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SIMULATING THE EFFECTS OF FREQUENT FIRE ON SOUTHERN CALIFORNIA COASTAL SHRUBLANDS

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Abstract. Fire disturbance is a primary agent of change in the mediterranean-climate chaparral shrublands of southern California, USA. However, fire frequency has been steadily increasing in coastal regions due to ignitions at the growing wildland–urban interface. Although chaparral is resilient to a range of fire frequencies, successively short intervals between fires can threaten the persistence of some species, and the effects may differ according to plant functional type. California shrublands support high levels of biological diversity, including many endangered and endemic species. Therefore, it is important to understand the long-term effects of altered fire regimes on these communities. A spatially explicit simulation model of landscape disturbance and succession (LANDIS) was used to predict the effects of frequent fire on the distribution of dominant plant functional types in a study area administered by the National Park Service. Shrubs dependent on fire-cued seed germination were most sensitive to frequent fire and lost substantial cover to other functional types, including drought-deciduous subshrubs that typify coastal sage scrub and nonnative annual grasses. Shrubs that resprout were favored by higher fire frequencies and gained in extent under these treatments. Due to this potential for vegetation change, caution is advised against the widespread use of prescribed fire in the region.

Key words: chaparral shrublands; coastal sage scrub; fire frequency; functional types; LANDIS; simulation modeling; southern California (USA); vegetation-type conversion.

INTRODUCTION

The coastal ranges and interior foothills of southern California (USA) support shrubland vegetation that is adapted to the mediterranean climate of the region, characterized by winter rain and summer drought (Keeley 2000). The most extensive vegetation type is chaparral, which is composed of densely spaced, evergreen sclerophyllous shrubs. Coastal sage scrub is the next most extensive vegetation type and consists of drought-deciduous subshrubs that occur in drier locations and at lower elevations than chaparral (Westman 1981).

Chaparral shrublands are quite flammable due to low decomposition rates, high dead-to-live fuel ratios, dense community structure, and low fuel moisture (Rundel et al. 1980). The fire season in southern California occurs from late summer through fall when the fuel moisture is lowest and when strong northeastern Santa Ana winds are most likely to occur. Under high-wind conditions, fire cannot be effectively controlled until the wind dies down or the fire runs out of fuel (Radtke et al. 1982). Therefore, chaparral typically burns in large, stand-

replacing, high-intensity fires (Keeley and Fotheringham 2003).

Although these periodic crown fires kill all aboveground vegetation, chaparral is resilient to fire and returns rapidly to its pre-fire composition (Hanes 1971, Bond and van Wilgen 1996). Shrubs are classified based on three post-fire regeneration modes: obligate resprouters (e.g., *Quercus berberidifolia*) respond to fire through vegetative propagation from underground root crowns or lignotubers; obligate seeders (e.g., *Ceanothus megacarpus*) are unable to regenerate vegetatively, but recruit from long-lived dormant seed banks that are cued by fire to germinate; and facultative seeders (e.g., *Adenostoma fasciculatum*) regenerate using both strategies of fire-cued germination and vegetative resprouting.

Because chaparral burns in stand-replacing fires, it is difficult to reconstruct precise fire histories using dendroecological methods (Keeley and Fotheringham 2001). Determining the natural fire regime is also complicated because humans have set fires in the region for hundreds to thousands of years (Keeley and Fotheringham 2003). Nevertheless, chaparral is thought to be resilient to fire at rotation intervals ranging from 20 to 150 years, with an average historic fire rotation interval of ~50–80 years (Keeley 1981, Minnich 1983, Zedler 1995*a*). A "fire rotation interval" (FRI) is defined

as the time it takes to burn an area equivalent to the size of the area of analysis.

