This dynamic could be exacerbated if these forests were to burn (Zouhar et al. 2008).

We also observed statistically significant increases in tanoak understory cover associated with tanoak mortality. This is caused by extensive stump sprouting from tanoaks that have been top-killed by SOD. This has been observed throughout the area impacted by SOD and is concerning from a fire behavior stand point because this shrub layer eventually dies from SOD and creates dry ladder fuels which further increase the potential for torching and passive crown fire.

Conclusions

This research documents clear patterns of increased fuel loads associated with increased SOD severity in Douglas-fir and redwood forests. In addition, our work suggests that fires in SOD-affected forests could burn with greater intensity. These results are consistent with the work of Valachovic et al. (2011) and Metz et al. (2011) although our results do suggest more potential for increased fire intensity and severity than those reported by Metz et al. (2011). Additionally, we observed increases in exotic species in the herbaceous layer that were associated with increasing levels of tanoak mortality. This suggests that SOD could tip the balance in these forests toward a novel state.

Redwood and coastal California Douglas-fir forests have evolved with primarily low and moderate severity fire since pre-EuroAmerican settlement times (Lorimer et al. 2009). However, our work suggests that as these forests are impacted by *P. ramorum*, the potential for uncharacteristically intense fire behavior may be increasing. These increases could present challenges to fire managers and make fire suppression efforts in SOD-impacted redwood forests more difficult. In addition, there may be undesirable ecological impacts associated with more intense fires in these forests. Such impacts could include reduced diversity of below-ground communities, changes to soil or increased erosion, decreased plant regeneration, and negative impacts on wildlife species such as the northern spotted owl (*Strix occidentalis* ssp. *caurina* Merriam). Fortunately, as fuels decompose, we expect these risks to gradually decrease. Although redwood and Douglas-fir forests are undoubtedly undergoing substantial changes due to SOD, we are hopeful about the ability of these forests to persist relatively intact even if the tanoak understory is lost and some forests experience uncharacteristically severe wildfire.

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TABLES

Table 1. P-values for t-tests of change in fuels over time (2007 to 2011) by forest type, disease status and timelag fuel class. With Bonferroni correction for multiple comparisons, $p<0.01$ is considered significant at the $\alpha=0.05$ level. Significant changes are denoted with an *. Many of the healthy stands were diseased by the end of the study period.

Timelag Fuel Class	**Douglas-fir Healthy**	**Douglas-fir Diseased**	**Redwood Healthy**	**Redwood Diseased**
1	0.0000*	0.0009*	0.0005*	0.0011*
10	0.0098*	0.0032*	0.1084	0.0223
100	0.1884	0.1175	0.2686	0.0028*
1000	0.0175	0.1050	0.0156	0.2192
all	0.0122	0.0053*	0.0063*	0.0582

Table 2. Fuel characteristics for field data (gray) and standard fire behavior models TL3 and TL5.

Fuels	**Healthy**	**TL3**	**TL5**	**Diseased**
1 hr (tons/acre)	0.35	0.5	1.15	1.00
10 hr (tons/acre)	1.70	2.2	2.5	4.04
100 hr (tons/acre)	2.26	2.8	4.4	5.18
Fuel bed depth (ft)	0.25	0.3	0.6	0.93

Table 3. BehavePlus model inputs (above) and outputs (below). Input data are the 97th percentile weather conditions calculated using the nearest Remote Automated Weather Station (RAWS).

		HEALTHY	**DISEASED**
Surface fuel model		**TL3**	**TL5**
Foliar moisture content (%)		80	80
Fine dead fuel moisture (%)	**1 hour**	3	3
	10 hour	4	4
	100 hour	10	10
Live woody fuel moisture (%)		61	61
Wind speed (km/hr)		24	24
Rate of Spread (m/min)		1.6	11.8
Heat Per Unit Area (kJ/m^2)		2,606	4,676
Fire Line Intensity (kW/m)		71	921
Flame Length (m)		0.6	1.8

FIGURES

Figure 1. Map of Point Reyes National Seashore, California, showing forest types and plot locations.

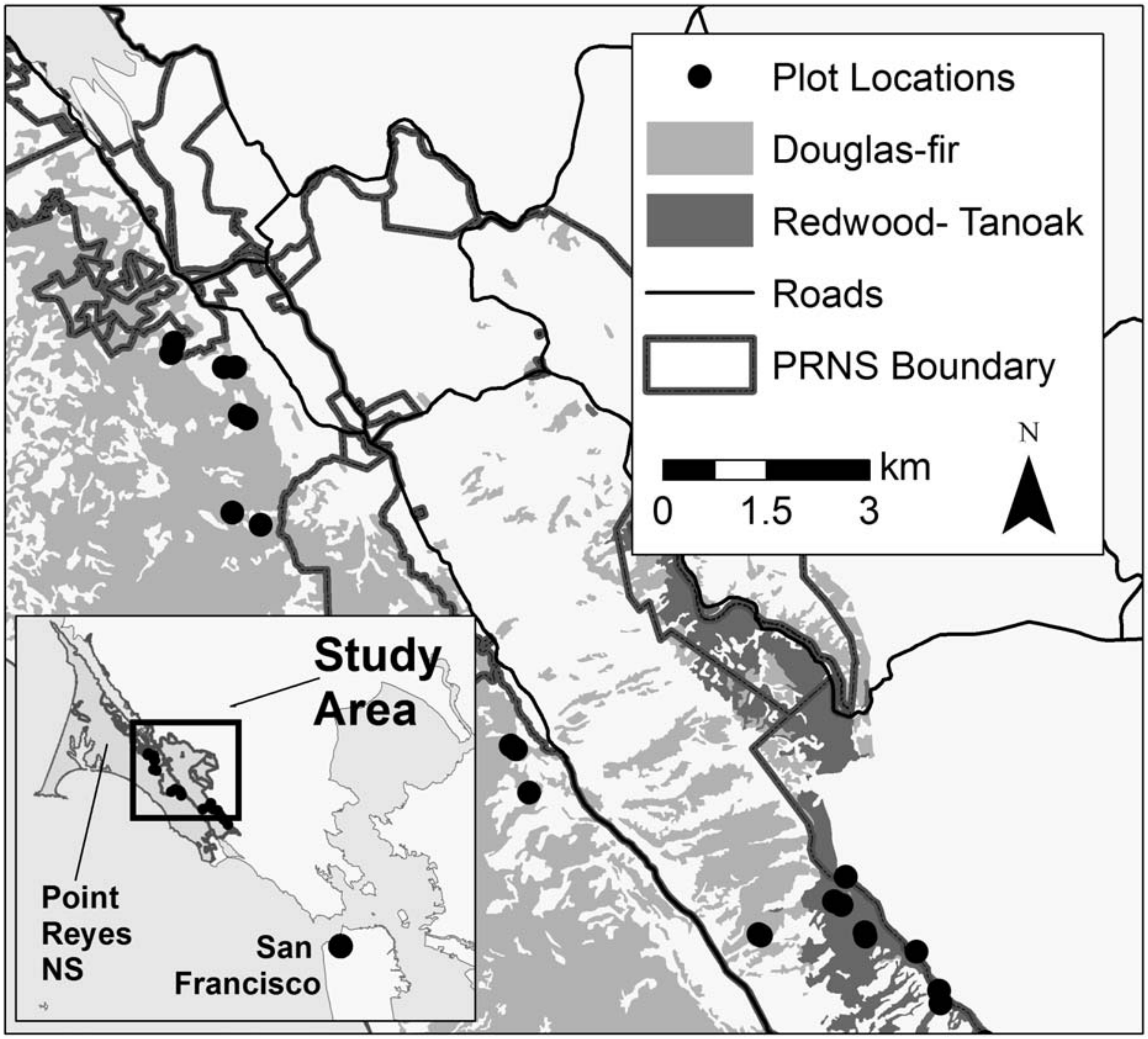

Figure 2. Disease progression, shown as proportion of live tanoak, over the study period for diseased and healthy redwood (dashed line) and Douglas-fir (solid line) plots. Vertical lines show plus plus/minus one standard error.

