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## Calibrating a forest landscape model to simulate frequent fire in Mediterranean-type shrublands

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### Abstract

In Mediterranean-type ecosystems (MTEs), fire disturbance influences the distribution of most plant communities, and altered fire regimes may be more important than climate factors in shaping future MTE vegetation dynamics. Models that simulate the high-frequency fire and post-fire response strategies characteristic of these regions will be important tools for evaluating potential landscape change scenarios. However, few existing models have been designed to simulate these properties over long time frames and broad spatial scales. We refined a landscape disturbance and succession (LANDIS) model to operate on an annual time step and to simulate altered fire regimes in a southern California Mediterranean landscape. After developing a comprehensive set of spatial and non-spatial variables and parameters, we calibrated the model to simulate very high fire frequencies and evaluated the simulations under several parameter scenarios representing hypotheses about system dynamics. The goal was to ensure that observed model behavior would simulate the specified fire regime parameters, and that the predictions were reasonable based on current understanding of community dynamics in the region. After calibration, the two dominant plant functional types responded realistically to different fire regime scenarios. Therefore, this model offers a new alternative for simulating altered fire regimes in MTE landscapes. © 2007 Elsevier Ltd. All rights reserved.

**Keywords:** LANDIS; Mediterranean-type ecosystems; Southern California; Fire regime; Plant functional type; Calibration; Scenario analysis; Landscape model

### Software availability

Name of software: LANDIS v. 4.0A

Developer: Dr. Hong S. He

Contact address: School of Natural Resources, University of Missouri-Columbia, 203 ABNR Building, Columbia, MO 65211, USA

First release: July 1, 2004

Hardware and software requirements: It runs under Windows 2000/XP with at least 215 MB of memory. Successful runs on large models have been performed on computers with 512 MB to 1 GB RAM. However, 1 GB or more RAM is recommended

Program language: C++

Program size: 800 KB

Availability: It can be downloaded from the website: [www.missouri.edu/~landis](http://www.missouri.edu/~landis)

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### 1. Introduction

In Mediterranean-type ecosystems (MTEs), fire disturbance is a primary agent of change, shaping the distribution and

composition of most plant communities in these regions (Henkin et al., 1999). Although many plant species in MTEs are resilient to fire (Naveh, 1975), impacts on land cover condition and community dynamics may be extreme and/or irreversible if the disturbance regime exceeds its natural range of variability (Dale et al., 2000). The natural fire regimes in the world's MTEs have been altered through intensive and extensive land use change as well as intentional use and suppression of fire (Espelta et al., 2002; Pausas, 2003). The magnitude and direction of these changes vary from region to region; however, the impact of altered fire regimes may be more influential than climate factors in shaping future Mediterranean-type ecosystem dynamics (Noble and Gitay, 1996; Pausas, 1999).

In southern California, a typical MTE, population growth and urban development in low-elevation chaparral shrublands have increased ignitions to the point that they have increased fire frequency beyond the historic range of variability in some areas (Keeley et al., 1999). Biological invasion of non-native grasses also interact with the natural fire regime, creating feedbacks that further increase fire frequency (e.g., Haidinger and Keeley, 1993; Keeley, 2006). Although California chaparral is generally resilient to a range of fire frequencies (Zedler, 1995), successively short intervals between fires threaten the persistence of some species and habitat types (Zedler et al., 1983; Jacobsen et al., *in press*). The immediate post-fire response strategies of many chaparral plant species are well documented; however, little is understood about the long-term dynamics of shrubland ecosystems in the face of increasing urbanization, invasion of non-native grasses, and altered fire regimes (Zedler and Zammit, 1989).

Because anthropogenic disturbances and alteration of natural disturbances are expected to continue with rapid global change (Tilman and Lehman, 2001), computer simulation models have become effective tools for testing and generating hypotheses about ecological dynamics under various landscape change scenarios (Brown, 2006; Rudner et al., 2007). Due to the strong influence of wildfire on vegetation dynamics (Henkin et al., 1999) and the sensitivity of fire regimes to human-induced environmental change (Aber et al., 2001), landscape fire succession models have recently evolved as an important group of these simulation models (Keane et al., 2004). However, few of these landscape forest succession models can simulate the high fire recurrence and unique post-fire response strategies characteristic of MTE shrublands at long temporal and broad spatial scales (Pausas, 1999, 2003).

Malanson et al. (1992) developed a model for MTE shrublands in southern California to investigate succession as a function of climate and life history traits; however, this model did not account for differential impacts of varied fire regimes or resulting spatial patterns. The SIERRA model (Mouillot et al., 2001) was developed specifically for evaluating the relationship between fire regimes, vegetation dynamics, and landscape patterns characteristic of MTE shrublands. However, SIERRA is a process-based simulator, similar to forest gap models (Shugart, 1998), that requires detailed physiological parameters to simulate phenomena such as

photosynthesis, soil evaporation, and root water uptake. Pausas and Ramos (2006) recently developed a model, LASS, to be used specifically for fire regimes and plant species characteristic of MTEs at landscape scales. LASS is designed to simulate a wide range of landscape and disturbance scenarios with varying degrees of complexity.

Pausas and Ramos (2006) developed LASS because of problems involved with implementing existing landscape models to simulate MTE characteristics. They argued that one of the most well documented and widely used forest landscape models in recent years, LANDIS (Mladenoff and He, 1999), is hard to apply to MTEs “because fire responses and seed bank characteristics are not modeled, and because the time step (10 years) is not appropriate for simulating short-lived species, short-lived seed banks, and/or short fire intervals.”

Despite these concerns, we calibrated LANDIS for fire regimes and vegetation dynamics in the foothills and mountains of southern California in previous research (Franklin et al., 2001, 2005; Syphard and Franklin, 2004) because it can simulate long-term, broad-scale effects of varying fire rotation intervals on plant species composition and distribution while maintaining reasonable mechanistic detail about fire and successional processes. We also modified the model to simulate fire-cued germination from a persistent seed bank (an important post-fire response strategy in MTEs). We were able to use LANDIS for the foothills and mountains landscape because the historical fire rotation intervals in that region (ranging from 30 to more than 500 years) exceeded the 10-year time step of the model. However, in the lower-elevation shrublands in other parts of southern CA and other MTEs, fire rotation intervals and other temporal processes are frequently shorter than 10 years.

The purpose of this research was to further refine the LANDIS model to operate on an annual time step and to calibrate it for a southern California landscape that experiences fire rotation intervals as low as 5 years. The specific objectives were: to develop a comprehensive set of spatial and non-spatial variables and parameters for a region that experiences very high fire frequency; to calibrate the model using the standard LANDIS calibration approach (Mladenoff and He, 1999; Franklin et al., 2001); and to conduct a scenario analysis to evaluate how the model responded to alternate parameter combinations reflecting hypotheses of system dynamics. The goal was to ensure that observed model behavior would simulate the fire regime characteristic of the region, and that the predictions were reasonable based on current understanding of community dynamics in the region. Modifications to LANDIS offer a new alternative for modeling potential long-term effects of altered fire regimes on the distribution and composition of vegetation in MTE landscapes.

## 2. Methods

### 2.1. Study area

The Santa Monica Mountain National Recreation Area (hereafter referred to as Santa Monica Mountains) is an administrative unit that protects the

largest expanse of mainland Mediterranean ecosystem in the USA's national park system (NPS, 2005) and encompasses approximately 60,000 ha of land adjacent to the Pacific Ocean and the Los Angeles, CA metropolitan area (Fig. 1). The mountains are a rugged east–west trending range with a Mediterranean climate, characterized by cool, wet winters and warm, dry summers. Although there is tremendous floristic diversity in the region, much of the vegetation is physiognomically similar, falling primarily into two types of shrubland, chaparral (approximately 60% of the landscape) and coastal sage scrub (25%) (Radtke et al., 1982; Dale, 2000). Chaparral shrublands are quite flammable due to low decomposition rates, high dead-to-live fuel ratios, dense community structure, and low fuel moisture (Countryman and Philpot, 1970; Conard and Regelbrugge, 1994; Keeley and Fotheringham, 2003).