Within the last century, unprecedented human-population expansion and associated land-use change, in addition to fire-management policies such as suppression and prescribed fire, have undoubtedly altered the region's fire regime. However, there is controversy over how the fire regime has changed (Keeley and Fotheringham 2001, Minnich 2001). It has been suggested that fire suppression has successfully excluded fire and allowed the buildup of old age classes, which have resulted in fewer, yet larger and more intense fires across the entire southern California landscape (e.g., Minnich 1983, 2001, Minnich and Chou 1997). Because this model assumes that young age classes can prevent the rapid spread of these fires, prescribed fire has been recommended to restore what has been claimed to be the natural condition for southern California: one of frequent, small fires that fragment the landscape into a fine-grained mixture of age classes. Evidence for this "age-mosaic" model, however, has been refuted for areas where fire is strongly influenced by Santa Ana winds (Keeley et al. 1999, Keeley and Fotheringham 2001, Moritz 2003, Moritz et al. 2004). Data from 20th-century fire records have indicated that shrubland fires have not become fewer and larger. Instead, fire frequency increased beyond the historic range of variability, and this increase was correlated with population density and human-caused ignitions at the wildland–urban interface (Keeley et al. 1999, Rundel and King 2001, Keeley and Fotheringham 2003). Furthermore, young age classes have not prevented fire spread during high-wind conditions (Keeley et al. 1999, Moritz 2003).

Local fire regimes influence the distribution of plant communities due to species' differences in post-fire regeneration strategies (Keeley 1986, Franklin et al. 2001, Meentemeyer and Moody 2002). Extremely short intervals between fire events can threaten the persistence of some shrub species (Zedler 1995a). In fact, these shrublands may irreversibly convert to other vegetation types ("type conversion") such as coastal sage scrub or alien annual grasslands that can tolerate (and even promote) repeated burns (Zedler et al. 1983, Minnich and Dezzani 1998). Alien grasses invade native shrublands via residential areas at the wildland–urban interface, through burned areas that have been seeded with annual ryegrass (Lolium multiflorum) to try to prevent erosion, or from areas that have been planted with grass and cleared for fuelbreaks (Zedler et al. 1983, Keeley 1986). Consequently, certain fire-management activities can ironically contribute to positive feedbacks that further increase fire frequency.

Although the immediate post-fire response of many chaparral plant species is well documented, little is understood about the long-term dynamics of shrubland ecosystems, especially in future scenarios with increasing population growth and fire frequency (Zedler and Zammit 1989). The need to understand and predict these effects is driven not only by issues of fire protection for humans but also to protect these native vegetation communities for their ecological and economic importance. These communities support high levels of biological diversity as well as a large number of endangered and endemic plant and animal species (Stephenson and Calcarone 1999).

The complex feedbacks between fire and vegetation dynamics make it difficult to evaluate the consequences of altered fire regimes through short-term field studies. Single-event observations of composition change are not sufficient to make well-informed conclusions about future scenarios over broad regions or to determine what the cumulative effects of an altered fire regime might be (Franklin et al. 2004). Therefore, we used a landscape-scale simulation model of fire disturbance and succession (LANDIS) to examine the effects of high-frequency fire on the distribution and extent (defined as the total area of cover across the landscape) of dominant plant species in southern California shrublands, represented by the three chaparral life-history types plus coastal sage scrub and annual-grass functional types (Pausas 1999). Three fire-regime treatments of increasing fire frequency were analyzed to answer these questions: What broad-scale effects on the distribution and extent of native plant species could occur if fire frequency continues to increase in the region? And, will different plant functional types be more susceptible to vegetation change than others? We expected that the obligate seeders would be most susceptible to type conversion; that the facultative seeders would also decline with frequent fire; and that obligate resprouters would be favored by the shortest fire rotation intervals. We also anticipated that parts of the landscape would shift from chaparral shrubland to coastal sage scrub and alien grasslands at higher fire frequencies.