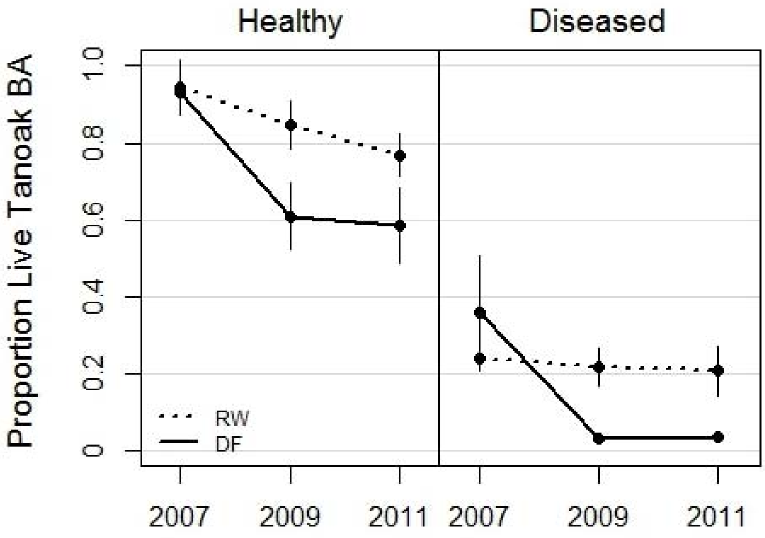

Figure 3. Change in fuel load over time for each time-lag fuel class and for total fuels. Healthy plots are shown in the top row and diseased plots in the bottom row. Douglas-fir plots are depicted with a solid line and redwood plots are shown with a dashed line. Vertical lines show plus plus/minus one standard error.

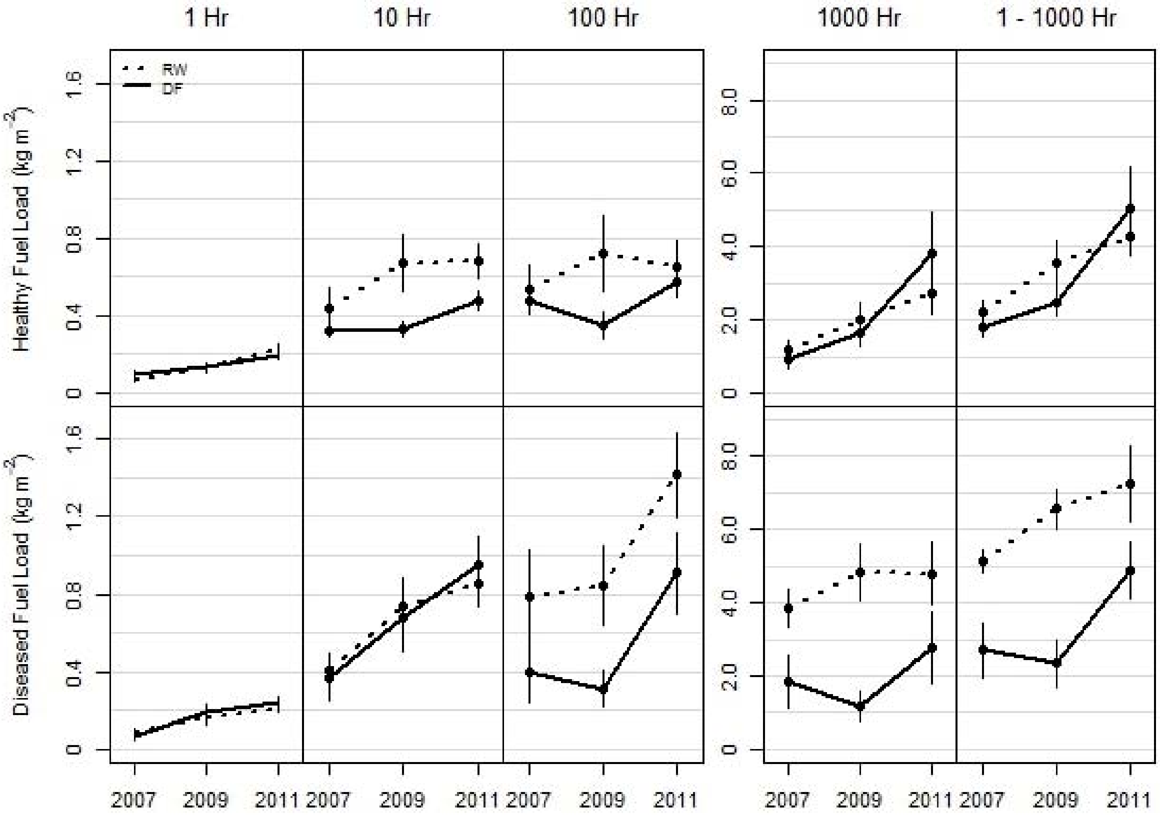

Figure 4. Total fuels (1- through 1000-hour fuels) as a function of tanoak mortality for each sampling year. Data are combined for forest type and disease status. Healthy plots are depicted with open circles and diseased plots are depicted with closed circles.

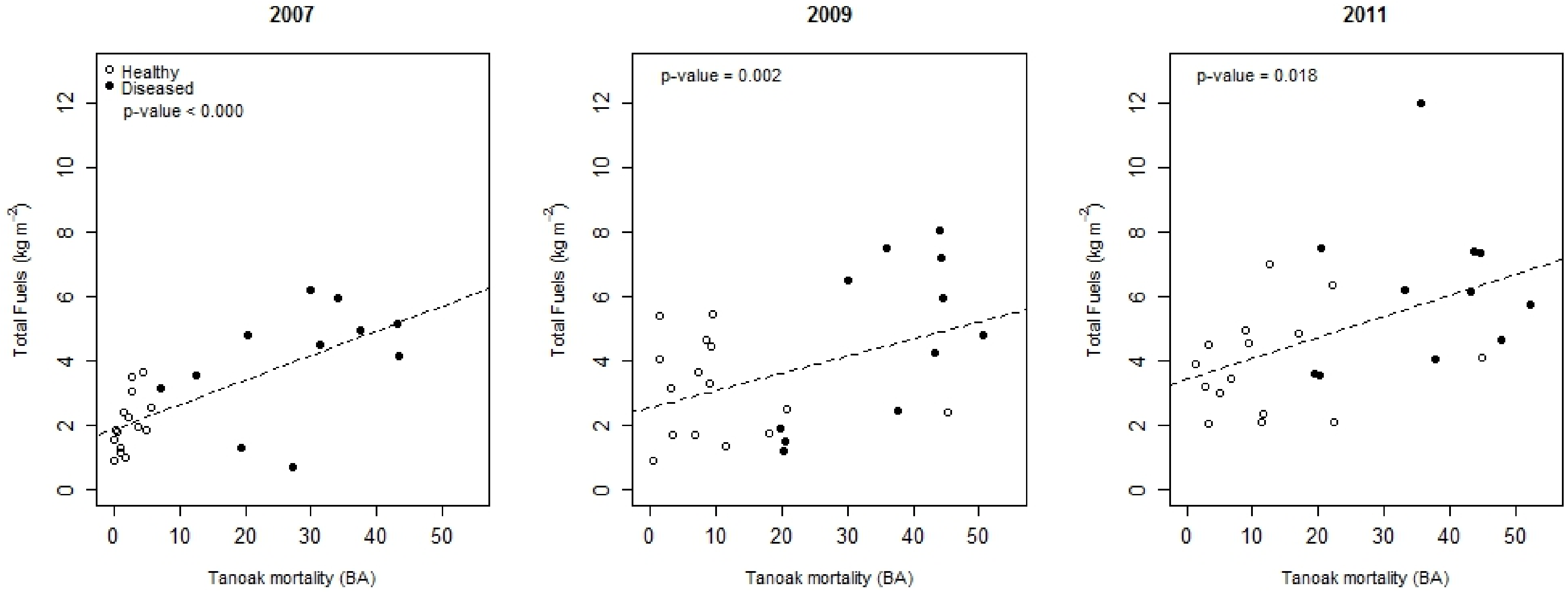

Figure 5. Percent cover of (a) non-native forbs, (b) native forbs, (c) non-native grasses, (d) native grasses, (e) native shrubs and (f) tanoak regeneration as a function of tanoak mortality. Data are combined across forest type and disease status and are shown for 2011 only.

