

# Altered Fire Regimes Affect Landscape Patterns of Plant Succession in the Foothills and Mountains of Southern California

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## ABSTRACT

In the southern California foothills and mountains, pronounced and complex topographic gradients support fire regimes that vary over short distances. We used LANDIS, a spatially explicit landscape model of disturbance and plant succession, to examine the resilience of dominant plant species, representing different disturbance response strategies, to the effect of varying fire rotation intervals (FRI). The simulated fire regimes represented natural, current and very long FRIs for the foothill shrublands less than 1,400 m (90, 30 and 150 years) and montane forest greater than 1400 m (30, 150, 500 years). The 30-year FRI allowed obligate resprouting shrubs to dominate over obligate seeders, whereas the 90-year FRI resulted in a stable spatial distribution of both of these shrub functional types. This is consistent with the literature that suggests that shifts in shrubland composition are most likely to result from human-caused

increases in fire frequency at the low-elevation urban-wildland interface. An ecotone conifer, *Pinus coulteri*, showed dramatic shifts in distribution under different FRIs, and retreated to the portion of the landscape representing its temporal regeneration niche. Both low and high frequency fire maintained the fire tolerant dominant pine (*P. jeffreyi*) in the montane zone. This contradicts the literature that suggests that a high frequency ground fire regime is required for the persistence of a pine-dominated forest, but is consistent with studies showing that conifer forests in the western U.S. have experienced, and are resilient to, a broad range of natural FRIs that include low frequency, high intensity crown fires.

**Key words:** chaparral; ecotone; LANDIS; landscape simulation model; obligate seeder; pine forest; plant functional type.

## INTRODUCTION

An ecosystem's disturbance regime is defined by parameters describing the recurrence, location, and severity of natural disturbance such as fire, for example, size, return interval, intensity (Pickett

and White 1985; Turner and others 1989; Johnson 1992). When disturbance is infrequent, average parameters can be hard to define as the frequency of the disturbance is of the same order of magnitude as changes in the causal factors, such as decadal fluctuations and longer-term trends in climate, and human impacts (Zedler 1995a; Keeley and Fotheringham 2003). Simulation modeling provides a method for studying the effects of long-term

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processes at larger spatial scales (Mladenoff and Baker 1999).

In southern California, the plant communities comprise species that tolerate fire by various methods of resistance or resilience, or in some cases require fire for regeneration (Keeley 1986; Zedler 1995a). The shrublands that cover the greatest area in the foothills and remaining undeveloped coastal plain burn in stand-replacing fires (Keeley and Fotheringham 2001). Therefore, it is difficult to reconstruct fire histories and vegetation response using dendroecological methods (fire scars) that, when combined with palynological data, have proved so useful in forests. Charcoal and pollen in ocean basin sediment cores (Mensing and others 1999), as well as historical and ethnographic data (Lewis 1973; Keeley 2002), provide insights into long-term trends in the shrubland fire regime in southern California, but lack spatial detail. Fire perimeter mapping has only been carried out for the 20th century, while in contrast humans have affected the fire regime in this region in various ways throughout the Holocene (reviewed by Keeley and Fotheringham 2003).

The available data suggest that in the second half of the 20th century, the frequency of small fires increased in southern, coastal California, while their average size decreased (Keeley and others 1999; Moritz 2003). In San Diego County, for example, this has resulted in an increased rate of burning (area burned per decade) in coastal shrublands (the coastal sage scrub plant formation), although no trend could be detected for the chaparral formation of the foothills and mountains, more distant from urban development (Wells and others 2004). This pattern is consistent with a causal explanation of increased human-caused ignitions along the lower-elevation wildlands-urban interface (with suppression efforts keeping many of those fires small), contrasting with effective fire suppression in the upper-elevation montane forests (Keeley and Fotheringham 2003). Further, it appears that for at least 560 years (predating the Spanish period), large fire events in the region have been associated with extreme fire weather, and most of the land area burned is consumed in those large fires (Moritz 1997; Mensing and others 1999), most recently in 2003. It has also been suggested that 20th century fire suppression has caused fewer, larger, high-intensity fires in chaparral owing to fuel accumulation (Minnich 2001 and references therein), but the evidence for this has been refuted (Keeley and Fotheringham 2001; Moritz 2003).

Although most shrub species dominating the chaparral and coastal sage shrublands are resilient

to a wide range of fire return intervals (Keeley 1981, 1986), few are resistant to extremely frequent fires (much less than a decade between fires), as occur now near coastal urban areas, and those areas are at risk of losing endangered native shrublands (O'Leary 1990) as they are replaced by invasive exotic grasses and forbs (Mack and D'Antonio 1998; Keeley 2001). In contrast, there is concern that the montane conifer forests of southern California (Minnich 1988; Stephenson and Calcarone 1999), like other 'yellow-pine' and mixed conifer forests in the western US (Allen and others 2002), are suffering an increasing risk of catastrophic, stand replacing crown fires because 20th century fire suppression has allowed the establishment of shade-tolerant understory conifers as ladder fuels (but see Ehle and Baker 2003).