METHODS

Study area

The Santa Monica Mountains are a rugged, coastal mountain chain with a mediterranean climate in the east–west trending Transverse Range in southern California, USA (Fig. 1). Within the boundary of the Santa Monica Mountains National Recreation Area (SMMNRA), administered by the National Park Service, approximately half of the 60 000 ha is publicly owned and protected land. The major vegetation types in the mountains include chaparral (~60% of the area); coastal sage scrub (25%); oak woodland (3%); and (primarily alien) grasslands (3%) (Radtke et al. 1982). The biologically rich region is home to nearly 1000 plant species, 50 mammal species, 400 bird species, and 35 species of reptiles and amphibians (NPS 2004).

The SMMNRA has a largely anthropogenic fire regime; humans cause >95% of all fires. Over the last 75 years, fire frequency and total area burned have increased, and some areas have burned up to 10 times
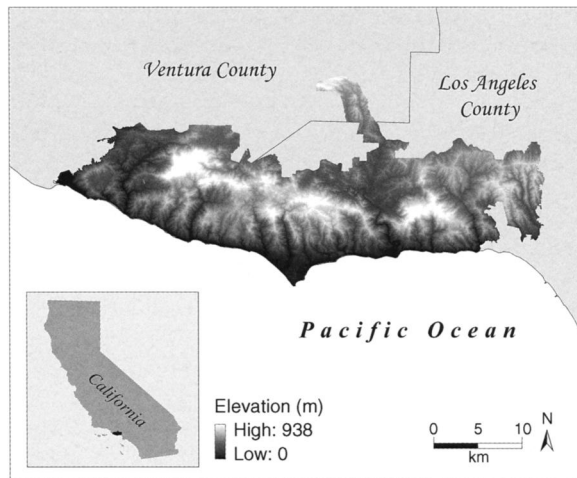
FIG. 1. The Santa Monica Mountains National Recreation Area in southern California, USA.

(NPS 2004). The steep terrain and alignment of the Santa Monica Mountains promotes intense fires that rapidly move from north to south with extensive lateral spread (Radtke et al. 1982).

The LANDIS model

LANDIS is a landscape fire-succession model that has been extensively evaluated and is the focus of a special issue of *Ecological Modelling* [**180**(1), 2004]. LANDIS is raster based, stochastic, and spatially explicit, and simulates multiple disturbance types (although only fire disturbance was applied in this study) and resulting multiple pathways of succession (He and Mladenoff 1999). Successional dynamics result from interactions among fire regimes, plant life history, and site conditions, and can be simulated over broad spatial extents and long time periods. Life-history parameters of the simulated species include longevity, maturity, dispersal distance, ability to resprout, and relative shade and fire tolerance. The cell size for the model is user specified, and multiple plant species and age cohorts may be present within one site. Within an individual cell, local, temporally dynamic processes occur, and the model keeps track of species presence by age and disturbance history. At a landscape scale, spatially explicit processes occur, such as dispersal and spread of disturbance.

Fire ignition and spread are stochastic, but the probability of a fire starting and spreading is conditioned by specified fire-return intervals and disturbance history. Fire size is also stochastic and follows a lognormal distribution function. Fire severity is determined by the time since the last fire and through fuel-accumulation curves that specify how long it takes for a severe fire to occur. Fire-induced mortality depends on species' age and fire tolerance (younger age cohorts with lower fire tolerances are most susceptible).

Several changes have been made to the model (LANDIS 4.0) to adapt it for fire regimes and plant functional types that are characteristic of mediterranean-type ecosystems (Syphard 2005). These include fire-cued germination from a dormant seed bank (characteristic of obligate and facultative seeders) and an annual life-history form to simulate the fine-scale temporal dynamics characteristic of these regions. Additional details on calibration of LANDIS for another southern California landscape can be found elsewhere (Franklin et al. 2001, 2005, Syphard and Franklin 2004).

Input data

LANDIS requires non-spatial and spatial inputs, including (1) species life-history parameters for the simulation of dispersal, establishment, competition, persistence, and mortality, (2) a map of species distribution by age class, and (3) land-type map representing site classes of species' affinities and rates of fuel accumulation. We developed the spatial data using a 30-m cell size (equivalent to the resolution of the raw data used for the land-type map), but we aggregated the maps to 90 m for the model simulations.