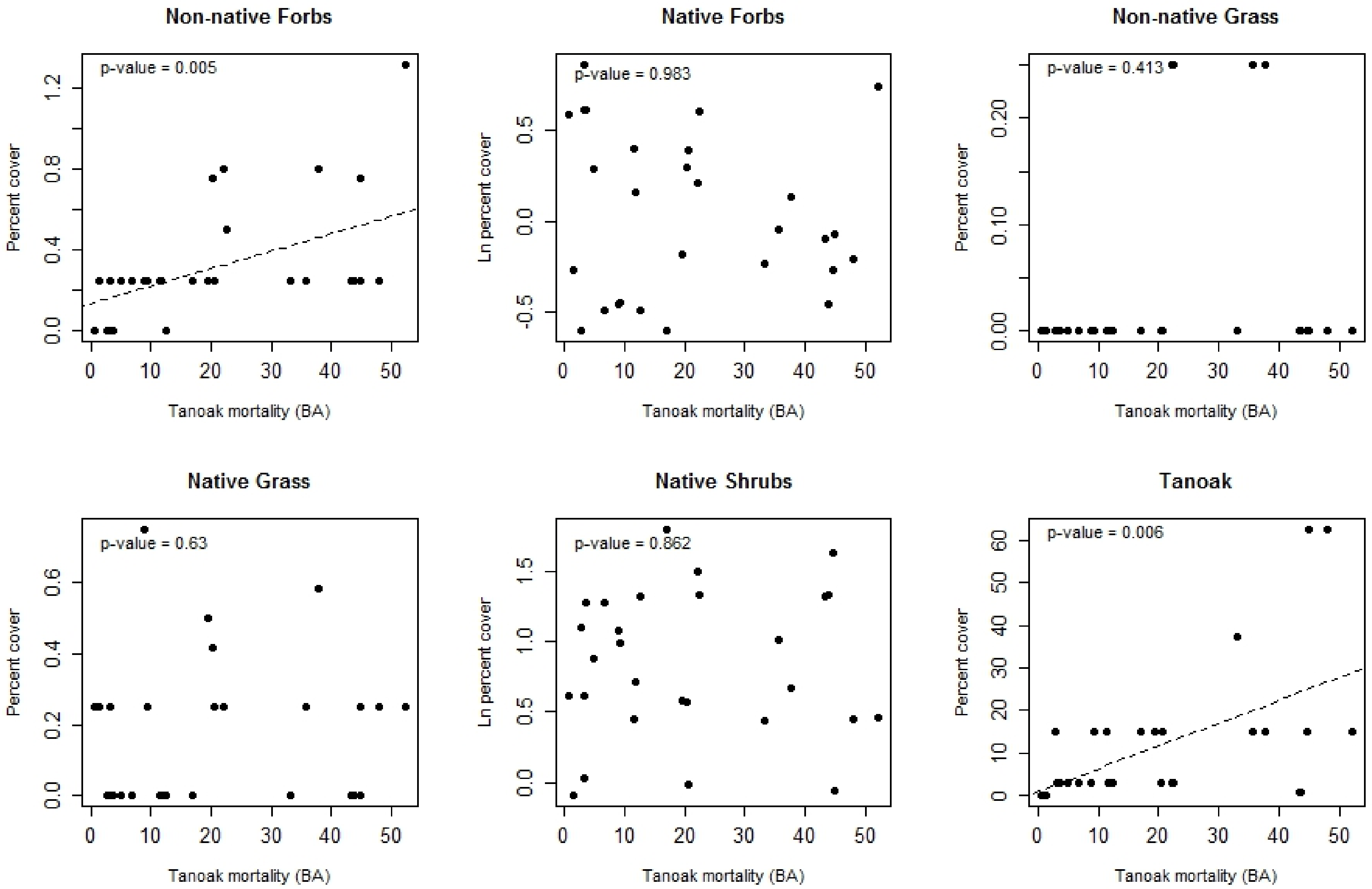

Figure 6. Fuel accumulation associated with fallen tanoaks in a redwood forest at Point Reyes National Seashore, California, USA.

CHAPTER 3

Fire History and Forest Structure at Crater Lake National Park, Northern Cascades, Oregon

INTRODUCTION

The west side forests of Crater Lake National Park (CLNP), Oregon, are unique in that they represent one of the few places in the Cascade Range where an elevational gradient from low-elevation mixed conifer to high-elevation mountain hemlock forests remains intact and has never been logged. The fire history along this gradient is not well documented or understood. Park management documents, including the Fire Management Plan, describe the fire regime of these forests as ranging from mixed severity (mean fire return interval of 40-70 years) in mid-elevation red fir (*Abies magnifica* A. Murr.) forests to a low frequency, high severity regime (mean fire return interval greater than 100 years) for high-elevation mountain hemlock (*Tsuga mertensiana* (Bong.) Carr) forests (National Park Service 2007). However, both the patch mosaic structure of these high-elevation forests as well as the fire behavior and fire effects in recent wildland fires in this region suggest that the fire regimes may be more mixed in severity and that fire return intervals may be shorter than previously thought (Farris 2008, Perry et al. 2011). In addition, there may be potential for fire spread from lower- to higher-elevation forests that is absent in more fragmented ecosystems.

Along the western slope of Mount Mazama, at CLNP, a gradient of forest types are found. At the highest elevations, from 1800 to 2300 m, forests are dominated by open stands of mostly pure mountain hemlock. Mountain hemlock is a long-lived, slow growing species, adapted to long winters and short growing seasons (Taylor 1995, Bekker and Taylor 2010). As elevation decreases, forests are dominated by a mix of red fir and mountain hemlock. Red fir exhibits a dual strategy of both post-fire regeneration and shade-tolerant establishment in areas that have not burned recently (Taylor and Halpern 1991, Scholl and Taylor 2006). The lowest elevations, ranging from 1500 to 1700 m, are dominated by mixed conifer forests which are comprised of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), white fir (*Abies concolor* (Gord. Glend.) Lindl.), incense-cedar (*Calocedrus decurrens* (Torr.) Florin), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western white pine (*Pinus monticola* Dougl.). Lodgepole pine (*Pinus contorta* Loudon) forests are found across the elevational gradient within the study area, primarily on flat cold air drainages with poor soils (Zeigler 1978). Lodgepole pine stands are characterized by even-aged establishment following high severity fire. Although lodgepole pine in the southern Cascade range is not serotinous, it establishes in high severity post-fire gaps via seed from surviving trees and stand density is related to the proximity of these seed trees (Zeigler 1978, Pierce and Taylor 2011). CLNP was established in 1902 and most of the forests within the park boundary, including all of the forests in the study area, have never been logged. CLNP practiced full fire suppression until management ignited fires began in the 1980’s.

