Patterns of Fire Severity and Forest Conditions in the Western Klamath Mountains, California

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Abstract: *The Klamath-Siskiyou region of northwestern California and southwestern Oregon supports globally outstanding temperate biodiversity. Fire has been important in the evolutionary history that shaped this diversity, but recent human influences have altered the fire environment. We tested for modern human impacts on the fire regime by analyzing temporal patterns in fire extent and spatial patterns of fire severity in relation to vegetation structure, past fire occurrence, roads, and timber management in a 98,814-ha area burned in 1987. Fire severity was mapped by the U.S. Department of Agriculture Forest Service as low, moderate, and high based on levels of canopy scorch and consumption. We found (1) a trend of increasing fire size in recent decades; (2) that overall fire-severity proportions were 59% low, 29% moderate, and 12% high, which is comparable to both contemporary and historic fires in the region; (3) that multiaged, closed forests, the predominant vegetation, burned with much lower severity than did open forest and shrubby nonforest vegetation; (4) that considerably less high-severity fire occurred where fire had previously be absent since 1920 in closed forests compared to where the forests had burned since 1920 (7% vs. 16%); (5) that nonforest vegetation burned with greater severity where there was a history of fire since 1920 and in roaded areas; and (6) that tree plantations experienced twice as much severe fire as multi-aged forests. We concluded that fuel buildup in the absence of fire did not cause increased fire severity as hypothesized. Instead, fuel that is receptive to combustion may decrease in the long absence of fire in the closed forests of our study area, which will favor the fire regime that has maintained these forests. However, plantations are now found in one-third of the roaded landscape. Together with warming climate, this may increase the size and severity of future fires, favoring further establishment of structurally and biologically simple plantations.*

Key Words: Douglas-fir, fire regimes, fire severity, hardwoods, Klamath-Siskiyou region, roadless areas, silviculture

Patrones de Severidad de Fuego y Condiciones del Bosque en las Montañas Klamath Occidentales, California

Resumen: *La region Klamath-Siskiyou (Noroeste de California y Suroeste de Oregon) sostiene una biodiversidad templada globalmente sobresaliente. El fuego ha sido importante en la historia evolutiva que moldeó a esta diversidad, sin embargo, influencias humanas recientes han alterado el ambiente del fuego. Probamos los impactos humanos modernos sobre el régimen de fuego analizando los patrones temporales de la extensión del fuego y los patrones de severidad del fuego en relación con la estructura de la vegetación, incidencia de fuego en el pasado, caminos y manejo de madera en un área de 98,814 ha quemada en 1987. La severidad del fuego fue clasificada en el mapa por el Servicio Forestal de EE. UU. como baja, moderada o alta tomando en cuenta el grado de chamuscado y consumo del dosel. Encontramos (1) que hubo una tendencia hacia un aumento del tamaño del fuego en décadas recientes; (2) que las proporciones totales de severidad de fuego fueron: 59% bajo,*

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29% moderado y 12% alto (lo cual es comparable tanto para incendios contemporáneos como históricos en la región); (3) que los bosques cerrados, de edades múltiples, la vegetación predominante, se quemó mucho menos severamente que los bosques abiertos y la vegetación arbustiva no boscosa.; (4) que hubo considerablemente menos fuego de alta intensidad donde no habían ocurrido incendios en bosques cerrados desde 1920 en comparación con bosques que se han quemado desde 1920 (7% vs. 16%); (5) que la vegetación no boscosa se quemó con mayor severidad donde había una historia de fuego desde 1920 y en áreas con caminos; y (6) que las plantaciones de árboles tenían dos veces la cantidad de fuego severo que los bosques de edades múltiples. Concluimos que la acumulación de combustible en ausencia de fuego no causó incremento en la severidad del fuego, como se planteó. En cambio, el combustible que es receptivo a la combustión puede disminuir en la larga ausencia de fuego en los bosques cerrados de nuestra área de estudio. Esto favorecerá al régimen con fuego que ha mantenido a estos bosques. Sin embargo, las plantaciones se encuentran en un tercio del paisaje con caminos. En combinación con el calentamiento del clima, esto puede incrementar el tamaño y severidad de futuros incendios, lo que favorecerá el establecimiento de plantaciones estructural y biológicamente simples.

Palabras Clave: áreas sin caminos, intensidad de fuego, maderas duras, Pino de Douglas, regímenes de fuego, región Klamath-Siskiyou, silvicultura

Introduction

The effects of human alteration of natural disturbance regimes such as fire are fundamentally important issues for biological conservation. The persistence of endangered species, maintenance of ecological integrity, and safeguarding of ecosystem processes (e.g., hydrologic and nutrient cycling) are threatened by such alterations (World Conservation Union 1994; Dale et al. 2000). The significance of these threats is particularly high in the Klamath-Siskiyou ecoregion of northwestern California and southwestern Oregon (U.S.A.). This approximately 4,000,000-ha region has special significance in the vegetation history of the Pacific States as a center of endemism and speciation (Whittaker 1961; Stebbins & Major 1965). Recent analyses recognize the ecoregion's biodiversity as globally outstanding (DellaSala et al. 1999).

A complex, mixed-severity fire regime has shaped the composition and structure of Klamath-Siskiyou vegetation. Because of steep climatic, edaphic gradients, and rugged topography, fire frequencies and severities have been highly variable (Agee 1993; Taylor & Skinner 1998, 2003). Such spatial and temporal variation in disturbance is believed fundamental to promoting species diversity because nonequilibrium processes enhance habitat heterogeneity (Connell 1978; Huston 1979). Biodiversity is likely to be threatened where changes in fire regime become incompatible with evolutionary history (Bond & van Wilgen 1996; Swetnam et al. 1999). Understanding fire regimes and human impacts on them will be essential to conserving the globally outstanding biodiversity of the Klamath-Siskiyou ecoregion.