In the Santa Monica Mountains, fire frequency and total area burned has steadily increased over the last 75 years (NPS, 2005). The majority of fire ignitions in the region are human-caused, and some areas have burned up to 10 times over the last century. Although the majority of the fires in the region are small (less than 50 ha), the largest fires (more than 15,000 ha) account for most of the total area burned (NPS, 2005). The bulk of the landscape burns in the autumn after the summer dry season and during extreme fire weather fanned by hot, dry Santa Ana winds. Because fire cannot be effectively controlled during these high-wind conditions (Radtke et al., 1982), chaparral typically burns in large, stand-replacing, high-intensity fires that explode across the landscape (Keeley and Fotheringham, 2003).

## 2.2. The LANDIS model

The LANDIS model has been described extensively in the literature and was recently the focus of a special issue of Ecological Modelling (Volume 180, 2004). LANDIS is a raster-based, spatially explicit model that simulates forest landscape dynamics, including stochastically driven interactions between fire regimes, plant life history behaviors, and site conditions (He et al., 1999). Species-level successional dynamics can be simulated for large, heterogeneous landscapes over long time periods.

Each cell on the simulated landscape is a spatial object that tracks the presence or absence of age cohorts of individual plant species. Multiple plant species and age cohorts may be present within one cell. LANDIS enables ecological processes to occur at the scale of individual cells (including seedling establishment, birth, death, growth, vegetative reproduction, random age-dependent mortality, and inter-species competition) and at a landscape scale (including seed dispersal and fire disturbance). The probability of successful dispersal and establishment depends upon available propagules as well as current plant species composition (e.g., shade characteristics) of neighboring cells within the radius of specified dispersal distances for each plant species.

Fire is spatially explicit with contagious spread and higher probabilities of spread to neighboring cells with longer time since last fire (greater fuel load).

Fire severity increases with time since last fire and this function varies on the landscape. Younger age cohorts and species with lower fire tolerances are more likely to be consumed even by moderate severity fire. Ignition is stochastic, but occurs with increased probability with the time since last fire. Fire size is also stochastic, but small fires are more likely to occur than large fires, following a lognormal distribution, and the mean fire size is specified in the input parameters. More than one fire is allowed to occur within one time step.

Although most of the core algorithms of LANDIS Version 3.6 remained the same for this research, LANDIS 4.0A included several modifications in addition to an annual time step. LANDIS 4.0A is the annual time step version of LANDIS 4.0, which is a component-based program that breaks the monolithic program into multiple dynamically linked libraries (DLLs) that each have a standard interface and can simulate distinct processes such as succession, wind, and fire (He et al., 2002, 2005). The realism of fire disturbance simulation in LANDIS 4.0A has been greatly improved by using the hierarchical fire frequency model, which can simulate a wide range of fire regimes across heterogeneous landscapes with fewer parameters and a more moderate amount of input data (Yang et al., 2004). Moreover, landscape heterogeneity can now be stratified both through the landtype (or ecoregion) map and through individual disturbance regime maps that can be used as input. LANDIS 4.0A also includes an option to update the landtype maps, the disturbance regime maps, and/or the fire regime characteristics over time to meet the need of simulating the effects of climate change and human development on forest landscape change. Finally, LANDIS 4.0A can simulate a long-lived persistent seed bank that recruits after fire even if there are no species present on the site.

## 2.3. LANDIS input and parameters

### 2.3.1. Landtype map

The LANDIS landtype map stratifies the landscape into areas with uniform species establishment probabilities, rates of fuel accumulation, and fire regime characteristics. To create the map for the Santa Monica Mountains, we employed an unsupervised clustering approach using ISODATA (Ball and Hall, 1965) to classify five environmental variables (as in Franklin, 2003) (Table 1). These environmental variables were selected based on the primary factors known to affect plant distributions and productivity in the region – local climate and topographically mediated soil moisture availability (Franklin, 1995; Franklin et al., 2000). We normalized the variables to ensure that they would be equally weighted in the clustering, and then generated 20 classes using the Euclidean distance measure. Through an analysis of the environmental characteristics and spatial distribution of the classes, we merged them into seven landtypes and then overlaid these landtypes over maps of urban and other non-vegetated land (Fig. 2).

### 2.3.2. Species age map

LANDIS requires a map of species' presence by age class to establish initial distributions for the species included in the simulations (e.g., Wolter et al., 1995; He et al., 1998; Franklin, 2002). For the Santa Monica Mountains, the primary data source available to determine species distributions was a digital map of the Weislander Vegetation Type Maps (VTM) from the 1930s (Weislander, 1935) that provided detailed, species-level information for mapped vegetation stands that existed at that time based on extensive field surveys. Because no extensive changes have occurred in southern CA chaparral vegetation types since the VTM maps were developed (Bradbury, 1974; Franklin et al., 2004), we assumed that the maps represented plausible distributions of the species. For a small portion of the study area (8% of the landscape) not covered by the VTM maps, we used a contemporary, but less detailed, map of vegetation types that was developed using classification of remotely sensed imagery (Landsat TM) (Franklin et al., 1997).

For all species in the simulations (described below), we generated binary GIS maps of their distribution and overlaid them, producing 220 map classes with different combinations of species. We then used a hierarchical, agglomerative cluster analysis with PC-ORD Software (McCune and Mefford, 1999) to group the map classes into 24 vegetation types. The species assemblages comprising these vegetation types were compared to a classification of California vegetation (Sawyer and Keeler-Wolf, 1995) to ensure that the co-occurrence of these species realistically occurred in the field. Because fires

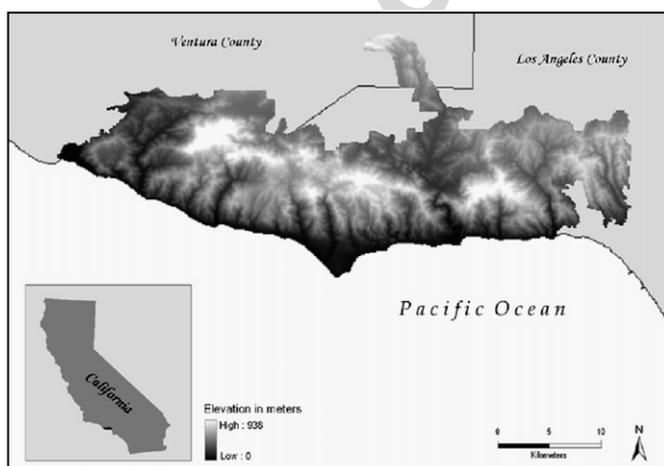


Fig. 1. The Santa Monica Mountains in southern California.

Table 1  
Variables used to create landtype classes in the SMMNRA

Variable	Resolution	Source, description	Range
Annual precipitation	1 km <sup>2</sup>	J. Michaelson, interpolated by kriging (see Franklin, 1998)	330.1 to 623.4 mm
January minimum temperature	1 km <sup>2</sup>	J. Michaelson, interpolated by kriging (see Franklin, 1998)	3.76 to 8.6 °C
July maximum temperature	1 km <sup>2</sup>	J. Michaelson, interpolated by kriging (see Franklin, 1998)	22.6 to 28.0 °C
Elevation <sup>a</sup>	100 m <sup>2</sup>	USGS Digital Elevation Model	106 to 948 m
Slope gradient	100 m <sup>2</sup>	Derived from DEM by first order finite difference	0 to 73°
Southwestness	100 m <sup>2</sup>	Transformed aspect derived from DEM, indicates potential solar radiation	0 (southwest) to 201 (northeast)

<sup>a</sup> Elevation was not used in the clustering due to its strong correlation with slope gradient and southwestness.