Prior to this study, there have been few published fire histories that include these forest types at CLNP. There is published fire history information from other forest types within CLNP and from similar forest types in other parts of the Cascades or Sierra Nevada ranges (Table 1). One study, in the Panhandle region of CLNP, reported fire return intervals of 9-42 years in ponderosa pine (*Pinus ponderosa* Laws.) forests (McNeil 1975). Another study, using a combination of tree stumps in the Winema National Forest adjacent to CLNP and tree cores from a burned area within park boundaries, reported a fire return interval of 39 years in red fir forests (Chappell 1991). Other studies of fire history in red fir forests south of CLNP report fire return intervals ranging from 20 to 100 years (Pitcher 1987, Chappell 1991, Taylor and Halpern 1991, Taylor 2000, Bekker and Taylor 2001, Taylor and Solem 2001, Scholl and Taylor 2006). The fire history of subalpine mountain hemlock forests is not well documented but they are thought to have fire free intervals of hundreds of years (Agee 1993). Bekker and Taylor (2001, 2010) found fire return intervals of 20 years (based on direct analysis of fire scars) and 100 years (based on fire extent maps using the same set of scars) for red fir – mountain hemlock forest in the southern Cascades. They found that moderate and high severity fires occurred in this forest type, but they were not able to detect impacts of fire on forest composition or structure (Bekker and Taylor 2010).

In addition to evidence for mixed severity fire regimes from similar systems, recent wildfires at CLNP have been mixed in severity. For example, the 2006 Bybee Fire burned over 1100 ha of lodgepole pine, red fir, and mountain hemlock forests within the study area. Burn severity, based on data obtained through the Monitoring Trends in Burn Severity program, was mixed and areas of both high and low severity occurred across all three forest types (Eidenshink *et al.* 2007). Although mixed severity fire regimes are likely widespread throughout the western United States, they are poorly documented (Perry *et al.* 2011). In addition, the term mixed severity has not been well defined in the literature. Agee (1993) defines mixed severity as those fire regimes where more than 20% but less than 70% of the tree basal area is killed by a typical fire. Other defining characteristics of mixed severity regimes are patchiness across the landscape at scales of 1-100's of ha and variation between fires in the proportion of high versus low severity patches due to small scale variation in fuel conditions and shifting weather conditions (Perry et al. 2011).

Understanding the fire regimes of mixed conifer, lodgepole pine, red fir, and mountain hemlock forests at CLNP is important for a variety of reasons. First, a clear understanding of fire history is important to guide the management of wildfires and prescribed fires into the future. Second, documentation of a mixed severity fire regime in a system such as this is useful in understanding mixed severity fire regimes elsewhere. This study uses stand structural and fire scar data to document fire history and forest successional trajectories across the gradient of forest types on the west side slopes of CLNP. Specifically, our study addresses the following hypotheses: 1. The fire regime in red fir and mountain hemlock forests is mixed severity with episodic tree establishment and fire return intervals of 40 to 70 years; 2. The fire regime in lodgepole pine forests is low frequency, high severity with even-aged stands and no fire scar evidence present; and 3. The fire regime in mixed conifer forests is high frequency, low severity with uneven aged stands without peaks of establishment and fire intervals less than 40 years.

METHODS

Study area

Field work was conducted at CLNP, which is located in the Southern Cascade Mountains of Oregon and covers more than 74000 hectares. Specifically, this study focused on the mountain hemlock, red fir, lodgepole pine, and mixed conifer forests on the west side of the Cascade crest, within two sub watersheds of the Upper Rogue River watershed encompassing 7031 ha (Figure 1). This area covers an elevational gradient from 1500 m to 2300 m. The climate in the study area is characterized by long, snowy winters and short, dry summers. Mean annual precipitation is 168 cm, most of which falls in the form of snow. The mean maximum July temperature is 20 °C and the mean minimum January temperature is -8 °C (Western Regional Climate Center 2008). Soils in the study area are volcanic and originated with the eruption of Mount Mazama approximately 6600 years ago (Williams 1942).

Plot selection and sampling

To characterize stand structure, 64 stand demography plots were established within the study area using a 1 km grid with a random starting point (Figure 1). Plots were located using a GPS and were rejected if the selected location was non-forested. Data collected at each plot included the following: aspect, slope, elevation, several measurements from the dominant canopy species, ocular estimates of canopy cover, and cover of dominant shrub and herbaceous species. Elevation assigned to each plot was divided into three categories: low, which included those plots in the lower third of elevations (< 1684 m); moderate, which included plots between the 33th and 66th percentile (1684 m -1818 m); and high, which included all plots in the upper third of elevations (> 1818 m). Stand demography data were collected using variable radius circular plots (Speer 2009). At each plot, the 20 closest trees to plot center with a diameter at breast height (DBH) of 10 cm or greater were identified and species, DBH, status (live or dead) and canopy class (dominant, co-dominant, intermediate, or understory) were recorded. Each tree was cored at maximum 15 cm above the ground and core height was recorded. The distance to the furthest tree from plot center was also recorded. No more than five trees with a DBH less than 20 cm were cored; if more than five such trees were present, plot radius was expanded to include larger trees and trees less than 20 cm were measured, but not cored. This ensured that older trees were adequately sampled, and also balanced our results such that recent recruits were less likely to be captured.

Fire scars were sampled opportunistically throughout the study area from both living and dead trees. Such targeted sampling has been shown to yield comparable results to random or grid-based sampling (Van Horne and Fule 2006, Farris 2009). Intact fire scars were extremely rare within the project area; the majority of scars we encountered were rotten, presumably because firs and hemlocks, the dominant species in the study area, do not preserve scars well or tend to heal over during intra-fire intervals (Pitcher 1987, Taylor 1993). Using a chain saw, partial cross-sections were sampled from a total of 35 trees with visible scars, primarily from the mixed conifer forest areas. For each fire scar that was sampled, we recorded the location of the scar using a GPS as well as the species, status (live or dead) and DBH.

Tree cores and fire scars were sanded using progressively finer sandpaper and cross-dated using standard methodology as described in Stokes and Smiley (1968), utilizing several published master chronologies from nearby sites (NOAA 2011, Table 2). For cores that did not intersect the pith, but were within an estimated ten years of the pith, we estimated the pith date based on the curvature of the innermost rings (Applequist 1958). We did not adjust for the number of years it took for trees to reach core height, but because our analysis is based on ten-year bins of establishment dates, we expect this source of error to be relatively unimportant.

Data analysis

Each plot was assigned a forest type: mountain hemlock, red fir, lodgepole pine, or mixed conifer, based on the species with the maximum basal area in that plot. For mixed conifer plots, the maximum basal area was Douglas-fir, white fir, incense-cedar, western hemlock or western white pine. We summarized the stand structural data within each forest type. Using our demography data, we summarized stand age structure by forest type and elevation and compared the age distribution between species using Kolmogorov-Smirnov two-sample tests with Bonferroni corrections for multiple comparisons. We used both land use history and reconstructed drought information to aid in interpreting age structure data. Specifically, for land use history, we used forest survey maps developed by the USGS around the beginning of the twentieth century that included the perimeters of recently burned areas (Leiberg 1900). We used reconstructed Palmer Drought Severity Index (PDSI; grid point 4) as an indicator of past climate (Cook et al. 1999). PDSI is a measure of seasonal drought with negative numbers indicating drier than average conditions and positive numbers indicating wet conditions (Palmer 1965). Summary statistics from the fire scars were obtained using FHAES software (USDA Forest Service 2011). All fire scars were analyzed together due to the small sample size. All statistical analyses used R statistical software version 2.11.1 (R Development Core Team 2010).