Fire regimes have been recently modified where fire has been successfully excluded, especially if biomass that is receptive to combustion accumulates in the absence of fire (Covington 2000; Dale et al. 2000). This scenario has been commonly cited as the primary factor contributing to recent large fires in forests of the western United States (Covington 2000; Arno & Allison-Bunnell 2002; Agee 2002). As a result, current land-management policies in the United States are calling for widespread tree harvests and other mechanical treatments aimed at reducing fuel. However, the effects of these treatments on biodiversity remain unclear. In addition, the problem of fuel build-up leading to increased fire severity has mainly been documented in formerly open forests of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) that have historically been maintained by remarkably frequent surface fire (Covington 2000). Fire plays a very different role in many other forests (Turner et al. 2003), raising concerns that the surface-fire model of fuel dynamics is uncritically accepted in forests where it may not apply (Baker & Ehle 2001; Gutsell et al. 2001; Ehle & Baker 2003; Johnson 2003).

Forestry practices other than fire exclusion also may influence fire regimes. Even-aged silviculture can increase fire hazard by creating more combustible fuel complexes (Perry 1994; Weatherspoon & Skinner 1995). Other silvicultural activities include harvest of small trees and suppression of other understory growth. These activities may reduce fire intensity and spread, but they may also adversely affect soils, vegetation, wildlife, and other biological resources (DellaSala & Frost 2001). To assess the net effects of forest-management activities on biodiversity, a better understanding of how these practices interact to influence fire is needed.

Extensive fires burned in the Klamath-Siskiyou region in 1987, creating a landscape well suited to test the following hypotheses: (1) within the same vegetation types, fire severity is greater where previous fire has been long absent, and (2) exclusive of where plantations are, the proportion of high-severity (crown) fire is lower in previously roaded and managed portions of the burned landscape. The study area in the Klamath National Forest of

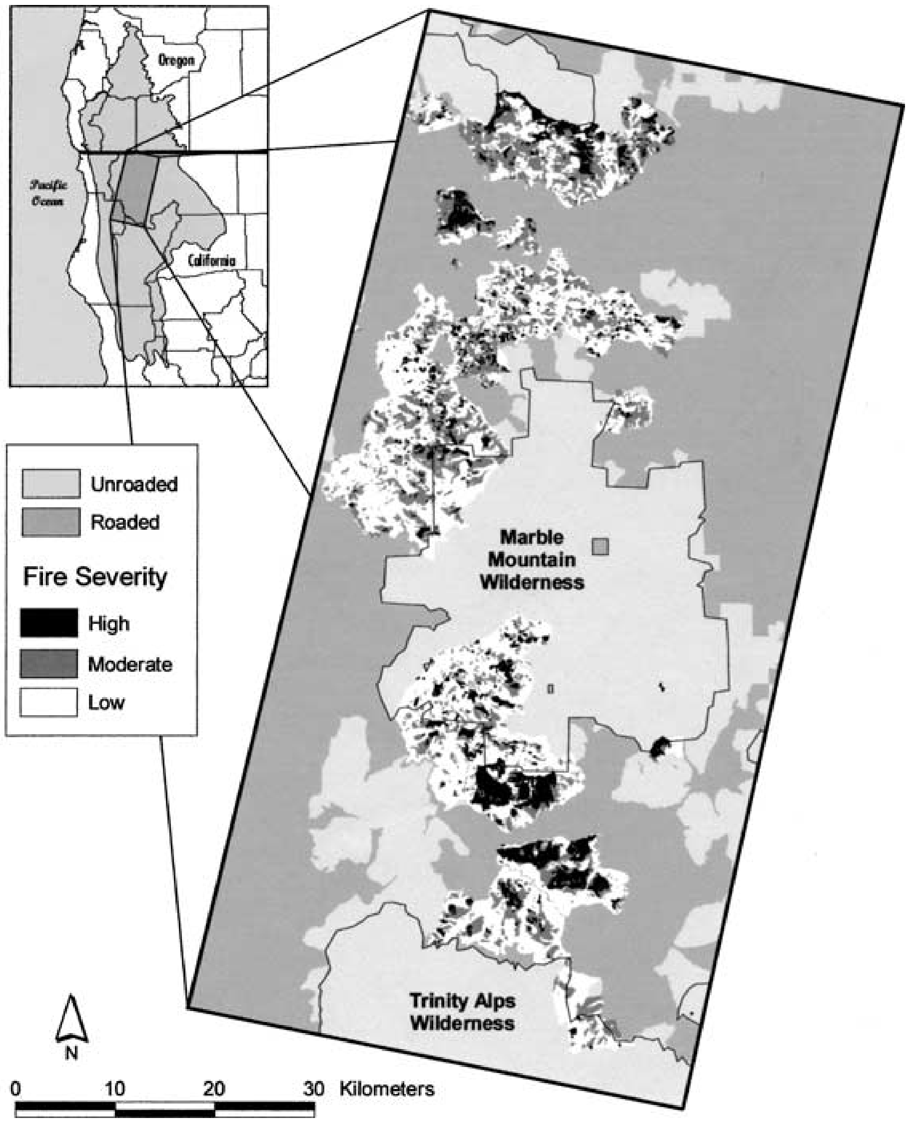

Figure 1. Map of the study area within the Klamath-Siskiyou region (light gray area on insert) showing location and severity patterns of 1987 wildfires and roaded and unroaded areas.

northwest California exhibits vegetation complexity for which the Klamath-Siskiyou ecoregion is well known and was ideal for evaluating the degree to which mixed-severity fire regimes have been altered by recent human activity.

Methods

Study Area

The Klamath National Forest (KNF) is located in northwestern California (Fig. 1). Our study area, defined by satellite data coverage, was a 500,000-ha portion of the KNF, of which almost 100,000 ha burned in 1987. Elevations ranged from about 300 m along the Klamath and Salmon rivers to over 2000 m on select mountaintops. Most of the area was between 500 and 1500 m in elevation. The climate is characterized as Mediterranean, with warm, dry summers and cool, wet winters. Precipitation ranges from about 1100 mm to over 2000 mm based on the few stations with long-term data; 90% of precipitation falls between October and May. The dry summers are hot; the average July temperature for Happy Camp, 330 m in elevation in the north-central part of the study area, is 25.7° C (Taylor & Skinner 1998).