The purpose of this study was to predict the effects of varying fire rotation intervals (also called fire cycle, rotation period, or return interval), the average time required to burn an area equivalent to the study area (Johnson 1992; Johnson and Gutsell 1994), on the distribution and extent of dominant plant species in the southern California foothills and mountains. These species represent different functional types or disturbance response strategies (Pausas 1999; Pausas and Lavorel 2003; Pausas and others 2004). We were particularly interested in the predicted changes at the chaparral-forest ecotone, where species with different life forms, life history traits, and flammability, occur together. Ecotones can be sensitive indicators of synoptic environmental change (Holland and others 1991; Hansen and di Castri 1992). If the current southern California landscape were subjected to fire regimes with greatly differing rotation intervals, what changes would occur in the landscape distribution of those species that define the major plant communities in the region? Based on literature review and preliminary research (see Franklin and others 2001), we expected that a long rotation interval (a century or more) in the low elevation shrublands (foothills, below ~1,400 m) would favor those longer-lived species that can resprout following fire over those that must germinate from the seed bank but that are short-lived relative to the time between fires, for example, that would succumb to senescence risk (Zedler 1995a). However, it is relative abundance, rather than persistence of obligate seeders with long-lived seed banks that is likely to be negatively affected by longer rotation intervals (Keeley and Zedler 1978). Further, we expected that a long rotation interval in the upper elevation montane zone (above 1,400 m) would allow further fuel build-up and lead to high severity, stand-

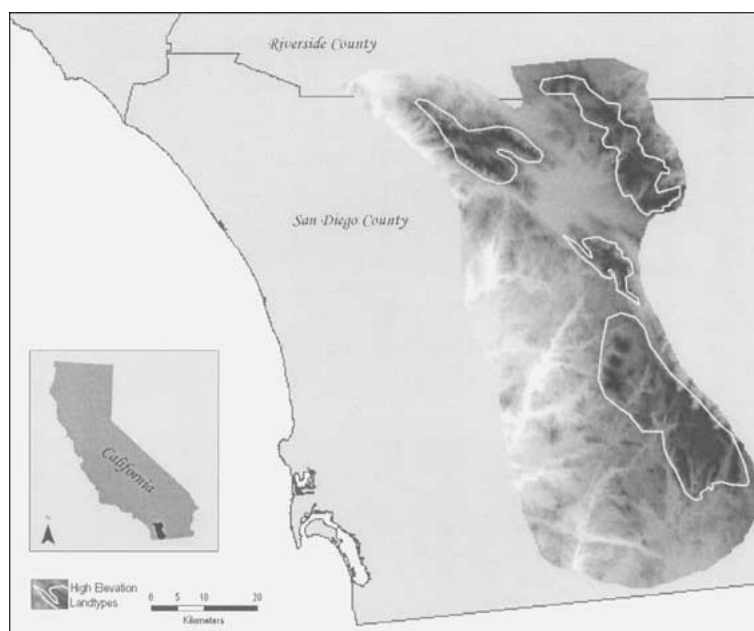


Figure 1. Study area, the foothills and mountains of the Peninsula Ranges primarily in San Diego County ( $\sim 3,880 \text{ km}^2$ ) showing elevation (157 to 1,981 m, darker tones are higher elevation) and delineating the low versus high elevation landtypes (white line).

replacing fire affecting ecotone species, fire-tolerant pines and shade-tolerant understory conifers. A spatially explicit landscape simulation model of disturbance regimes and plant succession allowed us to project topographically-varying fire regimes characterized by different rotation intervals onto the study region.

## METHODS AND MATERIALS

### Study Area

The study area (Figure 1), approximately  $3,900 \text{ km}^2$ , corresponded to the mountains and foothills ecological subsections of the Peninsular Ranges, primarily within San Diego County, California (Miles and Goudey 1997; Stephenson and Calcarone 1999). Elevations range from 157 to 1,981 m. The climate is Mediterranean with cool wet winters and warm to hot dry summers. Average annual precipitation ranges from 30 to 95 cm, mean minimum January temperature from  $-4$  to  $5^\circ\text{C}$ , and mean maximum July temperature from  $27$  to  $37^\circ\text{C}$  (Franklin 2003). On the ocean-facing (cismontane) slopes, semideciduous coastal sage scrub dominates lower elevation foothills (below  $\sim 1,000 \text{ m}$ ) with predominantly evergreen chaparral and oak woodland at middle elevations, and mixed conifer forest above  $1,400 \text{ m}$  in the montane zone. Great basin sage and grasslands are found in the interior. A more detailed description can be

found elsewhere (Stephenson and Calcarone 1999; Franklin 2003). The striking feature of this mountainous Mediterranean-type ecosystem is that the steep topography and maritime to continental climate gradient result in strongly patterned insolation, temperature and precipitation regimes, and therefore plant communities with differing physiognomy and correspondingly varying fire regimes, occur in close proximity on the landscape.

### The LANDIS Model

LANDIS (LANdscape DISTurbance and Succession) is a spatially explicit landscape model capable of simulating multiple disturbances and the resulting multiple pathways (Noble and Slatyer 1980) of forest succession (Mladenoff and others 1996; He and Mladenoff 1999b; Mladenoff and He 1999). In our study, only fire disturbance was simulated using LANDIS version 3.6. This raster-based model simulates the stochastically-driven interactions between disturbance regimes, site conditions and plant life history strategies over large spatial extents and time periods of centuries. The landscape is described by the species-age map, containing information about the presence of each modeled species in 10-year age classes, and therefore each cell can contain multiple species and age cohorts (He and others 1999a). The site conditions associated with each species' potential for establishment (Roberts 1996; He and others 1999b) and with

**Table 1.** Landtypes (proportion of the study area), and Simulated Rotation Interval (FRI, years) in the Three Fire Regime Treatments (10 replicates)