1. *Species life-history parameters.*—Based on a preliminary vegetation classification being developed by the National Park Service (NPS), a literature review, and consultation with NPS vegetation scientists, we selected 19 species to include in the simulations. Demographic attributes of southern California shrubland species have been extensively published (e.g., Zedler 1995b, Keeley 2000, Franklin et al. 2001). Therefore, we derived the life-history parameters for the LANDIS model from the literature. To avoid specifying parameters with false precision, we rounded off many of the values to highlight relative differences between functional types (Table 1).

2. *Species-age map.*—The initial distribution of species-age classes was based a digital copy of the Weislander Vegetation Type Maps (VTM) from the 1930s (Wieslander 1935) that provided detailed, species-level information about the vegetation that existed at that time. Areas not covered by the VTM maps (8% of the landscape) were filled in with a contemporary map of vegetation types (Franklin et al. 1997). We derived a binary GIS map for each of the 19 species used in the simulations to delineate that species' distribution in the study area. These 19 maps were then overlaid, producing more than 220 map classes, each with different combinations of species. A hierarchical, agglomerative cluster analysis using PC-ORD software (McCune and Mefford 1999) was used to group classes based on similarity of species membership, which reduced this number to 24 species assemblages. Because fires are stand replacing in California shrublands, we used a fire-history map to determine the age of the vegetation by subtracting the time of last fire from the current year.

3. *Land-type map.*—The land-type map was derived from the environmental variables that are known to

TABLE 1. Species life-history attributes and parameters used in LANDIS for five functional types.

Parameter	Obligate resprouters	Obligate seeders	Coastal Sage scrub	Facultative seeders	Annual grass
Number of species in group	6	2	6	2	1
Longevity (yr)	150	75	50	100	1
Age of maturity (yr) 20	10	2–3†	15	1	
Shade tolerance (ordinal class 1–5)	4	3	2	3–4†	1
Fire tolerance (ordinal class 1–5)	4	3	2	3–4	1
Effective seed dispersal distance (m)	100	75	75	75	10 000
Maximum seed-dispersal distance (m)	500	100	100	100	−1‡
Probability of resprouting (0–1)	0.80–1.0†	0	0.25–0.75†	0.70–0.80†	0
Minimum age of resprouting (yr)	3	0	4	3	0

† Indicates a range of values for the species within that functional type.

‡ A dispersal distance of −1 means the species can disperse to anywhere on the landscape.

affect plant distributions and productivity in the region—local climate and topographically mediated soil moisture availability (Franklin 1995). Based on methods described in Franklin (2003), five digital maps (January minimum temperature, July maximum temperature, annual mean precipitation, slope, and transformed slope aspect) were subjected to unsupervised classification using ISODATA (Ball and Hall 1965). The clusters that were generated through the unsupervised classification were then aggregated according to similarities in their environmental characteristics and their spatial contiguity on the landscape. The final land-type map, consisting of seven classes, was merged with maps of urban extent and other non-vegetated land. We prohibited fires from burning through urban land types; however, we allowed fires to spread across (or jump) road land types at low probabilities.

We derived the land-type parameters, including probabilities of species establishment and fuel characteristics, from the literature as well as through empirical calculation from spatial data. First, we approximated the species' establishment probabilities based on the proportion of area they covered within each land type. We then modified these values according to general site preferences documented in the literature and based on overall capabilities of different functional types to successfully establish (Syphard 2005). For example, obligate resprouters have higher probabilities of establishing in mesic, north-aspect land types than in xeric, south-aspect land types; however, because their recruitment rates are very low, their overall probabilities of establishment were also lower than for other functional types (Keeley 1986, Meentemeyer and Moody 2002).