Most of the natural vegetation in the study area is tall, temperate forest characterized by a relatively open Douglas-fir (*Pseudotsuga menzesii* Mirbel) overstory with a subcanopy of tan oak (*Lithocarpus densiflorus* Hook. & Arn.), an evergreen hardwood. According to KNF timber-type maps, these trees accounted for approximately 65% of forest cover in the portion of our study area that burned in 1987. Other evergreen trees included several conifers, notably sugar pine (*Pinus lambertiana*

Douglas), and the hardwoods Pacific madrone (*Arbutus menziesii* Pursh.), canyon live oak (*Quercus chrysolepis* Liebr.), chinquapin (*Chrysolepis chrysophylla* Hook.), California bay (*Umbellularia californica* Hook. & Arn.), and deciduous black oak (*Quercus kellogii* Newb.). These hardwoods can occur without a conifer overstory, particularly on rocky soils of steep canyon slopes and in recently disturbed areas.

With increasing elevation and moisture availability, the Douglas-fir–hardwood type is replaced by forests dominated by white fir (*Abies concolor* Gordon & Glend.) and Shasta red fir (*A. magnifica* var. *shastensis* Lemmon), which covered 10% and 4% of the burned landscape, respectively. Nonforest vegetation is mostly chaparral, a dense evergreen shrubland that is edaphically restricted to rocky soils or that is established following stand-replacing fire in areas with forest potential (Wills & Stuart 1994). Relatively short-statured hardwoods often occur in this vegetation and may dominate. Nonforest vegetation occupied 12% of the burned landscape at the time of the 1987 fires. Tree plantations affected by these fires accounted for 3965 ha (4%), all within roaded portions of the study area.

Wildfire Setting

Historical fire regimes for the study area and nearby are generally described as mixed, with fire-severity proportions ranging, in order of abundance, from low to moderate to high (crown fire) (Agee 1993). Fires also have had highly variable return intervals, depending on vegetation type, topography, and elevation. For Douglas-fir–hardwood forests, recent fire return intervals have ranged from 3 to 71 years (Wills & Stuart 1994; Taylor & Skinner 1998) within the study area. White-fir forests just west of the study area burned at intervals ranging from 12 to 161 years prior to fire suppression (Stuart & Salazar 2000). Fire suppression reportedly became effective in reducing the area burned on the KNF in the 1940s (Taylor & Skinner 1998). During the large wildfire event that began on 30 August 1987, however, initial attack was limited because so many lightning fires ignited simultaneously. Control actions related to these fires were limited by lack of resources and were compounded by prolonged drought and record-breaking temperatures that desiccated fuels to unusually low levels (Reider 1988).

Satellite Image Processing

We processed Landsat thematic mapper satellite imagery acquired on 19 August 1986 to examine vegetation structure prior to the wildfires of 1987. Following registration and geometric correction, we classified the image with standard software (ERDAS Imagine, Leica Geosystems, Atlanta, GA, USA) into three forest structural types characterized by closed canopies of differing texture and one forest type characterized by open canopy. Nonforest (shrub-hardwood) vegetation was also recognized.

GIS Data

From the U.S. Department of Agriculture Forest Service (USFS) we acquired geographic information system (GIS) data layers produced at 1:24,000 map scale for the study area, including maps of tree plantations, fire history, fire severity, and timber type. We also identified roaded and unroaded areas. All existing wilderness areas and most of the inventoried roadless areas of >2020 ha were included in the unroaded landscape, as were smaller areas mapped with 1:24,000 scaled road data (minimum size 405 ha; for details see Strittholt & DellaSala 2001).

The fire-history data layer displayed mapped perimeters for fires dating back to 1911 in the area that burned in 1987. There was an abundance of fire in 1917 and 1918 and a continuous record of fire after this period. However, we cannot be certain that some (particularly small) fires, especially those that occurred prior to 1920, are not included. Fire perimeters from this period were obtained from 1:126,720 fire atlases of ranger districts and transferred to 1:62,500 maps. In part for this reason, we considered all the landscape for which the previous burn date was 1920 or before to be "long unburned."

For the 1987 wildfire season, fire-severity data was obtained for a complex of fires within the study area (Fig. 1). Staff of the KNF mapped severity (low, medium, high) with 1:15,840 color infrared, post-burn, aerial photography. Low severity was represented by canopy vegetation with <50% scorch (brown foliage). These areas primarily experienced surface fire that tended to kill conifer seedlings and saplings and nonsprouting shrubs. Tree mortality was generally low. Moderate severity was represented by canopy vegetation with 50–100% canopy scorch. Forests experienced stand thinning, with mortality concentrated in smaller trees, and small patches of stand replacement. Effects on forest structure were variable, but a significant proportion of the larger fire-resistant conifers survived. Effects were lethal to nonsprouting shrubs. High severity was represented by canopy foliage that was 100% scorched or consumed to varying degrees by crown fire. These effects were generally lethal to conifers, and only root crowns of hardwoods and resprouting shrubs survived. However, crown fire rarely destroyed the foliage of all trees in an area, particularly large specimens, so an occasional large conifer may have survived.