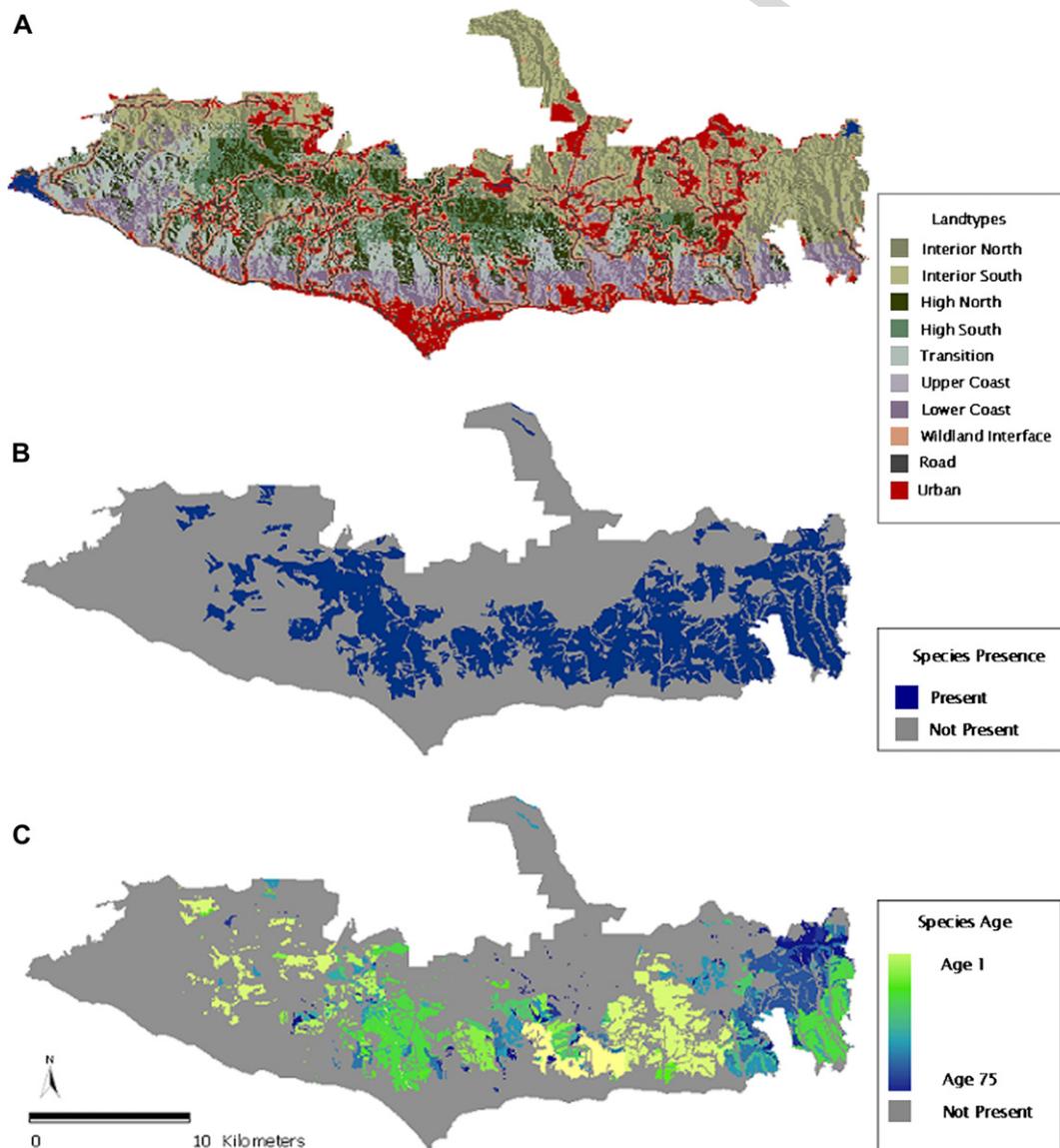


Fig. 2. LANDIS spatial inputs, including map of seven landtypes overlaid with roads, urban areas, and wildland urban interface (A); and distribution of *Ceanothus megacarpus* before (B) and after (C) classification into species-age classes for the LANDIS model.

are stand-replacing in California chaparral, we overlaid a fire history GIS map (J. Woods, unpublished data, 2004) on the map of vegetation classes to determine the age of the vegetation. We compared species distributions in our final species-age map to the original distributions selected out of the VTM maps to ensure that the merging process maintained most of the original extent for all species, as illustrated in Fig. 2.

### 2.3.3. Classification into functional types

Although the LANDIS model tracks the dynamics of individual species' age cohorts in the simulations, the model output can be reclassified into collections of species vis-à-vis functional types. Functional type classification has been an effective way to simulate and analyze vegetation dynamics in disturbance-prone ecosystems (Pausas, 1999, 2003; Franklin et al., 2001; Rusch et al., 2003). Species belonging to the same functional types share similar adaptations and responses to disturbance, so analysis of these species as groups provides a framework for understanding the mechanisms driving vegetation responses (Pausas, 1999). The calibration of LANDIS in the Santa Monica Mountains focused primarily on the behavior of two functional types that best represent the dominant post-fire response strategies characteristic of the chaparral vegetation in the region: obligate seeders and obligate resprouters (described below), an approach that has been used elsewhere (e.g., Pausas, 2003). We grouped other species into the following functional vegetation types: coastal sage scrub (drought-deciduous, short-lived shrubs that cover many of the coastal slopes); facultative seeders (chaparral species that can resprout following fire and also produce refractory seeds that are cued by fire to germinate); oak woodlands; early successional subshrubs; and annual grass. Some of the species in these groupings have overlapping post-fire response strategies (e.g., resprouting); however, our classification reflected a large range of demographic and physiognomic characteristics that, when combined, distinguished one group from another.

### 2.3.4. Obligate seeders and resprouters

Obligate seeders (e.g., *Ceanothus megacarpus*) recruit from long-lived dormant seed banks that are cued by fire to germinate (Keeley, 1998). They are incapable of regenerating vegetatively and rarely recruit new individuals in fire-free intervals. Although their plant and seed longevity (combined) generally exceeds 100 years, these species are believed to be resilient to a smaller range of fire frequencies than obligate resprouters (it takes 5–25 years to build a seed bank, and they have shorter life spans) (Keeley, 1977; Zedler, 1995). Obligate resprouters (e.g., *Quercus berberidifolia*) do not recruit seedlings but persist on burned sites because they resprout. These species recover rapidly after fire and are long-lived (Keeley, 1986).

### 2.3.5. Species life history database

In LANDIS, species are parameterized based on life history traits related to disturbance response (e.g., Noble and Slatyer, 1980). Instead of simulating physiological processes of individual trees as in gap models, these species-specific life history characteristics enable succession to take multiple pathways while reducing the computational load and potential false precision involved with estimating more detailed information such as growth. The life history attributes parameterized for each species in the model include longevity, age of first reproduction, potential seed dispersal distance, ability to resprout, shade tolerance, and fire tolerance (to fires of varying severity).

Based on literature review and consultation with National Park Service scientists, we selected 19 species to include in the simulations (Table 2). When specific life history values were published, they were used as the model parameters. However, to avoid false precision, many of the parameters reflected qualified estimates and highlighted the relative differences between functional types (and species within those functional types). Although obligate resprouters become sexually mature at an early age, successful recruitment of new individuals usually does not occur until a full canopy has been developed following fire. Therefore, we forced this behavior to occur by setting the maturity parameter to 20 years. The maturity parameter for the obligate seeders was set to 10 years to reflect the approximate time it takes to establish

a seed bank that will recruit following fire, which ranges from 5 to 25 years (Keeley, 1986).

## 2.4. LANDIS calibration

The standard method for calibrating LANDIS is based on manual optimization in which a 'trial-and-error' approach is used to step through parameter ranges until the best fit is determined between model results and parameter values. The fire regime is specified by the mean fire rotation interval (FRI), which is defined as the time it takes to burn an area equivalent to the size of the area of analysis. Mean FRIs are determined by dividing the area of the landtype(s) by the mean area burned per time interval. Calibration is performed through systematic comparison of observed average FRIs to specified values. In previous versions of LANDIS (1.0–3.6), two fire calibration coefficients had to be specified to manipulate fire on the landscape. In LANDIS 4.0A, these scalars that related specified to simulated fire frequency and size are no longer used. Instead, fire size follows lognormal distribution defined by the mean fire size and its variance, and fire frequency is determined by the fire ignition coefficient, which specifies the average number of ignitions attempted per hectare (ha) for each landtype (Yang et al., 2004).