RESULTS

Stand Demography, Forest Composition, and Structure

More than half of the plots had little or no shrub or herbaceous layer; this open, litter-dominated understory was particularly prevalent in the red fir forest type. Only seven plots (11 %), which were distributed among forest types, had a shrub dominated understory consisting of low-growing species (< 0.5 m in height), primarily huckleberry (*Vaccinium* spp.) and manzanita (*Arctostaphylos* spp.). Stand characteristics varied a great deal between the four forest types. Red fir forest had more basal area per plot than the other forest types while mountain hemlock forests had lower stem density (Table 3).

A total of 1025 trees were cored across the study area. Approximately 23% of cores were excluded because they could not be cross-dated or were too far from the pith to estimate an establishment date (Table 4). Of the entire sample, 45% of trees were established during the forty-year period centered around 1900. When broken out into forest type, this cohort was more dominant in lodgepole pine and mixed conifer stands. In those forest types, more than half of the trees we cross-dated were established during that forty-year time period (1880-1920) (Table 4, Figure 2). This cohort was also more pronounced at lower elevations (Figures 1 and 3) and in areas mapped as recently burned around the beginning of the twentieth century (Figure 1; Leiberg 1900).

Tree establishment dates varied by forest type in CLNP (Figure 2). Mountain hemlock forests exhibited a pattern of continuous establishment since the early 1600's. Red fir forests, showed continuous establishment since the mid- to late-1600's with a peak of increased establishment around 1900. Lodgepole pine and mixed conifer forests both exhibited a distinct peak of establishment around 1900 with very little establishment prior to 1850. These patterns were characteristic for each forest type rather than each species. For example, mountain hemlock individuals found in lodgepole pine or mixed conifer forest types showed the same 1900 establishment peak characteristic of those forest types. Reconstructed PDSI does not appear to explain peak patterns of establishment in the study area (Figure 2).

We compared the age distribution between species using Kolmogorov-Smirnov two-sample tests with Bonferroni corrections for multiple comparisons. Excluding the mixed conifer group (excluded because it includes multiple species), age structures were significantly different between mountain hemlock and red fir ($p \leq 0.005$), red fir and lodgepole pine ($p \leq 0.005$), and mountain hemlock and lodgepole pine ($p \leq 0.005$). We also compared the age distribution between elevation groups using the same method. Age structures were significantly different between elevation zones (High-Mod p ≤ 0.005; High-Low p ≤ 0.005; Mod-Low p ≤ 0.005).

Fire History

Of the fire scar samples collected, we were able to cross-date scars on 16 samples (Figures 1 and 4). Successfully dated scars were collected at lower to middle elevations in red fir and mixed conifer forests. A total of 32 scars were dated and the median point fire return interval was 37.5 years (range = 12-82 years). In only three of nine cases where fire scar samples were collected within 500 m of a stand demography plot did scars correspond with a peak in establishment (Figure 5).

DISCUSSION AND CONCLUSIONS

Stand structures observed in this study are typical for these forest types. Among the forest types considered, red fir forests stand out as having substantially higher basal area (Table 3). This may be because red fir are long-lived and become quite large and also grow at relatively high stem densities. Mountain hemlock individuals are also often large and long-lived, but these higher-elevation forests tend to be more open and had substantially lower stem densities than the other forest types studied.

Both stand demography and fire scar data indicate that each forest type in the study area has somewhat different fire ecology. Mountain hemlock forests tend to occur at higher elevation and are later successional. Contrary to our hypothesis, the continuous establishment of mountain hemlock over the last four centuries suggests that high or even moderate severity fires are rare in this forest type. Because mountain hemlock forests are covered in snow for so much of the year, there is a narrow window when wildfires can occur. When they do occur, they likely burn as low severity surface fires with small pockets of higher severity such as observed in the Bybee Fire. We were unable to find any fire scars in this high-elevation forest type to corroborate our stand demography data either because fire is relatively rare or fire scars rarely form, heal over, or tend to rot in these forests.

The dual regeneration strategy of red fir is apparent in the demography data for this forest type, which shows both continuous establishment for the last several centuries and peaks of establishment associated with fire events. Although the fire scar analysis combined red fir and mixed conifer forests, the 37.5 year fire return interval is consistent with a mixed severity fire regime and with what has been reported for other red fir forests in the region (e.g. Chappell 1991, Taylor and Halpern 1991, Bekker and Taylor 2001). Fire years were generally not consistent across the study area. The fire regime of red fir forests is probably the most characteristic of a mixed severity regime of the forest types considered in this study.

Lodgepole pine in the monospecific stands sampled in this study tended to have establishment dates in the last 100 to 150 years. Although no direct fire scar evidence was found, these stands likely regenerated following stand-replacing fire. Several of the lodgepole pine stands we sampled did have establishment dates around 1900 and were located in or near mapped fire perimeters from the same time period (Leiberg 1900). Some studies have hypothesized that lodgepole pine follows two successional pathways following fire, where it is self-replacing on flat, cold air drainages with poor soils and succeeds to mountain hemlock and red fir forests on better sites (Zeigler 1978, Agee 1993). However, all of our plots dominated by lodgepole pine, including those on flat, poor sites, had an understory of mountain hemlock and red fir and it is likely that they would succeed to a red fir-mountain hemlock forest type in the absence of disturbance over several centuries (Figure 6).

The mixed conifer forests sampled have few older trees with most individuals established since 1900. The lack of older trees suggests that these forests may have burned with high severity around the beginning of the twentieth century. This may reflect land use history, with increased fire associated with settlement and land use changes in southern Oregon during that period, particularly since the mixed conifer forests in the study area are near park boundaries and may have been more easily impacted by human activities in surrounding areas. Typically, mixed conifer forest fire regimes in this region are high frequency and low to moderate severity, so high severity fire is likely related to human influences (Agee 1993).

The peak in establishment we observed around 1900 has been seen in similar forest types in other locations (Taylor 1995, Bekker and Taylor 2010). This may be the result of a warm, mesic period in the region around this time (Taylor 1995). Land use and fire history may also be factors; forest survey maps produced for this region in 1900 show approximately 25% of the study area as recently burned (Leiberg 1900). However, our peak in forest establishment appears to be spread fairly evenly across the landscape; this turn of the century cohort does not appear to be associated exclusively with fires mapped around the same period (Figure 1). Lastly, CRNP fire suppression policy in the early 1900's through the 1980's is also a likely contributor to this pulse in regeneration.

Conclusions

Overall, our results are consistent with studies of the fire ecology of these forest types in surrounding areas. Our fire scar data, which is primarily for lower-elevation mixed conifer forests, supports the conclusion that this forest type has a relatively short fire return interval in relation to the period of fire suppression and may be in need of the most active management to restore fire as a natural process. The presence of mono-specific, even-aged stands of lodgepole pine, which are likely associated with past fire events, supports the conclusion that these forests are adapted to high severity, relatively low frequency fires. Red fir forests have the most mixed fire regime in the study area. Contrary to our hypothesis, our data did not support the idea that mountain hemlock forests in the study area had fire return intervals similar to red fir forests. Rather, continuous establishment in mountain hemlock forests over several centuries suggests that moderate to high severity fires have been relatively rare in these forests.

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TABLES

Table 1. Published fire histories for forests in Crater Lake National Park, northern Cascades, and similar forest types in Oregon and California. FRI, fire return interval.