Landtype	Percent Area	Natural FRI	Current FRI	Long FRI
<i>Low elevation landtypes</i>				
LOWNORTH, Low elevation, cismontane, north/neutral aspect	11.4	64 ± 5 (90)	37 ± 2 (30)	221 ± 29 (150)
LOWSOUTH, Low elevation, cismontane, southwest aspect	8.1	51	23	152
MIDNORTH, Mid elevation, cismontane, north/neutral aspect	10.1	64	35	223
MIDSOUTH, Mid-upper elevation, south aspect	13.9	62	33	202
LOWINTN, Lower-mid elevation, interior, north/neutral aspect	13.1	78	51	292
LOWINTS, Low elevation, interior, south aspect	5.8	76	54	302
LOWRIP, Low elevation, riparian	1.9	93	98	1144
MIDRIP, Mid-elevation, riparian	2.8	94	95	801
LOWINTRIP, Low elevation, interior, riparian	2.6	92	93	896
<i>High elevation landtypes</i>				
HIGHNORTH, High elevation, north/neutral aspect	9.9	32 ± 3 (30)	108 ± 4 (150)	682 ± 132 (500)
HIGHSOUTH, High elevation, south aspect	20.2	35	111	687

Average simulated FRI and standard error (10 replicates) are also shown for low elevation (foothills) landtypes, and high elevation (montane) landtypes. Fire rotation treatments (target FRI) are shown in parentheses.

primary productivity (fuel dynamics) are generalized using a landtype map (Franklin 2003). Life history parameters (longevity, maturity, dispersal distance, ability to respout, relative shade and fire tolerance) are used to simulate dispersal, establishment, competition, persistence, and mortality of each modeled species in every cell (He and Mladenoff 1999a).

In LANDIS, fire ignition and spread are stochastic, but the probability is conditioned by the rotation interval specified for each landtype, and fire size is drawn from a log-normal distribution function. Fire severity is determined by the time since the last fire (approximating fuel accumulation), and fire-induced mortality depends on species- and age-specific fire tolerance. Severity is represented as an ordinal variable (1–5), and fires of different severity classes are able to kill species cohorts of different age-dependent fire tolerance classes, also represented as an ordinal variable (1–5). Competition between species in a site is driven by broad ordinal categories of shade tolerance that are age-dependent, an approach also used in other models (for example, Pausas 2003). The model operates on a 10-year time step. A fire regime is simulated by specifying the targeted rotation interval for each landtype. The model is considered verified or calibrated if the difference between the specified and simulated rotation interval is minimal compared to the differences among rotations periods (treatments) that are being compared (He and Mladenoff 1999b), and has previously been calibrated for our study area using simplified input data (Franklin and others 2001). We made one change to the

standard version of LANDIS used by other research groups. To simulate fire-cued germination from a buried seed bank, the response that typifies the obligate seeders (discussed below), we modified the ‘grow’ and ‘fire’ subroutines. Obligate seeders that were present in a site and killed by fire were then given a seed bank from which germination could take place in that site for a specified number of decades.

## Input Data

A landscape model simulating processes such as disturbance and dispersal can be sensitive to the spatial resolution of the input data, and yet some explicit level of generalization is required in any ecological inquiry for theoretical (Levin 1992) as well as practical reasons (Davis and others 1991; He and Mladenoff 1999b). We have determined that simulated fire regime (rotation interval, area burned) is relatively insensitive to cell sizes between 90 and 210 m in our study area (Syphard and Franklin 2004), so we chose 180 m as the cell size for simulations (each grid cell represents an area of [180 × 180] m). A landtype map was developed from digital climate and topographic maps (Franklin 2003) using methods similar to Host and others (1996). Eleven landtypes (Table 1) were defined to capture the terrain-related variations in the temperature and moisture regimes (Keeley 2000) affecting potential species distributions (Appendix A.1, see online material at [www.springerlink.com](http://www.springerlink.com)) and fuel characteristics (Appendix A.2, see online material at [www.springerlink.com](http://www.springerlink.com)).

**Table 2.** Life History Attributes and Functional Type of Focal Species

Functional type	Species, Sources	Longevity		Maturity		Shade	Fire	Dispersal		Age
		(y)	(y)	(m)*	(m)			Max. Dispersal (m)	Resprout	
Obligate Seeder	<i>Arctostaphylos glauca</i> (a, b, c, d, e)	90	20	3	2	60	1000	0	0	
Obligate Seeder	<i>Ceanothus greggii</i> ssp. <i>perplexans</i> (a, b, c, e, i, j, k)	60	20	3	2	60	300	0	0	
Obligate Resprouter	<i>Cercocarpus betuloides</i> (b, c, f, h, j)	130	20	4	4	60	100	0.90	10	
Obligate Resprouter	<i>Quercus berberidifolia</i> (b, c, f, j, l)	120	40	4	4	60	1000	0.90	0	
Obligate Resprouter	<i>Arctostaphylos glandulosa</i> (a, b, c, d, e, f, g)	110	20	4	4	60	4000	0.85	10	
Ecotone Seeder	<i>Pinus coulteri</i> (f, m, n, o, v)	150	20	4	3	60	100	0	0	
Ecotone Fire, Shade Tolerant	<i>Pseudotsuga macrocarpa</i> (c, p, q)	500	50	5	5	60	200	0.80	50	
Fire Tolerant	<i>Pinus jeffreyi</i> (h, o, n, r, s)	400	20	4	5	60	750	0	0	
Shade Tolerant	<i>Abies concolor</i> (c, n, o, t)	300	50	5	3	60	100	0	0	
Shade Tolerant	<i>Calocedrus decurrens</i> (c, h, n, u)	450	50	5	4	60	100	0	0	

\*Dispersal (effective dispersal distance) set to 60 m if actual value from literature was less than that (as was the case for all of these species) because this distance of 1/3 cell length was required in LANDIS v 3.6 in order to have dispersal to adjacent cells (see text). Sources: a) Keeley 1977; b) Keeley and Keeley 1986; c) Keeley 1981; d) Keeley and Zedler 1978; e) Parker and Kelly 1989; f) Hanes 1971; g) Vogl and Schorr 1972; h) Prescribed Fire and Fire Effects Research Work Unit Rocky Mountain Research Station (FEIS) 1996; i) Zedler and Zammit 1989; j) Zedler 1995b; k) Zammit and Zedler 1992; l) Keeley 1992b; m) Mirmich 1991; o) Keeley and Zedler 1998; p) McDonald 1990; q) Bolton and Vogl 1969; r) Jenkinson 1990; s) Vander Wall 1992; t) Laacke 1990; u) Sawyer and Thornburgh 1988; v) Wells 2001.