### 2.5. Calibrating LANDIS for the Santa Monica Mountains fire regime

The approach for calibrating LANDIS for the SMMNRA was to begin running simulations using the most ecologically valid parameter values according to empirical calculations, literature review, and parameters used in the previous southern California study. The first objective was to adjust the ignition coefficients systematically using this parameter set until the simulated FRIs approximated the FRIs specified for three fire regime treatments using a fixed random number seed (with long, medium, and short FRIs) (Table 3). We developed the fire regime treatments based on average FRIs calculated for the whole study area and for each landtype using fire history data in addition to average FRIs cited in the literature for the two counties in which the study area is located (Keeley et al., 1999). The average FRI for the "long" treatment (60 years) was designed to approximate the historic fire frequency that maintained species' abundance and persistence on the landscape. The "medium" and "short" treatments (30 and 15 years, respectively) were designed to mimic the increasingly shorter FRIs that have been observed during the last half of the century resulting from human ignitions. Because the fire size distribution is strongly skewed in the SMMNRA (NPS, 2005), the average fire size was specified to be 40 ha, with a variance of 20,000 ha.

### 2.6. Objectives for scenario analysis

After calibrating LANDIS to simulate the specified fire regimes in the three treatments, we designed several parameter scenarios to evaluate the response of obligate seeders and obligate resprouters to variations in fire frequency. All parameter scenarios represented reasonable approximations of system dynamics in the SMMNRA, but differed according to hypotheses of how well these parameter combinations would translate into realistic model behavior. Our expectations were based on evidence that, although much of the vegetation in the region has remained stable over the last century (e.g., Bradbury, 1974; Franklin et al., 2004), extremely high fire frequencies in some locations are beginning to threaten the persistence of certain functional types (Keeley, 1981; Zedler et al., 1983; Haidinger and Keeley, 1993). The objective of the scenario analysis was to identify the parameter combination that produced the most realistic behavior of these functional types.

Specifically, we expected that the predictions intended to simulate the historic fire regime (the long treatment) would result in vegetation composition similar to the current landscape, with little change in species abundance over time. At the increased fire frequencies of the medium and short treatments, we expected the obligate seeders to progressively decline because if fire recurred before there was enough time to build a seed bank, the species would be killed by fire and unable to germinate. Obligate resprouters were

Table 2  
Final species life history attributes and parameters used in LANDIS for seven functional groups

	Obligate resprouters	Obligate seeders	Coastal sage scrub	Facultative seeders	Annual grass	Oak woodland	Early successional
Number of species in group	6	2	6	2	1	1	1
Longevity (year)	150	75	50	100	1	250	10
Age of maturity (year)	20	10	2–3 <sup>a</sup>	15	1	40	1
Shade tolerance (ordinal class 1–5)	4	3	2	3–4 <sup>a</sup>	1	5	2
Fire tolerance (ordinal class 1–5)	4	3	2	3–4	1	5	2
Effective seed dispersal distance (m)	100	75	75	75	10,000	100	100
Maximum seed dispersal distance (m)	500	100	100	100	–1 <sup>b</sup>	500	500
Probability resprout (0–1)	0.80–1.0 <sup>a</sup>	0	0.25–0.75 <sup>a</sup>	0.70–0.80 <sup>a</sup>	0	0.50	0
Minimum age of resprouting (year)	3	0	4	3	0	3	0

<sup>a</sup> Indicates a range of values for the species within that functional group.

<sup>b</sup> A dispersal distance of –1 means the species can disperse to anywhere on the landscape.

expected to persist at higher fire frequencies due to their ability to resprout successfully following fire at early ages, although there have been some circumstances in which they also experienced mortality after repeated fires (e.g., Haidinger and Keeley, 1993).

We used an elimination process for the scenario analysis, so if a parameter scenario resulted in unrealistic species' response, it was eliminated. This evaluation continued until we identified parameter space that produced realistic functional type response to the fire frequencies in the three treatments. Using the final set of parameters, we replicated the simulations for all model treatments 10 times.

#### 2.6.1. Probability of establishment scenarios

We evaluated two scenarios based on establishment probabilities (Table 4). In one scenario, we based our assignment of species establishment probabilities solely on environmental preferences. In the other scenario, we lowered the probabilities of establishment for the obligate resprouters and increased those for the obligate seeders and coastal sage scrub species. The reason we created a gap in site advantages between the obligate resprouters and the other species was to reflect differences in recruitment success. Despite the higher shade tolerance of the obligate resprouters, their overall rate of successful seedling establishment is very low, even in long fire-free periods (Keeley, 1986).

#### 2.6.2. Fire tolerance scenarios

In previous simulations in southern CA, the obligate seeders were assigned lower fire tolerance values than obligate resprouters because obligate seeders suffer 100% mortality during the stand-replacing fires they experience (Keeley and Zedler, 1978; Zedler, 1995). Similarly, we parameterized the obligate seeders to be less fire tolerant than obligate resprouters for our first fire

tolerance scenario. Because obligate seeders and obligate resprouters may also co-exist in mixed stands that would then experience the same intensity of fire, we evaluated another scenario in which both functional types were assigned the same fire tolerance values.

#### 2.6.3. Fuel accumulation scenarios

In LANDIS, fire severity curves capture the relationship between fuel accumulation and fire severity such that the longer the time since the last fire, the greater the fire severity when a fire occurs. In southern CA chaparral, fuel accumulation varies due to factors such as elevation, topography, slope aspect, and weather (Payson and Cohen, 1990), but regardless of site conditions, biomass increases so rapidly that fires can burn through young age classes, particularly during high-wind conditions (e.g., Zedler et al., 1983; Keeley et al., 1999; Keeley, 2000). Nevertheless, the highest-intensity fires typically occur within 10 years for coastal sage scrub species, within 15 years for south-slope chaparral communities, and within 20 years for north-slope chaparral communities (Radtke et al., 1982). To create fuel accumulation curves to represent these differences, we classified the landtypes according to whether they were dominated by coastal sage scrub, south-slope chaparral, or north-slope chaparral. We then compared two scenarios using different fuel accumulation curves (Fig. 3). In one scenario, we assumed that all landtypes could eventually burn at the highest severity class (class 5), but the length of time required to burn at the highest severity differed according to landtype. Because lower overall fuel quantity generally leads to lower intensity fires (Christensen, 1985), the second scenario scaled the curves so that the maximum fire severity class possible varied according to the landtype, assuming that the dominant vegetation types on the different landtypes ultimately burned at different intensities, even when full canopy had been developed.

Table 3  
Targeted and mean simulated fire return intervals (FRI, by year) for the whole landscape and by landtype for three fire regime treatments (in parentheses are standard deviations of the FRIs for 10 replicated runs)

Landtype	Proportion of study area	Targeted and simulated FRIs short treatment		Targeted and simulated FRIs medium treatment		Targeted and simulated FRIs long treatment	
Entire landscape	1.0	15	13 (0)	30	28 (1)	60	58 (2)
Interior North	0.18	25	20 (1)	40	35 (3)	80	76 (7)
Interior South	0.20	20	19 (1)	35	34 (1)	70	73 (10)
High North	0.15	15	13 (0)	30	30 (2)	60	56 (5)
High South	0.11	15	12 (0)	30	28 (2)	60	54 (5)
Transition	0.16	10	8 (0)	25	24 (1)	50	44 (4)
High Slope Coast	0.06	5	5 (0)	20	18 (1)	35	43 (3)
Low Slope Coast	0.14	5	5 (1)	20	18 (1)	35	38 (3)

Table 4  
Probabilities of species establishment on landtypes for 19 species under two scenarios