To evaluate how the 1987 fires compared with other large contemporary fires in the Klamath-Siskiyou region, we obtained additional fire-severity maps from the USFS for all fires larger than 1500 ha that had occurred on federal lands since 1977. Although the methodologies used to classify and map fire severity varied for the most recent

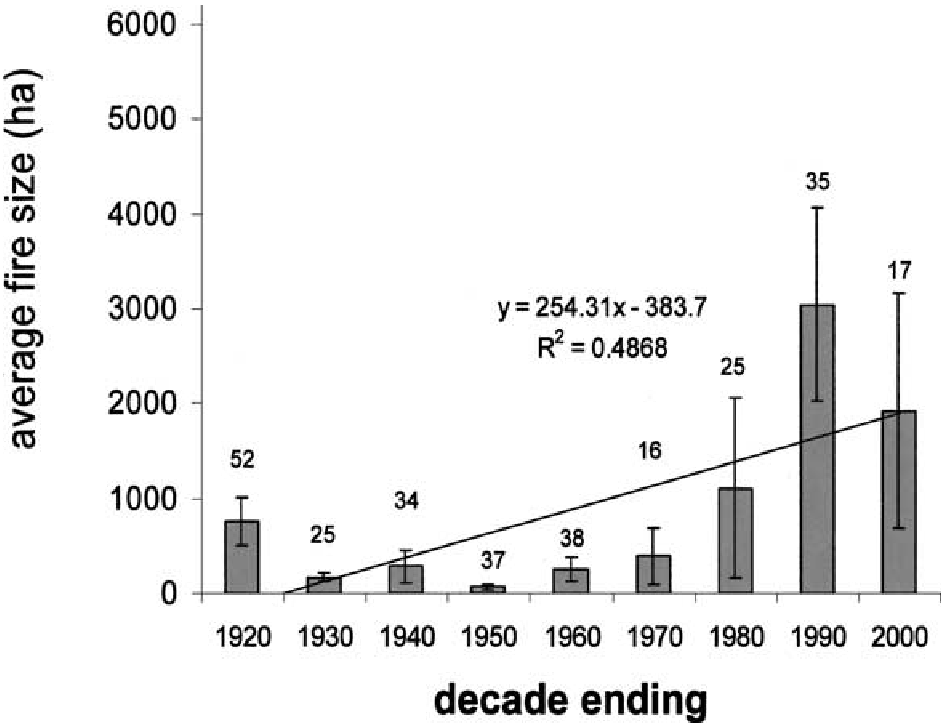

*Figure 2. Average fire size per decade from 1911 through 1999 (*F = 6.6, p < 0.047*). Error bars show 1 SE above bar, and numbers are number of fires.*

fires, criteria are sufficiently similar to allow for general comparisons.

GIS and Statistical Analyses

We regressed fire size (mean value calculated by decade) over time with standard least-squares regression. We analyzed fire-severity data from 1987 in vector format—using the mapped polygons—in relation to past fire occurrence, tree plantations, timber-type maps, and fire severity in an area that burned previously in 1977. Fire-severity data from 1987 and preburn vegetation-structure data were analyzed in raster format at a common grid size of 30 m. To eliminate spatial dependency and perform diagnostic statistics, we determined the spacing at which point locations of the dependent variable, fire severity, no longer exhibited spatial autocorrelation by constructing and evaluating a semivariogram (Jongman et al. 1987). We then generated a set of random points (100) separated by at least this distance (2000 m) for use in statistical analyses. We calculated the probability of the observed numbers of points falling into areas burned at high severity in a subset of the landscape based on the expected proportion in the burned landscape as a whole. We used the normal approximation (Zar 1999) to calculate *Z* and to obtain the probabilities. We only had sufficient sample sizes of independent points for testing large subsets of the landscape. So, for smaller landscape subsets, we performed selected chi-square tests, with the overall severity proportions for a given category representing the observed frequencies. These observed versus expected comparisons provided a sense of how different severity proportions in 1987 were in a particular type of vegetation that had burned in recent decades when the entire burned landscape was taken into account (i.e., not just spatially independent points).

Results

A total of 98,814 ha (19.1%) of the approximately 500,000-ha study area burned in 1987 (Fig.1). Based on the fire-history coverage, 202,700 ha burned between 1911 and 1987. Therefore, 1987 accounted for about half of all mapped burn area over a 76-year period ending then. From 1988 to 2002, an additional 33,803 ha burned. There have been fewer fires in the last few decades, however, and average fire size has increased (Fig. 2; $R^2 = 0.49$, $p = 0.04$). It would take 55 years to burn an area equal to the entire 500,000-ha landscape, based on the rate of burning in the last 15 years. This rate is strongly dependent on the continued occurrence of large fire events like those shown in Fig. 3.

Despite the multiyear drought that preceded the 1987 fires and a landscape of predominantly long-unburned vegetation, fire severity was mostly low. The overall proportions were 58.5%, 29.5%, and 12.0% for low, moderate, and high severity, respectively (Table 1). These proportions are typical of those found in other large fires in the Klamath-Siskiyou region in recent decades (Fig. 3).

Fire Severity and Vegetation

Closed forests accounted for almost 80% of the vegetation burned in 1987 (Table 1). Proportions of high-, moderate- and low-severity fire were similar among the three