Twenty seven species were included in the simulations. Because neither species distribution maps (for example, Wolter and others 1995), nor detailed vegetation inventory data (for example, He and others 1998) were available, species distributions were derived from a map of generalized vegetation types compiled for the study area (Stephenson and Calcarone 1999; Franklin and others 2000) combined with predicted distribution maps for eight of the most widespread chaparral shrubs. The resulting multiple species map closely matched validation data in the rank order of extent (constancy) of species, and the species co-occurrence patterns (Franklin 2002), and we assumed that these data adequately represented the current distribution of the dominant plant species for the purpose of long-term simulation.

Values for the species attributes were derived from the literature, (Appendix A.3, see online material at www.springerlink.com), and are shown for ten diagnostic species in six functional types (Table 2). The functional type classification developed for the study area (Franklin and others 2001) allowed us to select this subset of species to analyze the effect of fire rotation interval on persistence, dispersal, establishment and changing distributions. The plant functional types characterizing the foothills shrublands include obligate seeders and obligate resprouters. Obligate seeders germinate through fire-cued stimulation of long-lived seed banks while resprouters regenerate vegetatively following fire by sprouting from basal burls or lignotubers and tend to have short-lived seeds (Wells 1969; Mooney 1977; Keeley 1981, 1992a, 1992b; Zedler and Zammit 1989; Zedler 1995b). Two species of obligate seeders and three obligate resprouters, differing somewhat in their longevity and dispersal distance (Table 2), were selected to represent these functional types. They are widespread in the study area, occurring in many chaparral associations (Gordon and White 1994) where their average cover in mixed stands is roughly 10–50% (Gordon and White 1994; Franklin and others 2004). The important and ubiquitous facultative resprouter, *Adenostoma fasciculatum*, was included in the simulations, (Appendix A.1, see online material at www.springerlink.com), but because its ability to resprout and seed makes it robust to a wide range of simulated fire regimes (Franklin and others 2001), it was not used as a diagnostic species in this study.

The ecotone seeder, *Pinus coulteri*, is a relatively short-lived (but late maturing) pine that is not fire resistant (thin-barked and tends to be killed by fire) and that occupies the transition zone between chaparral and conifer forest. It has variable cone

serotiny (retention of seeds in closed cones until exposed to fire) with higher levels of seed retention in trees occurring in chaparral (Table 2). We simulated this by giving the species a 10-year (one time step) seed bank (cone serotiny is functionally equivalent to obligate seeding from an above ground seed bank). *P. coulteri* was expected to be resilient to longer (50+ years) rather than shorter (<20 years) intervals between fires (Wells 2001). Another ecotone conifer, the southern California endemic *Pseudotsuga macrocarpa*, is long-lived, capable of resprouting and fire resistant when large (Table 2). It has been suggested that high intensity, stand-replacing fires in foothill shrublands have led to almost a 20% decline in the extent of this species in some areas over the last 75 years (Minnich 1999). The dominant fire-resistant, long-lived pine found in the montane conifer zone is *Pinus jeffreyi*, while two common shade-tolerant conifers, differing in their longevity and fire tolerance (Table 2), have increased in extent and cover during the historic period of fire suppression (Minnich and others 1995; Stephenson and Calcarone 1999).

It should be noted that the minimum distance used for dispersal in these simulations (Table 2, Appendix A.3, see online material at [www.springerlink.com](http://www.springerlink.com)) was fixed at 60 m. This was required by the DISPERSAL subroutine in LANDIS version 3.6 in order to allow seed dispersal to an adjacent cell with 180-m resolution. The model was designed for ecosystems with many wind- and animal-dispersed species (dispersal distances  $\gg$  cell size), but in southern California shrublands, many species are gravity-dispersed with estimated dispersal distances of only a few meters (see Table 2 references). Subsequent versions of LANDIS will allow distance-dependent dispersal to adjacent cells of any resolution using biologically realistic dispersal values.

### Fire Regime Modeling Experiment

We calculated an 83-year average rotation interval for our chaparral-dominated (66% of the land area, Franklin 2003) study area from 20th century fire perimeter data. This corresponds roughly to an area-weighted average of the 60–70 year rotation intervals others have calculated for chaparral (Minnich and Chou 1997; Moritz 2003), 30–40 years when low elevation coastal shrublands are included (Keeley and others 1999), and 700 years for the limited area of montane mixed conifer forest subjected to effective fire suppression (Minnich and others 1995; Stephenson and Calcarone 1999). Three fire regime treatments (Table 1) were devel-

oped. The ‘natural’ treatment represented our assumption that an average rotation interval ranging from 50 to 100 years in the interior to coastal foothill shrublands, and 30 years in montane forests (low intensity ground fires, McBride and Laven 1976; Minnich and others 1995), is within the range of natural variability for the region. The ‘current’ treatment allowed the contemporary effects of increased fire frequency at low elevation (20–50 year) and effective suppression in the mountains (150 year) to play out over the course of the simulation. The ‘long’ treatment was used to define an endpoint—the conditions that would develop in the hypothetical case of very infrequent fire. Additional treatments representing all possible combinations of these rotation intervals on the landscape were also simulated, but their results were intermediate to those presented and are not shown.