Landtype name	Interior North		Interior South		High North		High South		Transition		High Slope Coast		Low Slope Coast	
	One	Two	One	Two	One	Two	One	Two	One	Two	One	Two	One	Two
Species name														
<i>Ceanothus megacarpus</i> <sup>a</sup>	0.4	0.8	0.7	0.9	0.3	0.7	0.6	0.9	0.5	0.9	0.3	0.7	0.1	0.5
<i>Ceanothus crassifolius</i> <sup>a</sup>	0.4	0.8	0.5	0.8	0.3	0.7	0.4	0.8	0.1	0.5	0.1	0.4	0.1	0.3
<i>Ceanothus spinosus</i> <sup>b</sup>	0.4	0.6	0.2	0.4	0.3	0.5	0.1	0.3	0.2	0.4	0.1	0.3	0	0.1
<i>Adenostoma fasciculatum</i> <sup>b</sup>	0.4	0.6	0.6	0.8	0.3	0.5	0.5	0.7	0.5	0.7	0.1	0.3	0	0.1
<i>Adenostoma sparsifolium</i> <sup>c</sup>	0.1	0.1	0.01	0.01	0.7	0.7	0.7	0.6	0.01	0.01	0	0	0	0
<i>Quercus berberidifolia</i> <sup>c</sup>	0.5	0.3	0.3	0.1	0.4	0.3	0.3	0.1	0.1	0.05	0.1	0.01	0	0.01
<i>Prunus ilicifolia</i> <sup>c</sup>	0.3	0.2	0.1	0.1	0.8	0.6	0.3	0.1	0.3	0.1	0	0.01	0	0
<i>Malosma laurina</i> <sup>c</sup>	0.3	0.4	0.3	0.1	0.1	0.1	0.2	0.05	0.5	0.3	0.4	0.2	0.4	0.2
<i>Cercocarpus betuloides</i> <sup>c</sup>	0.5	0.3	0.3	0.1	0.5	0.3	0.3	0.1	0.5	0.2	0.5	0.2	0.1	0.05
<i>Rhus integrifolia</i> <sup>c</sup>	0.1	0.1	0.01	0.01	0.1	0.1	0.1	0.1	0.1	0.1	0.5	0.6	0.6	0.7
<i>Quercus agrifolia</i> <sup>d</sup>	0.3	0.2	0.2	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.05	0	0.01
<i>Salvia mellifera</i> <sup>e</sup>	0.3	0.9	0.4	0.8	0.2	0.8	0.3	0.9	0.5	0.9	0.5	0.9	0.5	0.9
<i>Salvia leucophylla</i> <sup>e</sup>	0.5	0.8	0.4	0.7	0.01	0.01	0.01	0.2	0.3	0.6	0.5	0.8	0.4	0.7
<i>Encelia californica</i> <sup>e</sup>	0.01	0.01	0.01	0.01	0	0	0	0	0.2	0.5	0.6	0.9	0.7	0.9
<i>Eriogonum fasciculatum</i> <sup>e</sup>	0.5	0.8	0.5	0.8	0.05	0.2	0.05	0.2	0.4	0.7	0.4	0.7	0.4	0.7
<i>Eriogonum cinereum</i> <sup>e</sup>	0.05	0.2	0.1	0.4	0.01	0.2	0.1	0.3	0.6	0.8	0.5	0.8	0.5	0.7
<i>Artemisia californica</i> <sup>e</sup>	0.3	0.6	0.5	0.8	0.01	0.2	0.01	0.2	0.4	0.7	0.5	0.8	0.5	0.8
<i>Lotus scoparius</i> <sup>f</sup>	0.2	0.5	0.2	0.5	0.01	0.2	0.05	0.2	0.5	0.9	0.4	0.8	0.3	0.7
Annual grass	0.3	0.7	0.3	0.8	0.1	0.6	0.1	0.6	0.2	0.7	0.2	0.7	0.5	0.9

- <sup>a</sup> Obligate seeder.
- <sup>b</sup> Facultative seeder.
- <sup>c</sup> Obligate resprouter.
- <sup>d</sup> Oak woodland.
- <sup>e</sup> Coastal sage scrub.
- <sup>f</sup> Early successional.

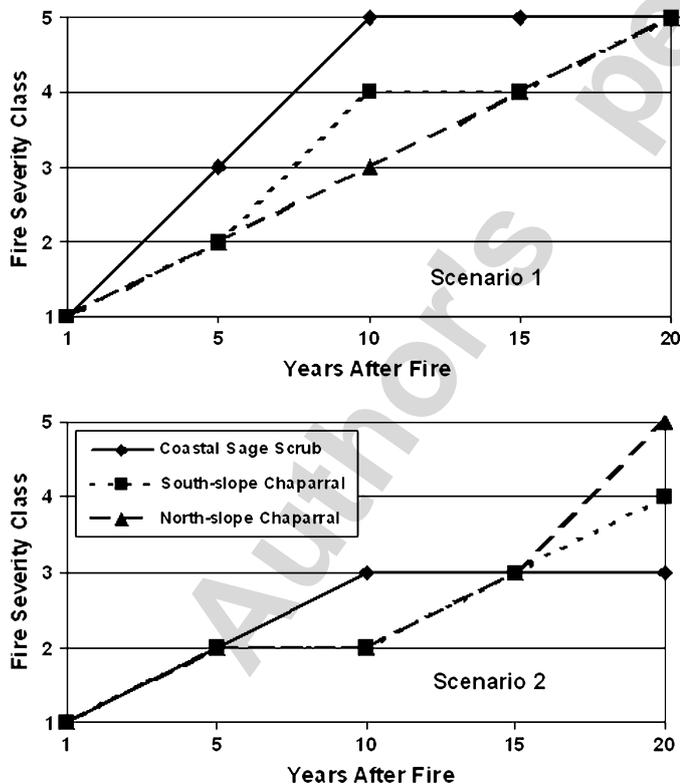


Fig. 3. Fuel accumulation curves under two scenarios. Coastal sage scrub landtypes include Upper Coast and Lower Coast; South-slope chaparral landtypes include Transition, High South, and Interior South; North-slope chaparral landtypes include High North and Interior North.

2.6.4. Dispersal distance scenarios

In LANDIS, species are parameterized with two dispersal distances, and the overall probability of seed dispersal follows a negative exponential distribution so that 95% of all seeds fall within the first parameter (effective distance), but a small percentage can reach the second parameter (maximum distance). Using LANDIS 3.6 (Franklin et al., 2005), it was necessary to inflate the effective distance parameter for species with short dispersal distances so they could disperse out of the cells (the distances had to be at least one quarter of the cell size). However, in LANDIS 4.0A, a random function was added to the model code to address this issue so that, if the effective distance were shorter than the cell size, the probability of the species dispersing out of the cell would increase with the magnitude of the effective distance. Although this new function enabled the short-dispersed obligate seeders to disperse to adjacent cells, their landscape extent substantially declined under all of the parameter scenarios, even in the long scenario. Therefore, because the new function is probability based, we evaluated additional simulations with increased effective dispersal distances (50, 75, and 100 m) for the obligate seeders.

2.7. Test of final parameter set across varying fire frequency

Because fire frequency is historically increasing in the SMMNRA, model treatments using longer FRIs were not considered necessary. However, for the purpose of model evaluation, we ran additional simulations with FRIs ranging from 5 to 150 years to test the range of the functional types' response to variations in fire frequency. Although long fire-free periods are currently uncommon in the CA chaparral, obligate seeders would be expected to decline in abundance because they are shorter-lived, rarely recruit new individuals between fires, and are less shade tolerant than obligate resprouters. On the other hand, because long fire-free periods are needed for obligate resprouters to expand their population, their cover would be expected to increase with longer FRIs. Therefore, we expected the hypothetical range of resilience of obligate seeders and obligate resprouters to resemble the pattern in Fig. 4, which was modified from Keeley (1986) so that obligate resprouters had

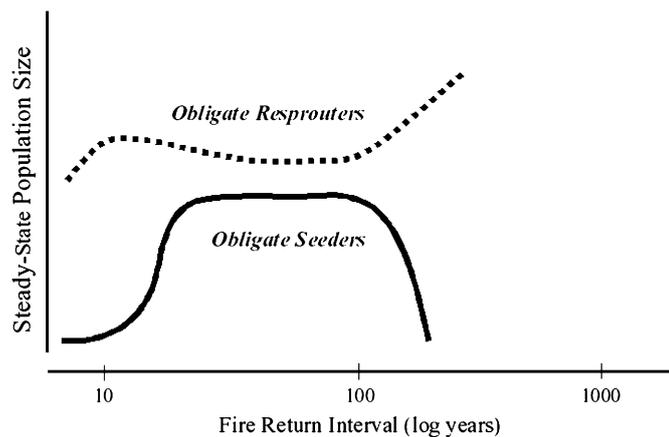


Fig. 4. Hypothetical resilience of obligate resprouters and obligate seeders across a range of fire return intervals in California chaparral (modified from Keeley, 1986).

a consistently larger abundance than obligate seeders. In the SMMNRA, obligate resprouters are mapped as covering 19,157 ha, and the obligate seeders are mapped as covering 16,784 ha.