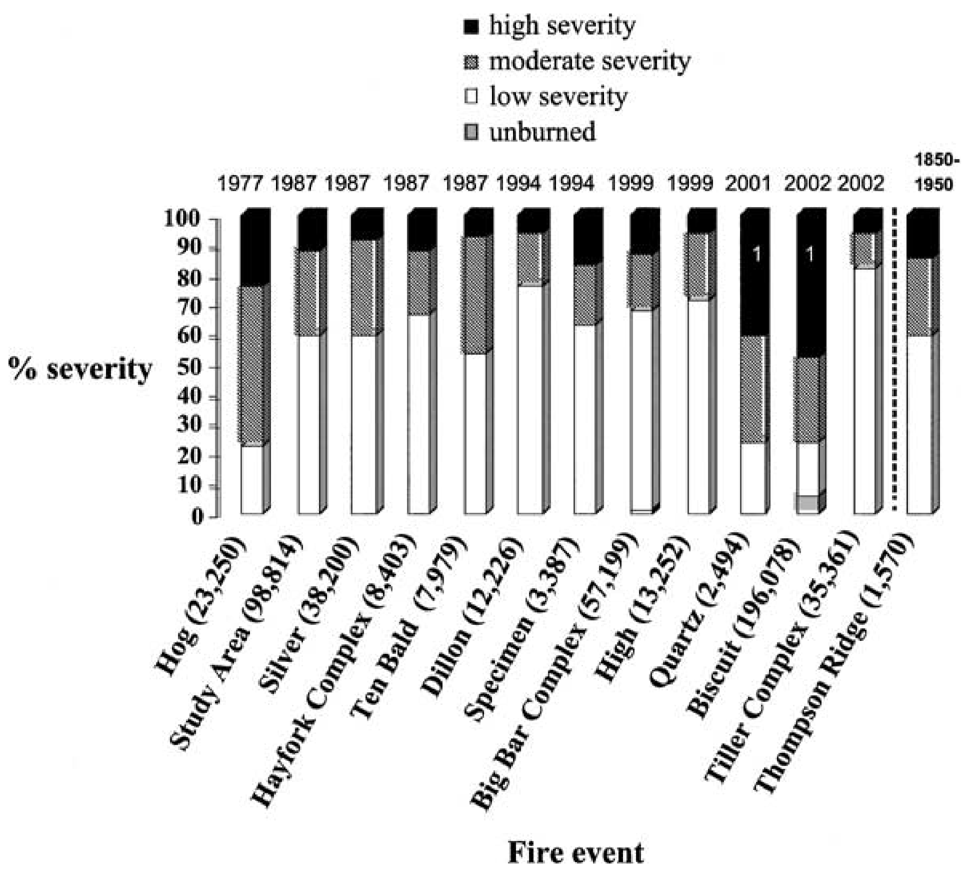

Figure 3. Severity of large fire events (>1500 ha) in the Klamath-Siskiyou region, 1977–2002. Year of burn is shown above bars. See Taylor and Skinner (1998) for historical estimate from study area and data for Hayfork complex. The number 1 in bars indicates that severity exceeding 75% scorch was mapped as high, a 25% lower threshold than used in other mapping.

closed-forest types (e.g., 8–11% high severity), so we grouped them together. Overall, closed-forest vegetation had significantly less high-severity fire than the burned landscape as a whole ($Z = -2.19$, $n = 77$, $p = 0.014$). Open forest and nonforest vegetation had considerably more high-severity fire. We also calculated burn severity where the timber-type maps indicated dominance by ponderosa pine. These pine forests (5748 ha) burned with only 6.6% high-severity fire.

Fire Severity and Time since Fire

The hypothesis that fire severity is greater where previous fire has been long absent was refuted by our study (Table 1). There was three times more high-severity fire in areas last burned since 1920 (recently burned landscape). The amount of high-severity fire in all areas previously burned in 1920 or earlier (long-unburned landscape) was significantly lower than in the burned landscape as a whole ($Z = -2.10$, $n = 86$, $p = 0.018$). Although long-unburned areas were dominated by closed forests (69,443 of 84,448 ha), only half of the more recently burned landscape supported closed forests. The other half was open forest and nonforest vegetation (Table 1). The amount of high-severity fire in long-unburned closed forests was the lowest of any portion of the landscape and differed from that in the landscape as a whole ($Z = -2.62$, $n = 66$, $p = 0.004$). However, the percentage of high-severity fire in recently burned areas in closed forests and nonforest vegetation was more than twice that found in long-burned areas. It was not possible to test whether these higher proportions differed from expectation with the 100 independent random points because very few of these points fell into each recently burned vegetation type. From a chi-square analysis we drew some inference about how improbable the fire severity amounts for recently burned closed forests, open forests, and nonforest vegetation were compared with severity in the same three vegetation types in the entire landscape. Probability values from these comparisons were 0.008, 0.021, and 0.003, respectively.

The 1987 fires reburned an area that had burned in 1977. The 1977 burn was unusually severe (Fig. 3). Sixty percent of the area that burned at high severity in 1977 reburned at high severity again in 1987 (2902 ha). Areas burned with moderate and low severity in the 1977 fire reburned with mostly low severity (54% and 63%, respectively).

One-third (3406 ha) of all the nonforest vegetation that burned in 1987 had burned in 1977, and fire severity was high in 54% of the area. Elsewhere, nonforest vegetation burned with only 20% high severity. Areas burned severely in 1977 were subsequently logged with helicopters. Activity fuels (branches and tops of trees) left untreated after such logging could have contributed to

Table 1. Proportions of the burned landscape mapped into low, medium, and high fire-severity categories.*

	Fire severity (%)			
*Landscape burned in 1987**	*low*	*medium*	*high*	*Area (ha)*
Entire landscape a	58.5	29.5	12.0	98,814
Vegetation				
all closed forests b	63.6	28.4	8.0	77,888
all open forests	38.7	40.2	21.1	8,894
all nonforest vegetation	39.6	28.9	31.4	12,033
all ponderosa pine forests	46.4	46.9	6.6	5,748
Time since fire				
last burned in or prior to 1920 b	62.0	29.4	8.6	81,913
last burned since 1920	41.0	30.2	28.8	16,901
Vegetation and time since fire				
closed forests burned in or prior to 1920 b	64.9	28	7.1	69,443
closed forests burned after 1920	53.2	30.9	15.9	8,445
open forests burned in or prior to 1920	42.9	42.0	15.1	5,785
open forest vegetation burned after 1920	30.9	36.6	32.2	3,109
nonforest vegetation burned in or prior to1920	49.1	32.0	18.9	6,686
nonforest vegetation burned after 1920	27.8	25.1	47.1	5,347
ponderosa pine forests burned in or prior to 1920	49.6	44.2	6.2	4,056
ponderosa pine forests burned after 1920	39.0	53.2	7.7	1,692
Management				
all roaded areas a	56.1	31.5	12.4	51,465
all unroaded areas a	61.0	27.4	11.7	47,368
plantations	42.0	41.5	16.4	3,965
roaded areas excluding plantations	59.4	30.6	9.9	47,495
Vegetation and management				
closed forests in roaded areas	62.3	29.6	8.1	39,450
closed forests in unroaded areas	64.9	27.1	8.0	38,444
open forests in roaded areas	36.8	45.4	17.9	4,723
open forests in unroaded areas	41.0	34.2	24.8	4,171
nonforest vegetation in roaded areas	35.3	32.4	32.2	7,285
nonforest vegetation in unroaded areas	46.2	23.4	30.3	4,748

**Different letters indicate significantly different proportions of high-severity burn ($p < 0.05$). Testing was based on spatially independent subsets of the landscape (see Methods).*

the elevated fire severity in nonforest vegetation in the 1987 reburn compared with elsewhere.