One challenge of applying LANDIS (originally designed for northern hardwood forests) to mediterranean-type shrublands was to mimic the stand-replacing fires characteristic of the region. Due to rapid post-fire fuel accumulation, chaparral and coastal sage shrublands can burn at young ages with no substantial change in fire intensity/severity after ~20 years (Zedler et al. 1983, Keeley et al. 1999, Moritz et al. 2004). Fire intensity also has more of an effect on the success of post-fire recovery than on mortality because all shrub species are usually killed aboveground. To simulate these characteristics, we parameterized the fuel-accumulation curves for the land types so that fires could reach intensities that were able to kill species within a short time after the previous fire. The highest-intensity fires could occur within 10 years on land types preferred by coastal sage scrub species; within 15 years for south-slope chaparral communities; and within 20 years for north-slope chaparral coastal sage scrub species (Radtke et al. 1982). Species' fire-tolerance parameters are directly related to the fuel-accumulation curves because susceptibility and fire intensity are connected on an ordinal scale. Therefore, we also specified fire-tolerance values of species to operate in conjunction with the fuel-accumulation curves to create the effect of stand-replacing fire. Additional details can be found in Syphard (2005).

Fire-regime modeling experiment

Three fire-regime treatments were developed and calibrated using fire rotation intervals (FRIs; the time it takes to burn an area equivalent in size to the area of analysis) that varied according to land type to capture the relative differences in fire frequency across the landscape (Fig. 2). We designed the landscape-averaged FRI for the "long" treatment (60 years) to approximate the historic fire frequency that maintained species' abundance and persistence on the landscape over the last century (Keeley et al. 1999). The "medium" and "short" treatments (average FRI of 30 and 15 years, respectively) mimicked the increasingly shorter FRIs that have been observed during the last half of the 20th century. The fire size distribution is strongly skewed in the study area (NPS 2004); therefore, we specified the average fire size to be 40 ha, with a variance of 20 000 ha. The model simulations were run for 50 years and were replicated 10 times each to quantify variability in results due to the stochasticity of the model. Although some species' longevities and FRIs were longer than the length of the simulations, the variation in initial species ages and the overall high frequency of fires on the landscape provided a sufficient number of post-fire regeneration
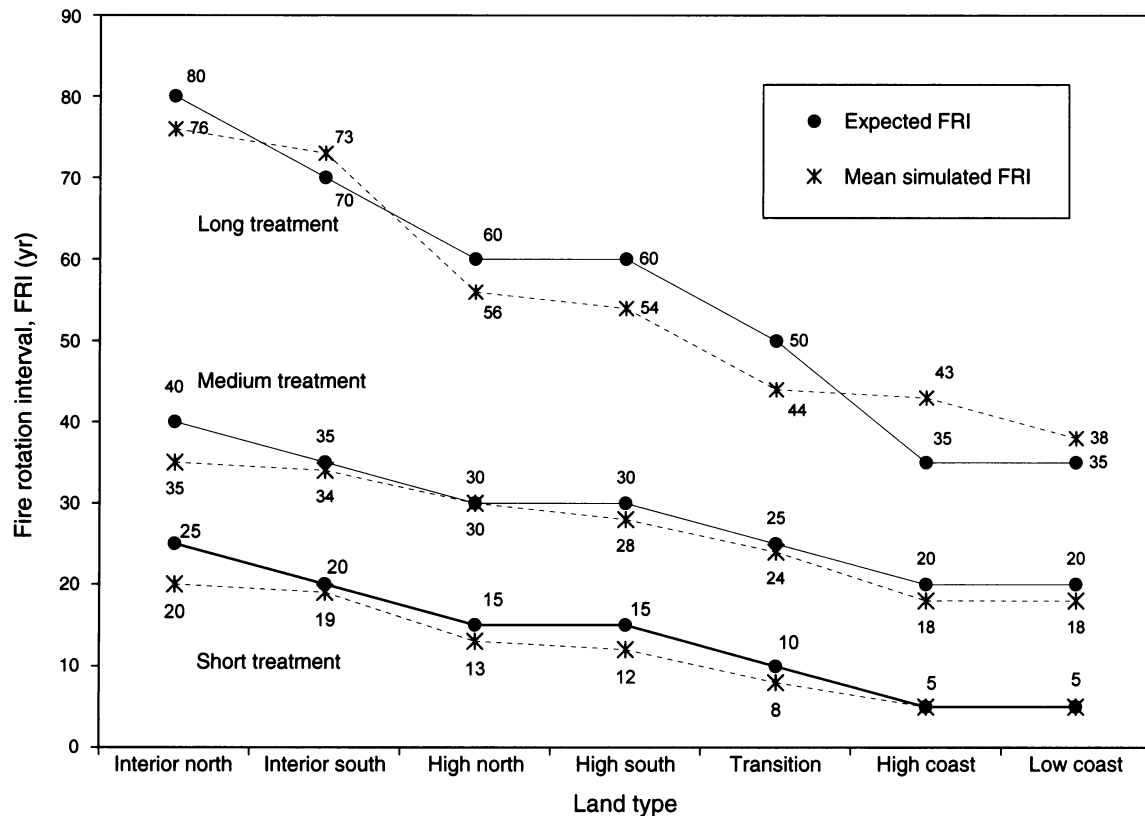
FIG. 2. Expected and mean simulated fire rotation intervals (FRI, by year), for the seven land types in the Santa Monica Mountains National Recreation Area, for the long (60 yr; upper curve), medium (30 yr; middle curve), and short (15 yr; lower curve) fire-regime treatments. Only one numeric label is used when the expected and simulated values are the same.