Forest Type	Location	FRI (years)	Analysis Unit for FRI	Sample Size	Citation
Red Fir	Sequoia National Park, CA	78	plot (.25-.5 ha)	16	Pitcher (1987)
Red Fir	Crater Lake National Park, OR	39	plot (.5 ha)	11	Chappell (1991)
Red Fir	Swain Mtn Experimental Forest, CA	40-42	plot (.5 - 1 ha)		Taylor & Halpern (1991)
Red Fir-Mtn Hemlock	Thousand Lakes Wilderness, CA	20 (9-91)	point	6	Bekker & Taylor (2001)
Red Fir-Mtn Hemlock	Thousand Lakes Wilderness, CA	100	point		Bekker & Taylor (2010)
Red Fir-Western White Pine	Lassen Volcanic National Park, CA	70 (26-109)	point	41	Taylor (2000)
Red Fir-Western White Pine	Caribou Wilderness, CA	66	plot (.04-.1 ha)		Taylor & Solem (2001)
Red Fir-Western White Pine	Lake Tahoe, CA	76 (25-175)	point		Scholl & Taylor (2006)
Lodgepole Pine	Caribou Wilderness, CA	67	plot (.04-.1 ha)		Taylor & Solem (2001)
Lodgepole Pine	Thousand Lakes Wilderness, CA	47 (28-54)	point	6	Bekker & Taylor (2001)
Lodgepole Pine	Thousand Lakes Wilderness, CA	50-76.5	point		Bekker & Taylor (2010)
Ponderosa Pine	Crater Lake National Park, OR	9-42	2 trees	48	McNeil (1975)

Table 2. Master chronologies used in cross-dating cores and fire scars (NOAA 2011).

Site Name	Location	Elev. (m)	Species	Time Period	Num. of Cores	Series Intercorr-elation	Mean Sensitivity	Contributor
Mt. Ashland	42.07°N 122.72°W	1860	Abies magnifica	1739-1983	22	0.606	0.182	Briffa, K., F.H. Schweingruber
Crater Lake	42.97°N 122.17°W	1752	Tsuga mertensiana	1564-1983	23	0.735	0.284	Briffa, K., F.H. Schweingruber

Table 3. Average stand characteristics by forest type in Crater Lake National Park, northern Cascades, Oregon.

	Forest Type			
	Mountain hemlock	Red fir	Lodgepole pine	Mixed conifer
Number of Plots	16	22	17	9
Elevation (m)	1975	1752	1688	1595
Basal Area ($m^2\ ha^{-1}$)				
Total	87.3	136.1	42.8	94.7
Mountain hemlock	68.5	19.1	0.4	8.6
Red fir	11.0	105.1	5.9	12.1
Lodgepole pine	6.9	3.3	34.3	2.1
Other	0.9	8.5	1.9	71.9
Density (stems ha^{-1})				
Total	591	986	779	841
Mountain hemlock	457	321	12	193
Red fir	65	536	88	123
Lodgepole pine	67	39	636	25
Other	2	90	44	500

Table 4. Tree cores and individuals established by time periods and species, Crater Lake National Park, northern Cascades, Oregon.

	All Trees	Mountain hemlock	Red fir	Lodgepole pine	Other
Number trees cored	1025	328	280	281	136
Number cross-dated	787	242	209	231	105
% Established pre1800	18.7	36.0	24.4	2.2	3.8
% Established 1880-1920	45.2	26.9	40.2	53.7	79.0

FIGURES

Figure 1. Location of study site in Crater Lake National Park, southern Cascades, Oregon. Plot locations are shown with symbol colors corresponding to the forest type of each plot, and symbol size corresponding to the percent of trees in each plot established between 1880 and 1920. Fires mapped around the turn of the 20th century are also shown (“Mapped Leiberg Fires”; Leiberg 1900). Labeled plots have establishment peaks corresponding with nearby fire scars and are also shown in Figure 5.

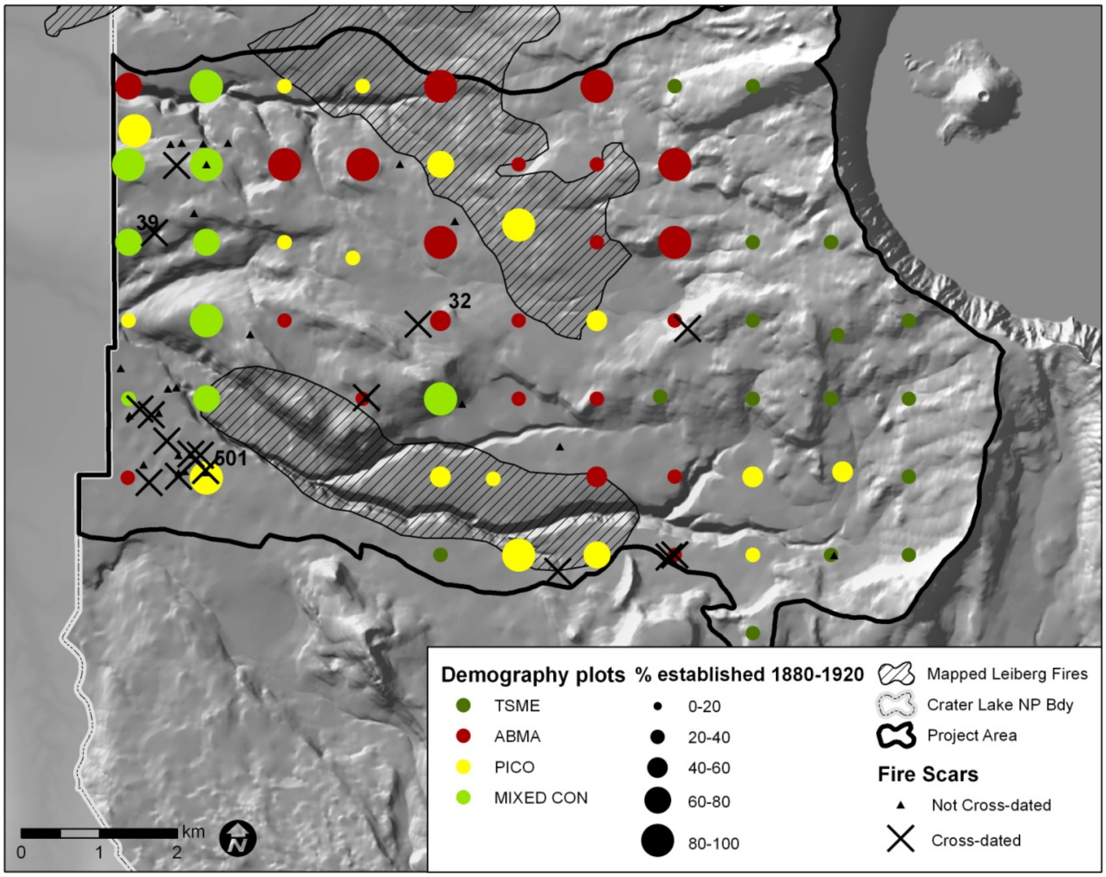


Figure 2. Age class distributions of red fir, mountain hemlock, lodgepole pine and other species (primarily Douglas-fir, white fir, western white pine, and western hemlock) across all plots at Crater Lake National Park, as well as the closest Palmer Drought Severity Index (gridpoint 4). Establishment dates are grouped into ten-year bins.