Fire Severity and Management

There was little overall difference in fire severity between roaded and unroaded areas, even though tree plantations had twice the burn severity of closed-canopy forests (Table 1). Fire severity tended to increase with plantation age (not shown). Severity proportions in closed forests in roaded and unroaded areas were almost identical (Table 1). Low-severity fire was more common in both open forest and nonforest vegetation in unroaded areas. We found a low chi-square probability that observed fire severity was not higher in roaded versus unroaded areas for nonforest vegetation ($p = 0.046$).

Discussion

The 1987 fires were typical of other relatively large fires in the region that have occurred in recent decades (Fig. 3). Despite human influences and a fire-suppression policy, most large wildland fires have been dominated by low-severity fire, with variable proportions of moderate and high severity. This is consistent with historical estimates inferred from stand age structure as shown in Fig. 3 (from Taylor & Skinner 1998). One factor that contributed to the heterogeneity in fire patterns in 1987, and presumably in other large fire events, is that the fires burned under a variety of weather conditions for many weeks (Reider 1988). Such extensive fires occurred in the Klamath-Siskiyou region prior to suppression, in 1910 for example (Agee 1993). During the past few thousand years, charcoal-accumulation rates in lakes in the region have been both higher and lower than rates in recent centuries, and there has been much variation (Mohr et al. 2000; Whitlock et al. 2003). In sum, extensive mixed-severity fires of variable frequency were likely instrumental in creating patchy landscape patterns and variable age-class distributions in this region for millennia. The importance of patchy landscape structure in maintaining species diversity has been demonstrated in studies of age mosaics created by stand-replacing fire (Baker 1992).

Such age mosaics have also demonstrated important temporal properties of fire regimes (e.g., Heinselman 1973, reviewed by Turner & Romme 1994), including the relative influence of climate and weather versus changes in vegetation combustibility in determining the occurrence and severity of fire (Turner et al. 2003; Moritz et al. 2004). We found evidence for important changes in combustibility over time because the probability of stand-replacing fire was lower in long-unburned forests. A number of factors may contribute to this pattern.

Whether a forest will experience surface or crown fire depends on the height of the tree canopy, the amount of available fuel it contains per unit volume, and rates of fire spread and surface heat output (Van Wagner 1977; Johnson 2003). Once crown-fire behavior begins, the frequency of spot-fire ignitions that coalesce with the main fire front may have a greater effect on fire behavior than fuel arrangement (Byram 1959). These ignitions are from embers cast ahead of the main fire (firebrands). Forest dynamics that could influence these factors in our study area include tree growth leading to increased levels of overstory shading. This would decrease waxy-leaved, combustible understory sclerophylls that are relatively shade-intolerant, such as chaparral shrubs and canyon live oak, in favor of species that tolerate shade well, such as tanoak and madrone (Minore 1979; Thornburgh 1982), which are not as receptive to combustion. In addition, shading decreases the leaf area of understory conifers (Waring & Schlesinger 1985); they may have relatively little high-energy foliar fuel per unit volume in their canopy. This is by far the most available aerial fuel in trees such as Douglas-fir (Fahnestock & Agee 1983). Understory temperatures are also reduced by shading, which can lower fire severity (Countryman 1955). Thus, the biological and physical effects of shading may lead to a reduction in surface-heat output during fire and, likely, in the production of firebrands. Average canopy height for mature trees may also be increased.

Because of such dynamics, in many regions of the world the long absence of fire causes vegetation that is relatively receptive to combustion to develop into vegetation that is not (Bond & van Wilgen 1996). In Tasmania, relatively long fire-return intervals (100+ years) result in the replacement of combustible vegetation with tall, open forests with a subcanopy of sclerophyll hardwoods, which are considerably less prone to combustion (Jackson 1968). These dynamics lead to alternative stable states that can be maintained by fire (Bond & van Wilgen 1996). The dynamics are similar to stand development in the structurally similar, moist temperate Douglas-fir–hardwood forests of our study area, as described by Stuart et al. (1993) and Wills and Stuart (1994).

The much greater fire severity we found in early successional, nonforest vegetation will tend to favor the persistence of this vegetation. In the long absence of stand-replacing fire, however, it is replaced by forests (Wills & Stuart 1994). Multi-aged, closed forests become less combustible with time since fire, and therefore become more likely to persist when fire does occur following a long fire-free interval. Temporal heterogeneity in fire, like its spatial counterpart, appears to be important to the maintenance of both successional types and a naturally patchy landscape structure in our study area.

Even-aged plantations are a patch type that can persist regardless of fire frequency. Plantations of any age are more receptive to combustion than co-occurring forests in our study area. Because plantations are often established following high-severity fire, a self-reinforcing relationship is possible (Perry 1995). An ecological analog may exist where exotic species invade and become abundant through positive feedback with fire (Mack & D'Antonio 1998). Plantations in our study area have grown to cover about one-third of the roaded area burned in 1987, increasing the likelihood of future positive feedback effects. In concert with climate change (McKenzie et al. 2004), these landscape dynamics provide reason to expect the trend of increasing fire size (Fig. 1) to continue, especially in roaded areas.

Weather conditions often override the sensitivity of a fire regime to internally regulated biomass processes operating over time. This has been demonstrated in empirical studies (e.g., Moritz 2003), through analysis of standard equations for predicting fire spread (Bessie & Johnson 1995), and in simulation modeling (Turner & Romme 1994). Extreme fire weather was previously invoked as the primary explanation for fire-severity patterns in the 1987 fires in the Klamath-Siskiyou region (Agee 1997), although strong local effects of plantations and logging were also observed (Weatherspoon & Skinner 1995).