First, the model was calibrated for the fire regime treatments in the foothills study area by varying the fire frequency and size parameters over several hundred replicated simulations (He and Mladenoff 1999b). Then, ten replicate runs (for example, Wear and others 1996; Pausas 2003; De Groot and others 2003) were performed per treatment using the final fire parameter values, and each simulation was run for 500 years (He and Mladenoff 1999a). Longer simulations (1,500 years) did not reveal any additional trends in the pattern or extent of fire or species (details not shown). Because the model tracks species’ age cohorts within cells, the results are evaluated by examining how the extent (number or proportion of cells occupied), persistence and location of species or functional types on the landscape vary with treatment (fire regime).

### RESULTS

The natural treatment imposed a short rotation interval (Table 1) on upper elevation landtypes that currently support a shade tolerant understory as a result of 20th century fire suppression. Therefore, a large proportion of that landtype burned (~12% of the study area) in high severity fire in one of the first time steps of each replicated simulation. Subsequent fires in the high elevation landtypes were low severity in the natural treatment. The current treatment imposed a short rotation interval on the low elevation landtypes, and so similarly, a large proportion of these landtypes burned early in the simulation (almost 30% of the study area), but also in subsequent decades (in order to achieve the short rotation interval). The proportion of the landscape that was burned in

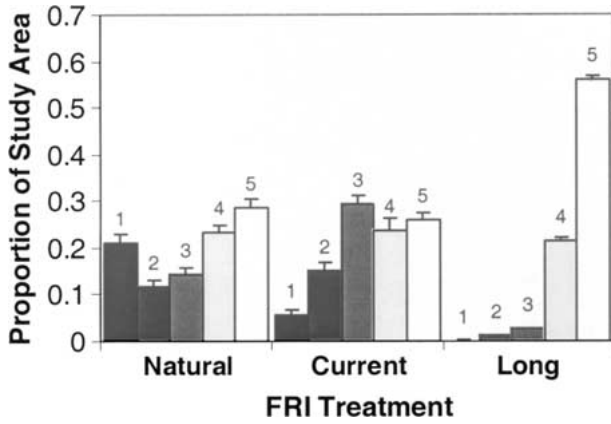


Figure 2. Proportion of landscape burned by fire severity class (1–5 in increasing order of severity) under three fire regime treatments (Table 1).

high severity fires increased as the fire rotation intervals increased among the treatments owing to fuel accumulation (Figure 2).

Differences in the landscape extent of all functional types (in the last time step) among the three replicated treatments were significant in most cases ( $P < 0.05$ ; Figure 3). The spatial extent of the obligate seeder functional type, comprising species restricted to low elevation landtypes (Appendix A.1, see online material at [www.springerlink.com](http://www.springerlink.com)), increased as rotation interval increased (Figures 3, 4). In other words, it succumbed to immaturity risk under the current treatment (short FRI), where it contracted in extent and persisted only at higher elevations (longer FRI, Table 1). The combined longevity of the adults (Table 2) and seed bank (50 years) was sufficient for persistence under rotation intervals of a century or more (natural, long treatments). In the current treatment the FRI of the lowest elevations was equal to the 20 years age at maturity parameter for the obligate seeders, and as a result this functional type was not able to persist there (succumbed to immaturity risk), but only at higher elevations (Figure 5).

The obligate resprouters increased in extent under the short FRI of the current treatment (Figure 4), especially at higher elevations (Figure 5) where they appeared to establish owing to the absence of the shade tolerant trees. Obligate resprouter extent was stable through time under the natural treatment, and lower under the long treatment (Figure 4) where this functional type established at low elevations (Figure 5), occurring there with obligate seeders and displacing short-lived subshrubs lacking seed banks (Appendix A.3, see online material at [www.springerlink.com](http://www.springerlink.com)).

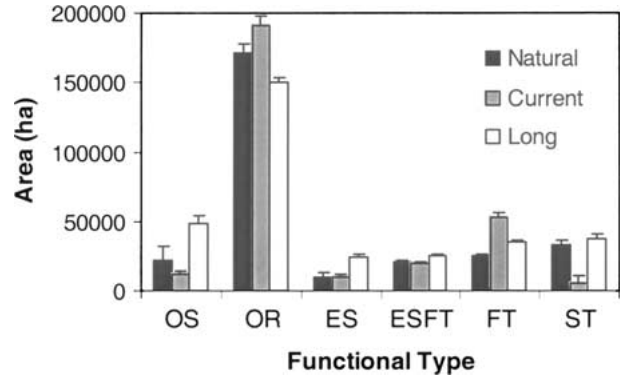


Figure 3. Mean area (extent) of functional type occurrence (in any age cohort) at the end of 10 replicates of a 500 year model simulation (standard errors shown) for the six functional types described in Table 2. OS, obligate seeder; OR, obligate resprouter; ES, ecotone seeder; ESFT, ecotone shade and fire tolerant; FT, fire tolerant; ST, shade tolerant.

The ecotone seeder, *P. coulteri*, showed the greatest extent (Figures 3, 4), occurring at high and low elevations (Figure 6) with longer rotation intervals (long treatment). Under the current treatment it declined drastically in response to frequent high intensity fire in the low elevation landtypes, and persisted only in the high elevation landtypes (Figure 6) with their longer FRI. Under the natural treatment it also declined initially in response to high intensity fire at high elevations, and then persisted at the ecotone between high and low elevation landtypes (Figure 6). The shade and fire tolerant long-lived conifer, *P. macrocarpa*, expanded (Figure 4) in the high elevation landtypes (Figure 6) under all simulated fire regimes. The long treatment, with infrequent but high severity fires, did not limit the occurrence of this species.