### 3. Results

#### 3.1. Fire rotation intervals

Except for two of the landtypes in the long treatment (Interior South and High Slope Coast), the mean simulated FRIs were consistently shorter than the targeted FRIs (Table 3), –13% in the short treatment, –6% in the medium treatment, and –2% in the long treatment. The error was slightly higher when disaggregated by landtypes; however, the ranking of simulated FRIs matched the specified FRIs across all of the landtypes in all three treatments. Variability in the FRIs became higher with more infrequent fire.

#### 3.2. Probability of establishment scenarios

When using the baseline parameter scenarios (FTDIFF, FUELS, and DISP5) indicated in Table 5, lowering the probabilities of establishment for the obligate resprouters resulted in slightly decreased cover and increasing those for the obligate seeders resulted in slightly increased cover (Fig. 5A vs. B). However, the overall effect of altering this parameter was minimal. Both scenarios resulted in a substantial net increase in obligate resprouter cover and net decrease in obligate seeder cover (Fig. 6A and B), even under the long treatment that was designed to maintain relatively stable cover over time for all functional groups. The direction of change in functional type cover in response to increased fire frequency was realistic in both scenarios because the obligate seeders declined at higher frequencies while the obligate resprouters favored the highest and lowest fire frequencies. Because the PHIGH scenario closed the gap between the net gain in cover for the obligate resprouters and the net loss of cover for the obligate seeders, we chose this parameter scenario to use in the next step of the evaluation.

Table 5  
Parameter scenarios listed in the order that they were evaluated

Parameter	Abbreviation	Scenario description
Probabilities of establishment	PLOW <sup>a</sup>	Species' probabilities of establishment based solely on site preference
Probabilities of establishment	PHIGH <sup>a</sup>	Species' probabilities of establishment increased for obligate seeders and decreased for obligate resprouters
Fire tolerance	FTSAME	Fire tolerance of obligate seeders and obligate resprouters is the same
Fire tolerance	FTDIFF <sup>b</sup>	Fire tolerance of obligate resprouters is higher than fire tolerance of obligate seeders
Fuel accumulation rate	FUELS <sup>b</sup>	Fuel accumulation curves scaled so the maximum severity fire differs by landtype
Fuel accumulation rate	FUELNS	Fuel accumulation curves allow all landtypes to reach fire severity class 5
Effective dispersal distance	DISP5 <sup>b</sup>	Biologically realistic dispersal distance (5 m) used initially for obligate seeders
Effective dispersal distance	DISP75	Dispersal distance (75 m) used for obligate seeders in the final parameter set

<sup>a</sup> Represents the first two scenarios that were evaluated.

<sup>b</sup> Represents the "baseline" scenario.

#### 3.3. Fire tolerance scenarios

Although the fire tolerance value for the obligate resprouters was not varied, their overall extent was lower when the obligate seeders had a lower fire tolerance value (A vs. C; Fig. 5). Correspondingly, the overall extent was also higher for the obligate seeders, substantially closing the gap in extent between the two functional types (A vs. C; Fig. 6). However, the obligate seeders' final extent was approximately the same for the long and short scenarios, but had a higher extent for the medium scenario (C, Fig. 6). These results were unrealistic because the obligate seeders cover is expected to continue declining with shorter FRIs (as in Fig. 2); therefore, evaluations continued with the PHIGH scenario and the FTDIFF scenario (A).

#### 3.4. Fuel accumulation scenarios

The simulations using the FUELNS scenario, allowing all landtypes to experience the highest severity (class 5) fires, resulted in a lower overall net loss of cover for the obligate seeders than that in the simulations using FTDIFF and PHIGH (D vs. A; Fig. 6). However, increasing the fire severity across

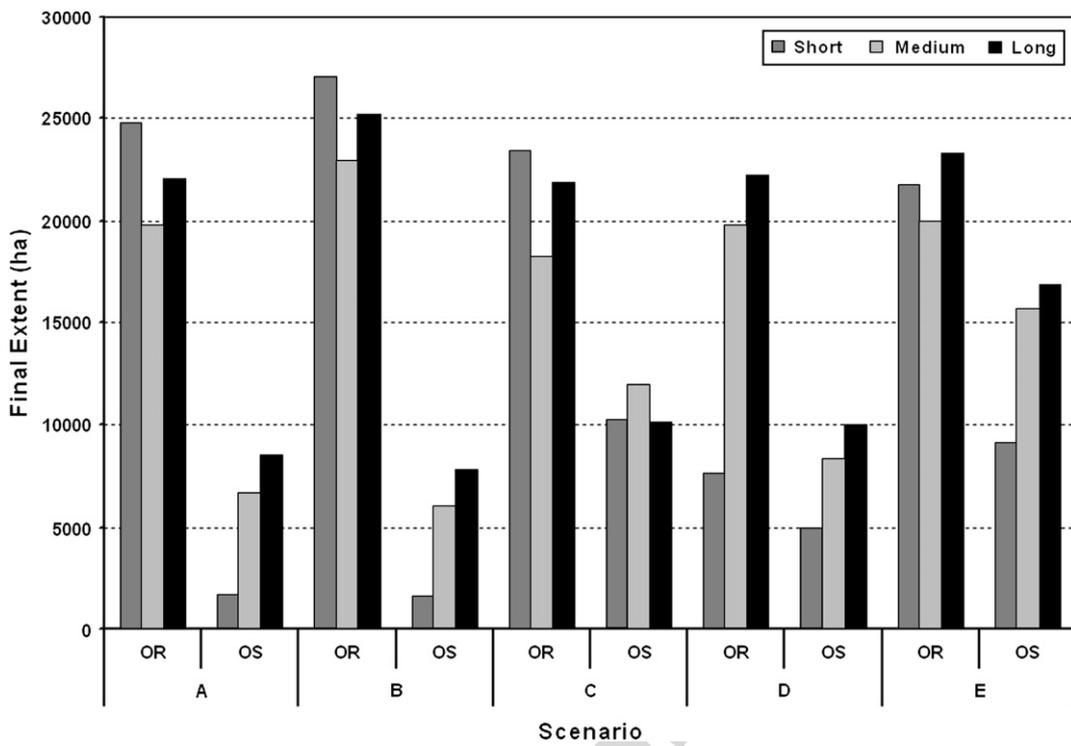


Fig. 5. Final extent (ha) of obligate resprouters and obligate seeders after 50-year model simulations under five parameter scenarios. A, PHIGH and FTDIFF; B, PLOW and FTDIFF; C, PHIGH and FTSAME; D, PHIGH and FTDIFF and FUELNS; E, final parameter set (PHIGH, FTDIFF, FUELS, and DISP75). See Table 5 for definition of scenarios.