Topography also influences fire behavior (Agee 1993), and, as with weather, we could not account for its effect. Further research in mixed-severity fire regimes is needed to answer questions about stand-age dependency and the role of fuel, weather, and topography. However, regardless of whether exogenous or endogenous forces were more important in determining the patterns we observed, time since fire was found to be an important predictor of lower fire severity, and this has implications for management.

Management Implications

Based on the empirical data we analyzed, the fuel-buildup model of dry, formerly open ponderosa pine forests does not apply to the natural forests of our study area. These findings further suggest that this model of fuel dynamics needs to be tested before it is exported to other forests (see also Gutsell et al. 2001; Johnson et al. 2001; Ehle & Baker 2003; Johnson 2003). This includes other ponderosa pine forests where heterogeneity in fire severity has been important (Shinneman & Baker 1997; Ehle & Baker 2003; Meyer & Pierce 2003).

In our study area, harvest treatments to reduce fire severity based on a model of fuel build-up in the absence of fire would be misdirected because long-unburned areas exhibited the lowest fire severity. Moreover, these treatments may be ecologically detrimental because stand-replacing or stand-thinning fire plays a key role in the regeneration of Douglas-fir and most other conifers and natural vegetation in our study area (Wills & Stuart 1994, Thornburgh 1995). Other elements of biodiversity may depend on these fire effects and the habitat heterogeneity that results. There are also more immediate biological consequences of harvest treatments—for example, to understory plants, soil organisms, and aquatic resources. The potential for these treatments to spread exotic forest diseases and plants also needs to be addressed.

Conversely, fuel treatments that reduce fire severity in portions of the landscape where human activities have increased available fuel will address the problem of unnaturally high fire severity. Not only have we found high fire severity in plantations, but, working in the same region, Key (2000) also found that plantations and adjacent vegetation burned more severely than natural forests (see also Weatherspoon & Skinner 1995).

Naturally ignited wildfires in the Klamath-Siskiyou region shape vegetation patterns that underlie biodiversity and are in alignment with the current climate. These fires are difficult for society to accommodate because they may burn for long periods, including when weather is extreme. Conservation objectives are affected by the need to protect people and property from such fires. In a detailed analysis of potential solutions to balancing the goals of human protection and conservation, modification of the edges of the built environment to slow or stop fire has been emphasized (Bradstock & Gill 2001). Treating the home-ignition zone as described by Cohen (2000) can almost eliminate the possibility of homes burning in wildfires. This would increase fire-management options and perhaps ultimately further conservation goals in the Klamath-Siskiyou ecoregion.

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Literature Cited

Agee, J. K., 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

Agee, J. K. 1997. Severe fire weather—too hot to handle? Northwest Science **71:**153–156.

Agee, J. K. 2002. The fallacy of passive management: managing for fire-safe forest reserves. Conservation Biology in Practice **3:**18–25.

Arno, S. F., and S. Allison-Bunnell. 2002. Flames in our forest: disaster or renewal? Island Press, Washington, D.C.

Baker, W. L. 1992. Effects of settlement and fire suppression on landscape structure. Ecology **73:**1879–1887.

Baker, W. L., and D. Ehle. 2001. Uncertainty in surface-fire history: the case of ponderosa pine forests in the western United States. Canadian Journal of Forest Research **31:**1205–1226.

Bessie, W. C., and E. A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. Ecology **76:**747–762.

Bond, W. J., and B. W. van Wilgen. 1996. Fire and plants. Chapman and Hall, London.

Bradstock, R. A., and A. M. Gill. 2001. Living with fire and biodiversity at the urban edge: in search of sustainable solutions to the human protection problem in Southern Australia. Journal of Mediterranean Ecology **2:**179–195.

Byram, G. M. 1959. Combustion of forest fuels. Pages 61–89 in K. P. Davis editor. forest fire; control and use. McGraw-Hill, New York.

Cohen, J. D. 2000. Preventing disaster: home ignitability in the Wildland-Urban Interface. Journal of Forestry **98:**15–21.

Connell, J. H. 1978. Diversity in tropical forests and coral reefs. Science. **199:**1302–1309.

Countryman, C. M. 1955. Old-growth conversion also converts fire climate. U.S. Forest Service Fire Control Notes **17:**15–19.

Covington, W. W. 2000. Helping western forests heal: the prognosis is poor for US forest ecosystems. Nature **408:**135–136.

Dale, V. H., S. Brown, R. A. Haeber, N. T. Hobbs, N. Huntly, R. J. Naiman, W. E. Riebsame, M. G. Turner, and T. J. Valone. 2000. Ecological principles and guidelines for managing the use of land. Ecological Applications **10:**639–670.

DellaSala, D. A., and E. J. Frost. 2001. An ecologically based strategy for fire and fuels management in national forest roadless areas. Fire Management Today **61:**12–23.

DellaSala, D. A., S. B. Reid, T. J. Frest, J. R. Strittholt and D. M. Olson. 1999. A global perspective on the biodiversity of the Klamath-Siskiyou ecoregion. Natural Areas Journal **19:**300–319.

Ehle, D. S., and W. L. Baker. 2003. Disturbance and stand dynamics in ponderosa pine forests in Rocky Mountain National Park, USA. Ecological Monographs **73:**543–566.

Fahnestock, G. R., and J. K. Agee. 1983. Biomass consumption and smoke production by prehistoric and modern forest fires in Western Washington. Journal of Forestry **81:**653–657.

Gutsell, S. L., E. A. Johnson, K. Miyanishi, J. E. Keeley, M. Dickinson, and S. R. J. Bridge. 2001. Correspondence. Nature **409:**977.

Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area. Quaternary Research **3:**329–382.

Huston, M. 1979. A general hypothesis of species diversity. The American Naturalist **113:**81–101.