The fire tolerant conifer, *P. jeffreyi*, initially declined in response to high intensity fire at high elevations under the natural treatment, but subsequently expanded under all three treatments (Figure 4). Its lesser extent under the natural treatment (Figure 3) resulted not only from the initial decline but also from competition with the shade tolerant functional type (Figure 7). There were periodic declines due to infrequent, high intensity fire under the long treatment, but this species was resilient to the longer rotation intervals simulated with current and long. It expanded under the current treatment in part due to lack of competition from the shade tolerant conifers in the southeast portion of the study area (Figure 7).

The shade tolerant conifers expanded under the long treatment, but also in the natural treatment (short FRI at high elevations; Figure 4). The mod-

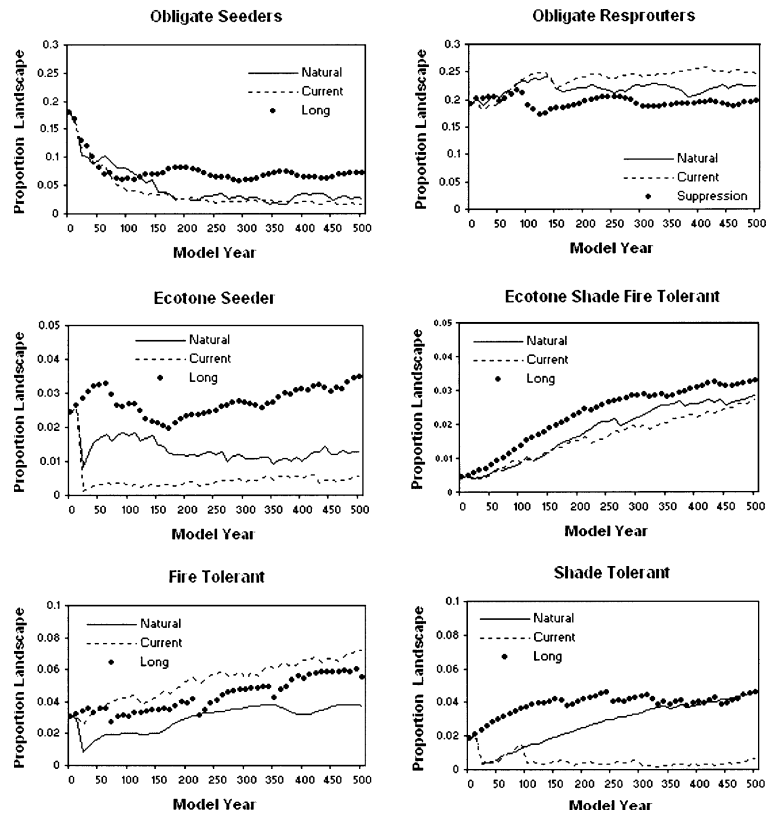


Figure 4. Proportion of the study area occupied (in any age cohort) by the six functional types (Table 2) in each time step of a single model run for the three fire regime treatments, Natural, Current and Long (Table 1).

erate fire tolerance of these species (Table 2) was sufficient to allow them to survive the low intensity fires occurring in the high elevation landtypes under this treatment. This functional type declined under the current treatment owing to extensive high intensity fire (resulting from fuel accumulation in high elevation landtypes) early in the model run, and never really recovered (Figure 7).

## DISCUSSION

We were able to use the LANDIS model to simulate fire regimes with rotation periods varying dramatically over short distances owing to the steep topographic gradient found in the study area (see also Franklin and others 2001). Although we did not expect that the FRIs in the current treatment would be sufficiently short for obligate seeders to succumb to immaturity risk in our simulations (Haidinger and Keeley 1993; Keeley and Swift 1995; Zedler 1995a), in fact they were. This supports the notion that the greatest threat to community structure in these shrublands is increasing fire frequency (Keeley and Fotheringham 2003) resulting from anthropogenic

ignitions. Obligate seeders with their long-lived fire-refractory seed bank remained on the landscape in our simulations even with low frequency (FRI 150–225 years), high severity fire in low elevation landtypes (Keeley 2000). Although the cover and density of short-lived obligate seeders (for example, *C. greggi* ssp. *perplexans*) declines with stand age (Zammit and Zedler 1992), this does not necessarily result in lower constancy or frequency among stands (for example, Franklin and others 2004), and it is the landscape extent or ‘presence’ of species age cohorts in sites that is simulated by LANDIS. It should be noted that obligate seeders declined under all treatments during the first 50 years, perhaps suggesting some generalization error in our spatial inputs (for example, the simulated decline could result from a mismatch between the actual and potential species distribution, the latter approximated by the landtype map).

Obligate resprouters were stable in their landscape extent under all treatments, showing resilience to a wide range of fire frequencies (Keeley and Zedler 1978; Keeley and Swift 1995), although significant differences were simulated. The spatially explicit LANDIS model showed that the obligate resprouters occurred at higher elevations to a