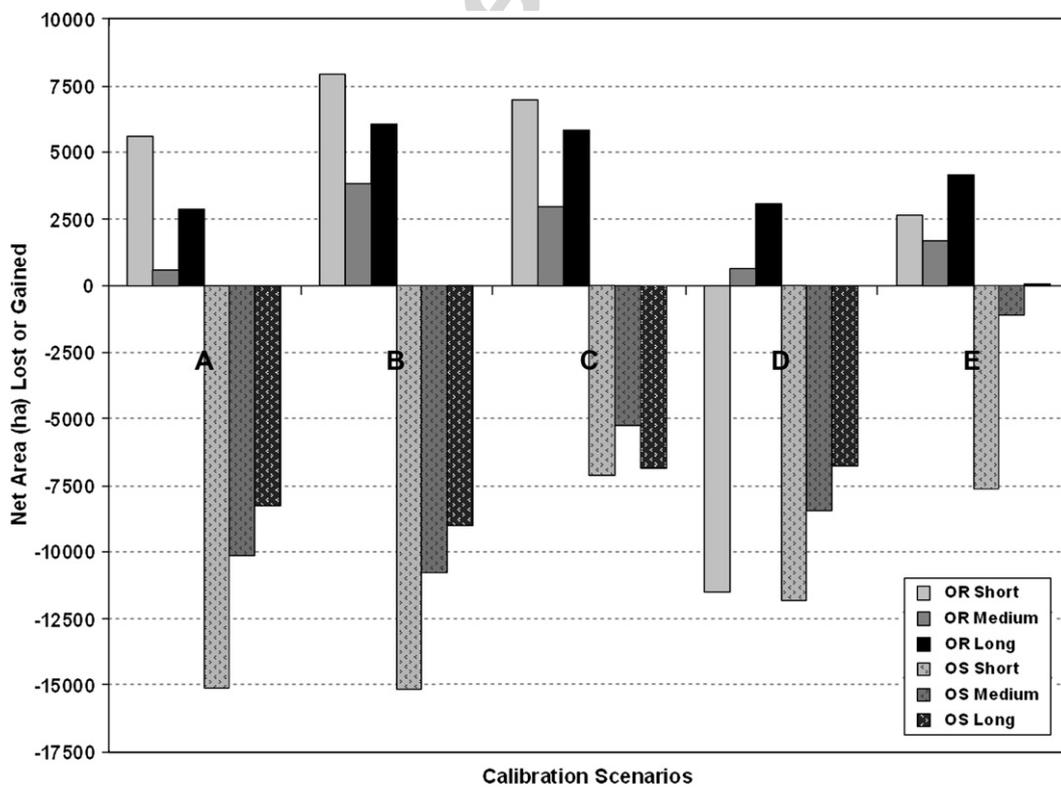


Fig. 6. Net area (ha) lost or gained for obligate resprouters and obligate seeders after 50-year model simulations under five parameter scenarios. A, PHIGH and FTDIFF; B, PLOW and FTDIFF; C, PHIGH and FTSAME; D, PHIGH and FTDIFF and FUELNS; E, final parameter set (PHIGH, FTDIFF, FUELS, and DISP75). See Table 5 for definition of scenarios.

the landscape substantially lowered the cover of obligate resprouters, especially in the short scenario that experienced the highest fire frequency (D; Fig. 6). Although the obligate seeders' response to this scenario was acceptable, the obligate resprouters' relative decline under high-frequency fire was less realistic.

### 3.5. Dispersal distance scenarios

Raising the dispersal distance in the long FRI scenario for the obligate seeders increased their cover proportionately to the increase in distance (A; Fig. 7), but this gain in extent did not affect the cover of the obligate resprouters (B; Fig. 7). Because the dispersal distance of 75 m resulted in the final extent most similar to the initial extent, this scenario was selected, along with the scenarios chosen from the previous simulations, as the final parameter set for model runs (E; Figs. 5 and 6). Although the real biological dispersal distances of obligate seeders are closer to 5 meters, inflating the dispersal parameter did not result in their unrealistic expansion under the long scenario.

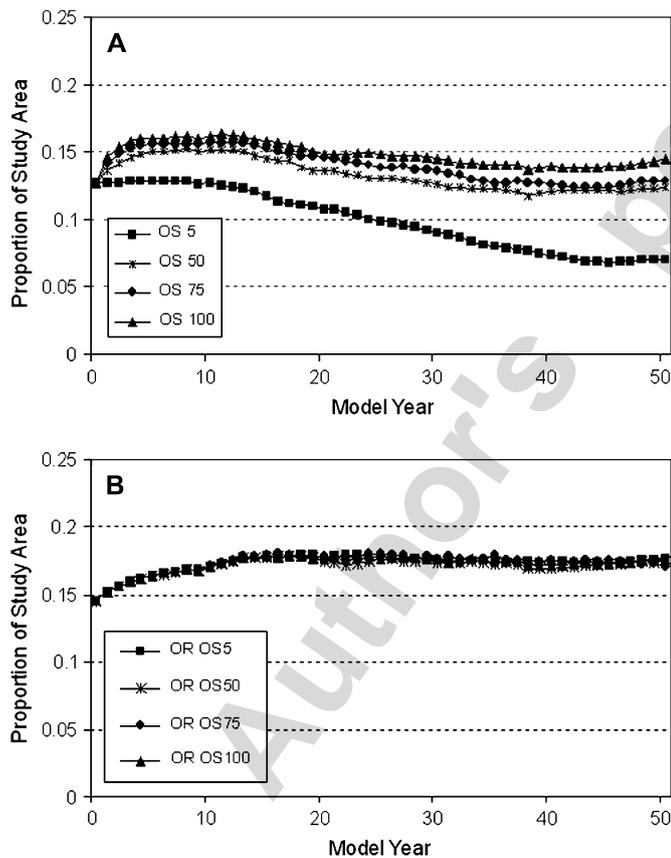


Fig. 7. Proportions of study area occupied by obligate seeders (A) and obligate resprouters (B) with dispersal distances of obligate seeders at 5 m, 50 m, 75 m, and 100 m in the “long” FRI scenario. OR OS 5 in the legend of B corresponds to obligate resprouter extent with obligate seeder dispersal distance set to 5 m; OR OS 50 in the legend corresponds to obligate resprouter extent with obligate seeder dispersal distance set to 50 m, etc.

### 3.6. Test of final parameter set across varying fire frequency

Although the obligate resprouters were expected to remain more stable across that range of frequencies (e.g., without the substantial drop in extent at FRIs between 15 and 40 years), the general trajectories in the simulations (Fig. 8) closely matched the hypothetical ones (Fig. 4). Using the final parameter set, all functional groups maintained stable cover over the 50-year simulations in the long scenario, although the obligate resprouters did increase slightly in cover under all three scenarios (Fig. 9).

## 4. Discussion

The FRIs specified for the three model treatments were designed to reflect the trend of increasing fire frequency in the study area to determine where and when vegetation change might occur under each scenario. The overall percentage error was fairly low in the calibration for FRI, but was higher for the short treatment than for the long treatment. However, the objective of creating three “different” treatments was met. As in other LANDIS applications (He et al., 1999; Franklin et al., 2001), the FRIs in the long treatment were more variable than those in the medium or short treatments because, as the average proportion of the landscape burning each year increases, there are fewer ways in which the area can burn to achieve the specified FRIs.

The complex relationships between LANDIS dynamics and model parameters were evident in terms of susceptibility to fire. The FTDIFF scenario resulted in the most realistic behavior of the functional types because, when the obligate seeders were given the same fire tolerance as the obligate resprouters (FTSAME scenario), the resprouters fared better in the medium treatment than in the long and short treatments. In field studies, the FRIs simulated in the medium treatment (average 30 years) are already threatening the persistence of obligate seeders in the SMMNRA because the shorter the FRIs, the more susceptible the obligate seeders are to becoming locally extinct (NPS, 2005). Therefore, even if the two functional

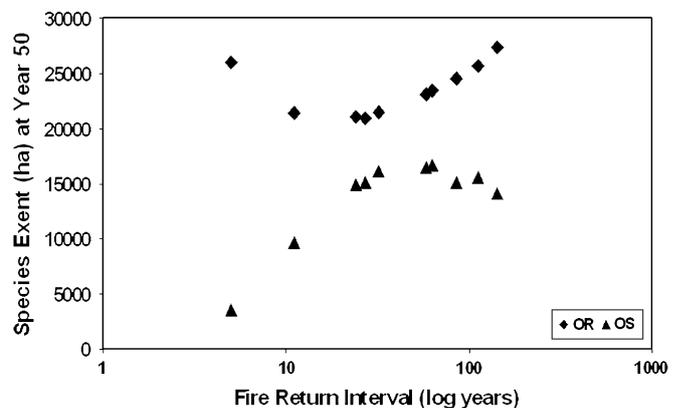


Fig. 8. Simulated resilience of obligate resprouters and obligate seeders across a range of fire return intervals in the Santa Monica Mountains, CA.