Jackson, W. D. 1968. Fire, air, earth and water—an elemental ecology of Tasmania. Proceedings of the Ecological Society of Australia **3:**9–16.

Johnson, E. A. 2003. Towards a sounder fire ecology. Frontiers in Ecology and Environment **1:**271.

Johnson, E. A., Miyanishi, K., and S. R. J. Bridge. 2001. Wildfire regime in the boreal forest and the idea of suppression and fuel buildup. Conservation Biology **15:**1554–1557.

Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. van Tongeren. Data Analysis in Community and Landscape Ecology. Centre for Agricultural Publishing and Documentation (Pudoc), Wageningen, The Netherlands.

Key, J. 2000. Effects of clearcuts and site preparation on fire severity, Dillon Creek Fire 1994. M.S. thesis, Department of Forestry, Humboldt State University, Arcata, California.

Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution **13:**195–198.

McKenzie, D., Z. Gedalof, D. L. Peterson, and P. Mote. 2004. Climatic change, wildfire, and conservation. Conservation Biology **18:**890–902.

Meyer, G. A., and J. L. Pierce. 2003. Climatic controls on fire-induced sediment pulses in Yellowstone National Park and Central Idaho: a long-term perspective. Forest Ecology and Management **178:**89–104.

Minore, D. 1979. Comparative autecological characteristics of northwestern tree species: a literature review. General technical report PNW-87. U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station Portland, Oregon.

Mohr, J. A., C. Whitlock, and C. N. Skinner. 2000. Postglacial vegetation and fire history, eastern Klamath Mountains, California. The Holocene **10:**587–601.

Moritz, M. A. 2003. Spatio-temporal analysis of controls on shrubland fire regimes: age dependency and fire hazard. Ecology **84:**351–361.

Moritz, M A., J. E. Keeley, E. A. Johnson, and A. A. Schaffner. 2004. Testing a basic assumption of shrubland fire management: does the hazard of burning increase with the age of fuels? Frontiers in Ecology and Environment **2:**67–72.

Perry, D. A. 1994. Forest ecosystems. John Hopkins University Press, Baltimore, Maryland.

Perry, D. A. 1995. Self-organizing systems across scales. Trends in Ecology & Evolution. **10:**241–244.

Reider, D. A. 1988. California conflagration—recounting the siege of '87. Journal of Forestry **86:**5–8.

Shinneman, D. J., and W. L. Baker. 1997. Nonequilibrium dynamics between catastrophic disturbance and old-growth forests in ponderosa pine landscapes of the Black Hills. Conservation Biology **11:**1276–1288.

Stebbins, G. L., and J. Major. 1965. Endemism and speciation in the California flora. Ecological Monographs **35:**1–35.

Strittholt, J. R., and D. A. DellaSala. 2001. Importance of roadless areas in biodiversity conservation in forested ecosystems: A case study—Klamath-Siskiyou Ecoregion, U.S.A. Conservation Biology **15:**1742–1754.

Stuart, J. D., M. C. Grifantini, and L. Fox III. 1993. Early successional pathways following wildfire and subsequent silvicultural treatment in Douglas-fir/hardwood forests, NW California. Forest Science **39:**561–572.

Stuart, J. D., and L. A. Salazar. 2000. Fire history of white fir forests in the coastal mountains of northwestern California. Northwest Science **74:**280–285.

Swetnam, T. W., C. D. Allen, and J. L. Betancourt. 1999. Applied historical ecology: using the past to manage for the future. Ecological Applications **9:**1189–1206.

Taylor, A. H., and C. N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecology and Management **111:**285–301.

Taylor, A. H., and C. N. Skinner. 2003. Spatial and temporal patterns of historic fire regimes and forest structure as a reference for restoration of fire in the Klamath Mountains. Ecological Applications **13:**704–719.

Thornburgh, D. A. 1982. Succession in the mixed evergreen forests of northwestern California. Pages 87–91 in J. E. Means, editor, Forest succession and stand development research in the Northwest. Oregon State University, Forest Research Laboratory, Corvallis.

Thornburgh, D. A. 1995. The natural role of fire in the Marble Mountain Wilderness. Pages 273–274 in J. K. Brown, R. W. Mutch, C. W. Spoon, and R. H. Wakimoto, editors. Proceedings of the Symposium on fire in wilderness and park management. General technical report INT-GTR-320. U.S. Department of Agriculture Forest Service, Intermountain Research Station, Ogden, Utah.

Turner, M. G., and W. H. Romme. 1994. Landscape dynamics in crown fire ecosystems. Landscape Ecology **9:**59–77.

Turner, M. G., W. H. Romme, and D. B. Tinker. 2003. Surprises and lessons from the 1988 Yellowstone fires. Frontiers in Ecology and Envrironment **1:**351–358.

Van Wagner, C. E. 1977. Conditions for the start and spread of crownfire. Canadian Journal of Forest Research **7:**23–24.

Waring, R. H., and W. H. Schlesinger. 1985. Forest Ecosystems: concepts and management. Academic Press, Orlando, Florida.

Weatherspoon, C. P., and C. N. Skinner. 1995. An assessment of factors associated with damage to tree crowns from 1987 wildfires in northern California. Forest Science **41:**430–451.

Whittaker, R. H. 1961. Vegetation history of the Pacific coast states and the central significance of the Klamath region. Madroño **16:**5–23.

Whitlock, C., S. L. Shafer, J. Marlon. 2003. The role of vegetation change in shaping past and future fire regimes in the northwest U.S. and the implications for ecosystem Management. Forest Ecology and Management **178:**5–21.

Wills, R. D., and J. D. Stuart. 1994. Fire history and stand development of a Douglas-fir/hardwood forest in northern California. Northwest Science **68:**205–212.

World Conservation Union. 1994. IUCN red list categories. IUCN Species Survival Commission, Kew, United Kingdom.

Zar, J. H. 1999. Biostatistical analysis. Prentice Hall, Toronto, Canada.