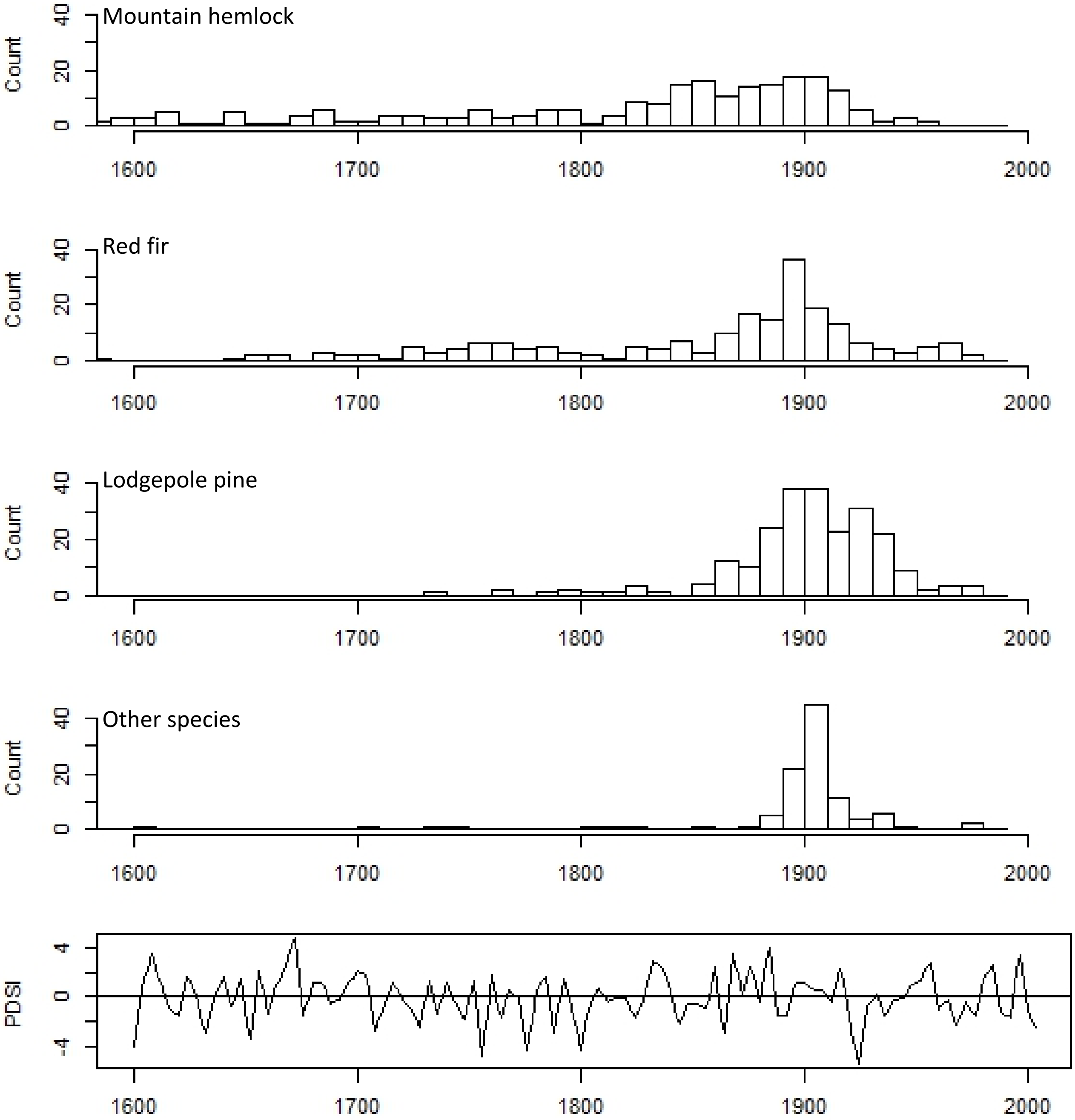
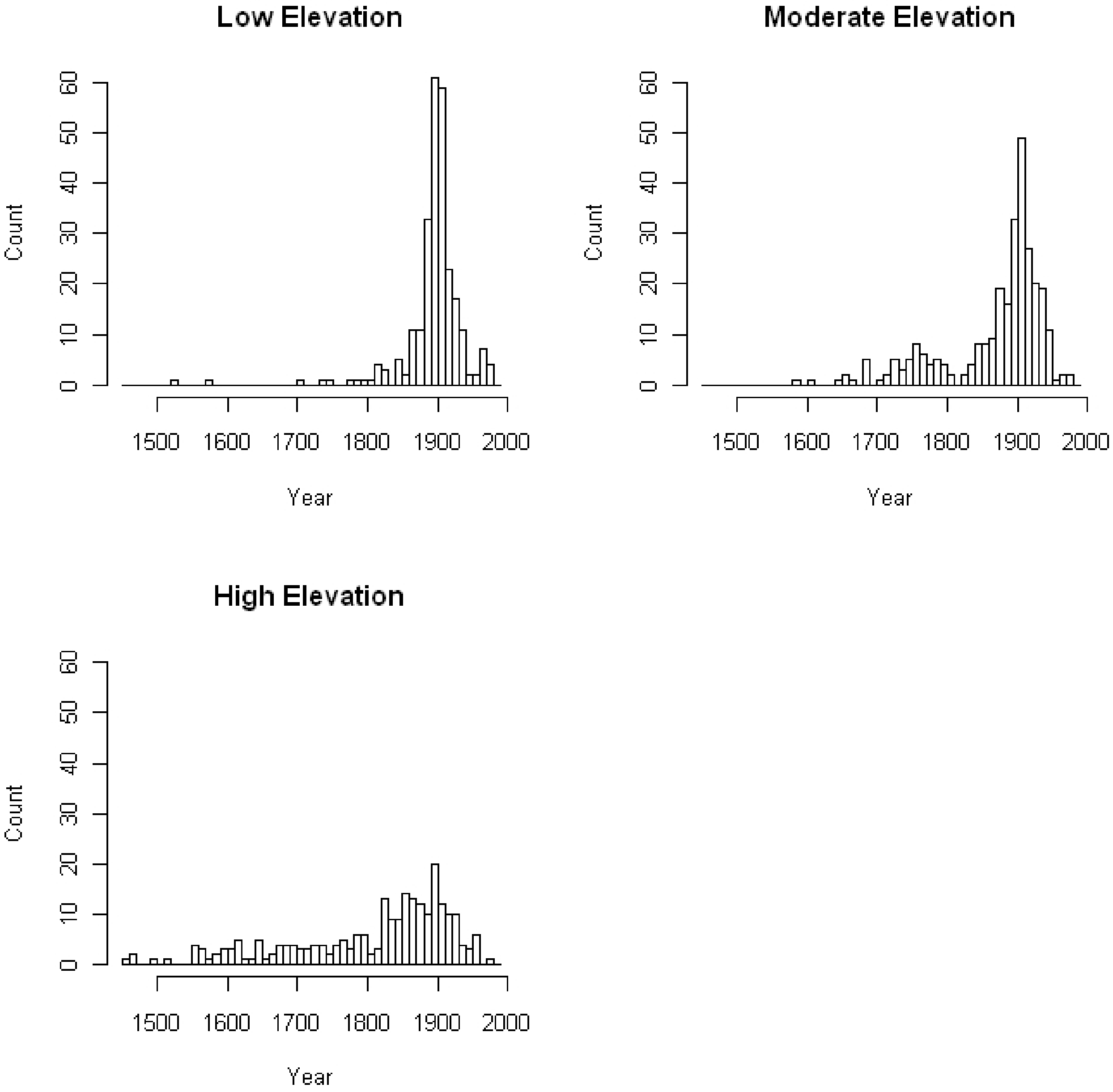


Figure 3. Tree establishment dates by elevation, Crater Lake National Park southern Cascades, Oregon (low includes plots less than 1684 m, moderate includes plots between 1684 m and 1818 m and high includes plots above 1818 m).



Low Elevation

Moderate Elevation

High Elevation

Figure 4. Fire history, scars sorted from high (top) to low (bottom) elevation, Crater Lake National Park, southern Cascades, Oregon. Composite filter shows years with at least two scarred trees.