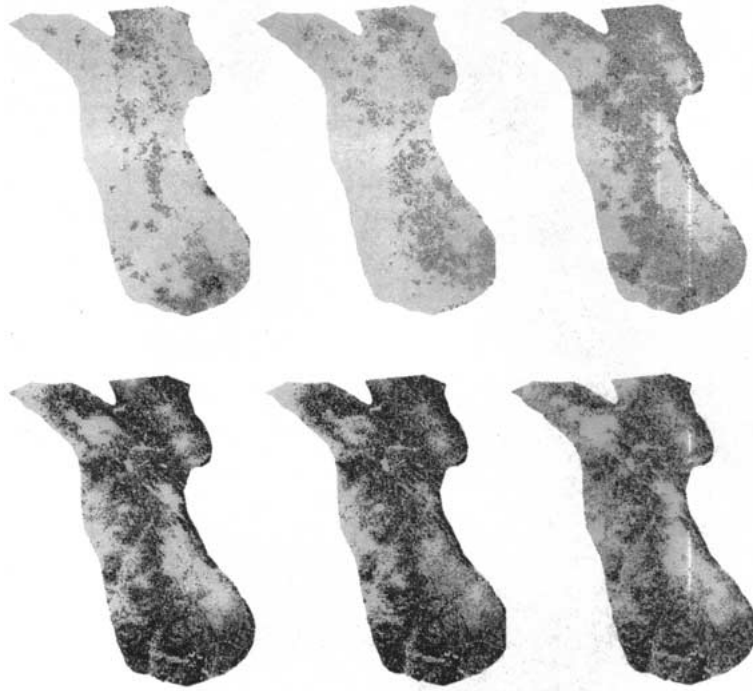


Figure 5. Map showing spatial persistence of the obligate seeder (*top row*), and the obligate resprouter (*bottom row*) functional types in each cell during the final 20 decades of a single model run for the three fire regime treatments, Natural (*left*), Current (*middle*), and Long (*right*; Table 1). Darker tones show that the species were present more often during the simulation.

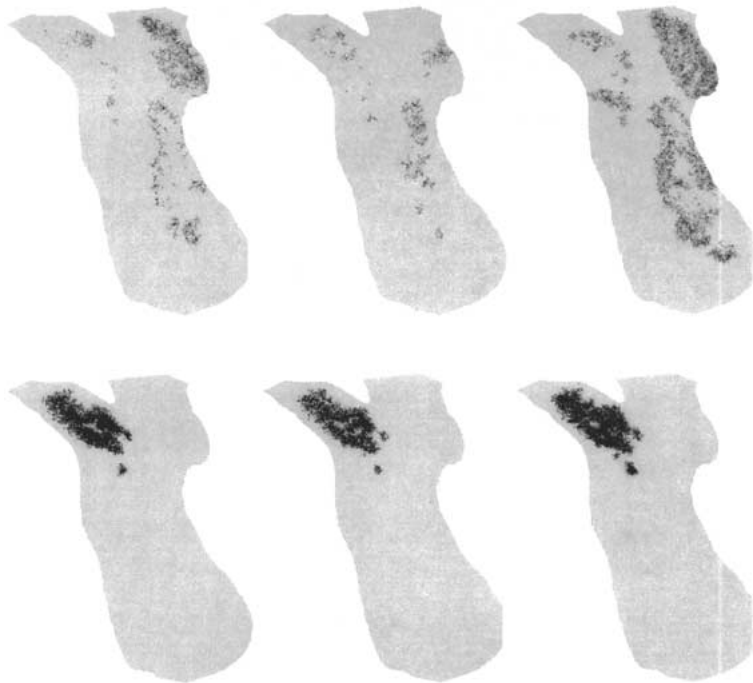


Figure 6. Map showing spatial persistence of the ecotone seeder *Pinus coulteri* (*top row*) and ecotone shade and fire tolerant *Pseudotsuga macrocarpa* (*bottom row*) in each cell during the final 20 decades of a single model run for the three fire regime treatments, Natural (*left*), Current (*middle*), and Long (*right*; Table 1). See caption, Figure 5.

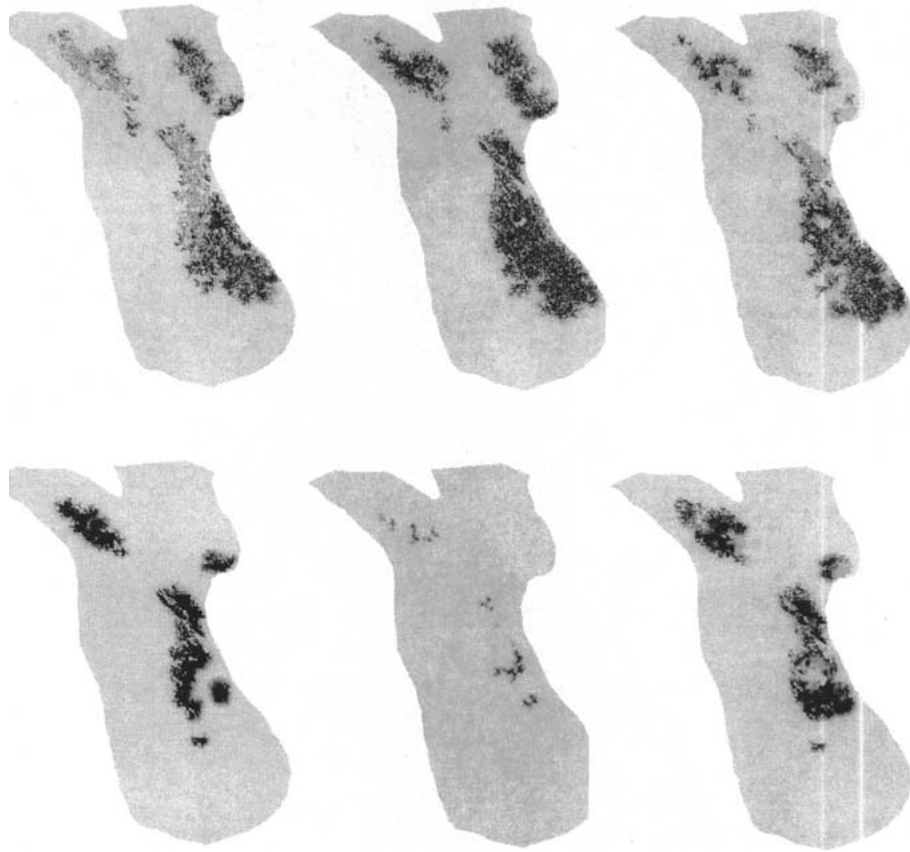


Figure 7. Map showing spatial persistence of the upper elevation fire tolerant *Pinus jeffreyi* (top row) and shade tolerant understory conifers (bottom row) in each cell during the final 20 decades of a single model run for the three fire regime treatments, Natural (left), Current (middle), and Long (right; Table 1). See caption, Figure 5.

greater extent under the current treatment (owing to the decline of shade tolerant understory trees there). Under the long treatment, they moved to lower elevations where they outcompeted short-lived shrubs, facilitated by the longer FRI, but occurred less frequently at middle elevations owing to competition from obligate seeders.