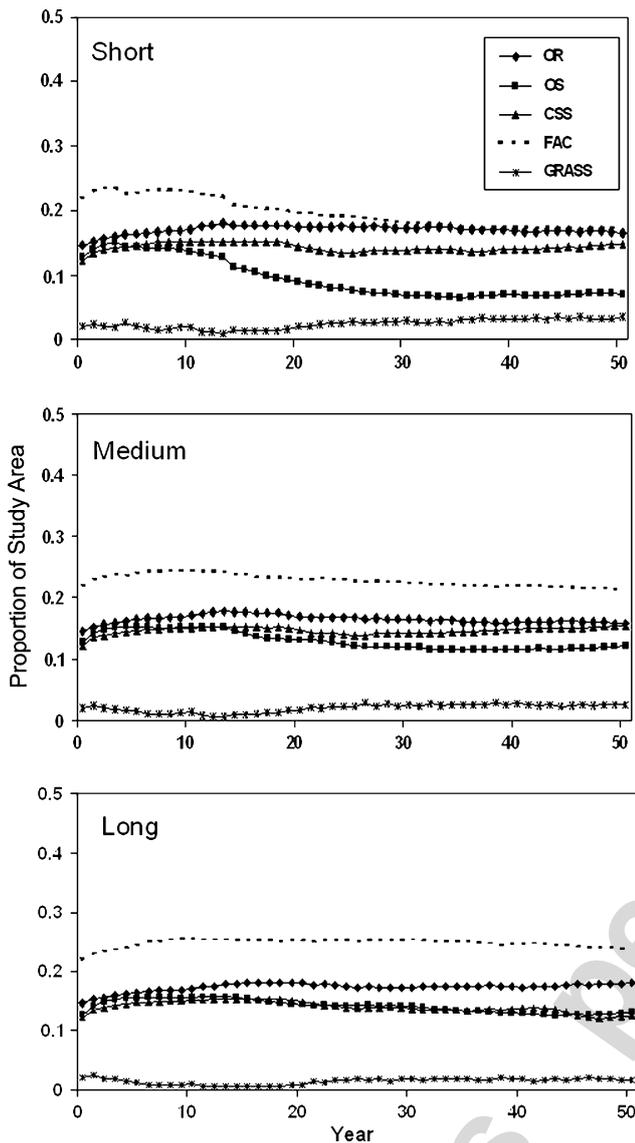


Fig. 9. Proportion of study area occupied by five functional groups for the short, medium, and long model treatments. OR, obligate resprouters; OS, obligate seeders; CSS, coastal sage scrub; FAC, facultative seeders; GRASS, annual grass.

types burn at the same intensities in mixed stands, as hypothesized, this does not translate into even resilience.

Although obligate seeders and obligate resprouters co-occur on certain parts of the landscape, they are more likely to be distributed according to site preferences. For example, obligate resprouters are generally more shade tolerant than obligate seeders, and obligate seeders will often replace them on xeric, equator-facing slopes (Keeley, 1986). While model results fit expectations when obligate resprouters were given higher fire tolerance values than the obligate seeders, allowing fires on all landtypes to reach the highest severity (the FUELNS scenario) resulted in a dramatic (and unrealistic) decrease in obligate resprouter extent when fire frequencies were the highest. Although some resprouters can succumb to repeated fires within a couple of years of each other (Zedler et al., 1983), they should be resilient to the fire frequencies

of the short treatment. However, in the FUELNS scenario, they could not regenerate at the same rate they were being killed by the frequent high severity fires. This behavior illustrates how convolved the fire susceptibility parameters are, and that species' response to fire is dependent upon interactions between fire tolerance values, age, post-fire response strategy, location on the landscape, time since last fire, and the maximum fire severity allowable by landtype.

Unlike the scenarios affecting the fire regime and species' response, the parameter scenarios affecting recruitment of new individuals (PLOW, PHIGH, and the dispersal scenarios) were not substantially influential on model results. Because of the relatively high fire frequency in all three of the model treatments, the functional types' regeneration was often dependent upon on-site post-fire response either through resprouting, fire-cued germination, or both. Furthermore, the age of maturity for the obligate seeders and obligate resprouters was set to 10 or 20 years. Therefore, although inflating the dispersal distance of the obligate seeders was biologically unrealistic, there were relatively few opportunities for recruitment via dispersal to occur, which is why the species' pattern on the landscape did not depart greatly from the initial distribution. Also, regardless of whether the distance was 5 m or 75 m, the species' could nevertheless only reach an adjacent 90 m cell during a dispersal event. Although fire was the primary mechanism affecting species' dynamics in these simulations, other factors such as shade tolerance and longevity (in addition to probability of establishment and dispersal) would likely become more influential under treatments with longer FRIs that do not occur under the present climate anyway.

The results from the final test of the parameter set across a range of FRIs from 5 to 150 years were largely consistent with the literature and very closely followed the hypothesized curve in Fig. 4. Although most chaparral species are resilient to a range of fire frequencies (Zedler, 1995), our simulations fit hypotheses that obligate resprouters are likely to replace obligate seeders at FRIs shorter than 10 years and longer than 100 years, while the obligate seeders are more likely to favor intermediate FRIs between 10 and 100 years (Keeley, 1986).

While it maintained integrity of the core LANDIS design, the model used for this research (4.0A) was also different in a number of ways, and this was the first test of that version on a real landscape. Overall, the modifications greatly added value and functionality to LANDIS, particularly for MTEs that experience very different fire regimes than the northern hardwood forests the model was originally developed to simulate. The results suggest that the current version of the model can be realistically applied to MTE landscapes for the evaluation of potential consequences of altered fire regimes. However, several aspects of the model design could be further improved to enhance the realism of model parameterization.

Although the inflated dispersal distance of the obligate seeders did not sacrifice too much ecological integrity in this research, it would be more desirable in the future to be able to specify biologically realistic distances as parameters. This version of LANDIS did improve upon the previous design by allowing species to disperse out of their cells, regardless

of their dispersal distance. Nevertheless, the obligate seeders declined dramatically over time using their real dispersal distance of 5 m because this distance was translated into a very low probability, and if the species is not able to disperse to another cell, no new recruitment is possible. Therefore, a useful improvement to the LANDIS design would be to allow a species to recruit in the same cell where it currently exists. Although this recruitment behavior was prohibited in previous versions of LANDIS to prevent species from recruiting under their parent plant, a modification to allow this behavior for selected species is planned for future versions of the model.

Another factor influencing the realism of modeling results (in MTEs) involves the maturity parameter. In chaparral shrublands, some species will regenerate following fire both through resprouting and fire-cued germination; and the age that these new individuals can reach sexual maturity differs according to whether the individual is a resprout or a seedling (Keeley, 2000). A related issue is that species with mixed sprouting and seeding strategies can have differential survival following fire depending on whether the individual originally came from seed or had already survived multiple previous cycles via resprouting. To enable the model to simulate these behaviors, a new type of species would have to be created that could recruit individuals that had one of two different sets of life history parameters.

These suggested features or others can be added to the newer version of LANDIS fairly easily due to the modular design of the model. Because each distinct ecological process is simulated in one DLL, development for a process is confined only to its corresponding DLL and its interface. Therefore, users who are capable of C++ programming can modify the code of an existing DLL or design a completely new DLL to satisfy their specific needs without producing undesirable changes in other DLLs.

## 5. Conclusion

Southern California and other MTEs are biologically rich, fire-prone regions experiencing extensive and intensive impacts from human activities. This new version of LANDIS, along with other simulation models, can be very effective tools for testing and generating hypotheses about vegetation dynamics under altered fire regimes in MTEs. Model results can help target areas for protection, can be used to evaluate the consequences of various fire management scenarios and future climate- and land-use change, and can help to focus field-based observations and experiments.

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