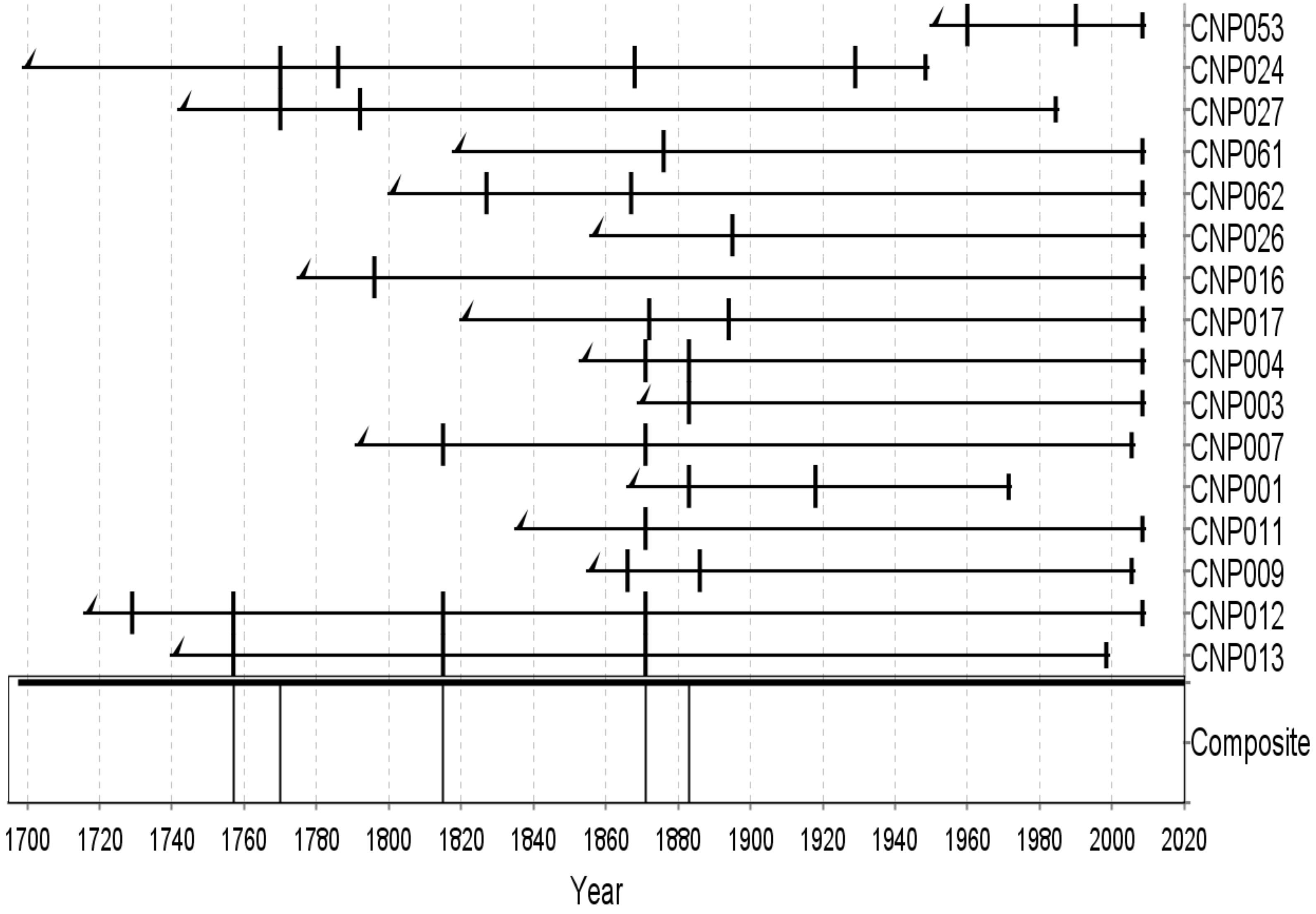


Figure 5. Plots where peaks in tree establishment were correlated with fire dates from conifer forests at Crater Lake National Park, southern Cascades, Oregon. Fire dates are indicated by arrows.

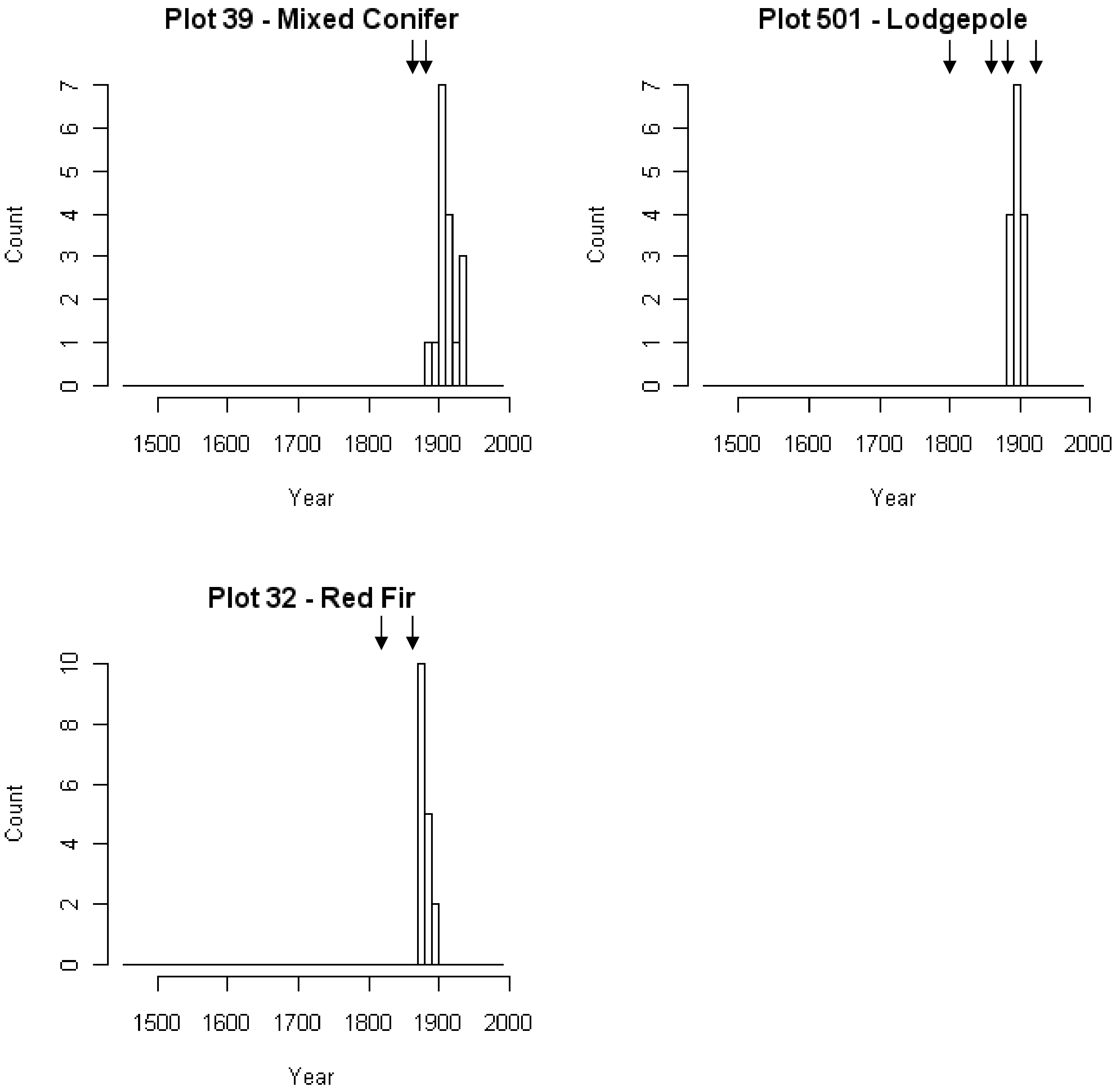


Figure 6. Red fir and mountain hemlock in the understory of a lodgepole pine stand, Crater Lake National Park, southern Cascades, Oregon.