*Pinus coulteri*, showed greatest resilience to longer FRIs. It virtually disappeared from lower elevation landtypes when FRI was very short there (current treatment), and persisted mainly at the ecotone (its contemporary distribution) when FRI was long in the foothills and short in the mountains (natural treatment). This is consistent with the predictions of Wells (2001). *P. macrocarpa* behaved as a super competitor in the simulations. This is not surprising given that it was parameterized as being long lived, fire resistant, shade tolerant, and resprouting, consistent with the literature on its life history traits. The simulated species did not decline as a result of high-intensity fires resulting from long FRIs (as suggested by Minnich 1999).

The predicted effect of FRI on fire- and shade-tolerant conifers in the montane zone was also somewhat unexpected. The longer high elevation FRIs under the current and long treatments (100–700 years), intended to simulate the effect of fire suppression, led to periodic small declines in the extent of *P. jeffreyi*, but it continued to expand in a range of age classes (details not shown). This occurred because the species is long lived, fire tolerant when mature, and was modeled as being moderately shade tolerant. Lower shade tolerance may have produced a greater impact from fire suppression, but this species, while light-requiring, can regenerate in small gaps (Jenkinson 1990). Again, because this model tracks the presence of cohorts in cells (not their abundance), lowering the shade tolerance would have the undesirable effect of requiring stand-replacing fire for this species to regenerate.

*P. jeffreyi* did show some effect of release from competition with the shade-tolerant conifers in that it occurred over the greatest extent in the

treatment where the shade tolerant species declined—but this was in the current treatment, not the natural treatment where it was expected to occur. A limitation of our input data (the species-age map) may have caused us to overestimate the success of this species under long and short fire regimes. We did not have information on the spatial variability in age structure (for example, He and others 1998), but assumed, because conifer forest in the study area was of limited extent, and had not been subjected to fire or logging for a century, that giving the species the same initial age structure wherever it was found would not greatly affect the simulations beyond the first few decades.

Although shade tolerant conifers expanded under extremely long FRIs (~700 years), as expected, they were knocked back by the initial high intensity fire event that occurred in both the natural and current treatments, for example, resulting from fuel build up. When the current scenario (100 year FRI) was played out, however, the shade tolerant species never recovered because they were displaced by resprouting shrubs (in spite of the shrubs' lower establishment probabilities at high elevation, (Appendix A.1, see online material at [www.springerlink.com](http://www.springerlink.com)), as noted above. On the other hand, imposing a short FRI (natural treatment) did not prevent the shade tolerant conifers from persisting on the landscape because they are moderately fire tolerant when they are large. However, they occurred over a lesser extent of the landscape for over 300 years during which time *P. jeffreyi* expanded in extent.

## CONCLUSION

This type of landscape model paints with a broad brush in time and space the projected effects of disturbance regimes with varied parameters on plant community dynamics. The current treatment projected a short FRI on the shrubland-cloaked foothills and a long FRI in the montane mixed conifer forest into future centuries. This resulted in primarily moderate to high severity fire events throughout the simulation and allowed obligate resprouting shrubs to dominate over obligate seeders at mid elevation and spread to higher elevation. In contrast, the natural treatment comprised a longer FRI in the foothills and shorter FRI in the mountains, and resulted in a stable spatial distribution of both of these shrub functional types. These results did not support our expectation that a longer FRI would cause a decline in obligate seeders due to senescence risk over the range of FRIs simulated, but instead were consistent with the literature suggesting that shifts in

shrubland functional type composition are more likely to result from human-caused increases in fire frequency at the low-elevation urban-wildland interface as a result of immaturity risk.

We predicted that ecotone species would be sensitive to changes in the fire regime, and this was supported in the case of the partially serotinous *P. coulteri* that showed dramatic shifts in spatial distribution as well as extent under different FRIs. This species was most sensitive to the catastrophic fire events that were predicted to occur early in the simulations in the montane landtypes due to fuel build up under both the natural and current scenarios, and retreated to the portion of the landscape representing its temporal regeneration niche. Montane mixed conifer forest composition was largely determined by this first major fire event, with subsequent low frequency, high severity fires causing shade tolerant understory conifers to decline. Both low and high frequency fire allowed the recovery of the fire tolerant *P. jeffreyi*. This contradicts the literature that suggests that a high frequency, low intensity ground fire regime is required for the suppression of shade-tolerant understory species that act as ladder fuels, and the persistence of a pine-dominated forest. However, it is consistent with studies showing that 'yellow' pine and mixed conifer forests in the western U.S. have experienced, and are resilient to, a broad range of natural FRIs that vary in time and space and include low frequency, high intensity crown fires (for example, Baker and Ehle 2001; Ehle and Baker 2003). The 110,000-ha Cedar Fire (the largest in California's recorded fire history) that burned the study area in October 2003 is the first large fire event affecting the montane conifer zone following 100 years of fire suppression there. It offers an unprecedented opportunity to assess the modeled predictions, in particular regarding the spatial heterogeneity of species- and age-specific tree mortality and establishment.

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