cycles to reveal substantial differences among the fire-regime treatments.

Classification of model output into functional types

Although LANDIS simulates the dynamics of individual species during model runs, our analysis focused on model output that was reclassified into five functional types occupying more than 96% of the landscape, three within chaparral and one each for coastal sage scrub and annual grass. The chaparral species were classified as obligate seeders, facultative seeders, or obligate resprouters based on their known life-history parameters (Table 1). The greatest distinction among these chaparral functional types was between the obligate resprouters and obligate seeders. The facultative seeders had intermediate parameter values. The obligate resprouters are longer lived, and have higher shade tolerance and longer dispersal distances than the facultative and obligate seeders. However, the parameterized dispersal distances for the seeders were longer than their biological dispersal distances because the parameter reflects a probability of dispersing out of the grid cell when the distance is shorter than the cell size.

The maturity parameter specifies the age at which species can begin recruiting new individuals. Although

obligate resprouters become sexually mature at a much earlier age, successful recruitment of new individuals usually does not occur until a full canopy has been developed following fire (Keeley 1986); therefore, the maturity parameter was set 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 effectively recruit new plants following fire, which ranges between 5 and 25 years (Keeley 1986). Because the seed banks of obligate seeders and facultative seeders can survive for decades to centuries (Keeley 1977), the life span of the dormant seed banks that were produced by these species in the simulations was set to 50 years, the duration of the model runs.

Although coastal sage scrub is less shade tolerant and more sensitive to fire than chaparral, the dominant species also mature earlier, have high probabilities of establishment on more xeric land types, and recruit continuously between fires (Westman 1982, Zedler 1995a, DeSimone and Zedler 2001). The coastal sage scrub species in the SMMNRA resprout following fire, with probabilities varying within genera (Malanson and O'Leary 1982).

The annual-grass functional type was parameterized to reflect an invasive habit with high dispersal capability

(Wells et al. 2004). Although the parameterization of grass was greatly improved with the annual time step in LANDIS 4.0, one of the limitations of our simulations was that this functional type took on ephemeral qualities that prevented it from persisting on the landscape in its original spatial configuration because it died in each time step. To overcome this limitation, we have proposed modifications to the LANDIS model to allow recruitment in the same cell where the species is located (Syphard 2005).

Analysis

We present the following final analyses of the simulation modeling in *Results*.

Extent.—LANDIS generated binary GIS maps of functional-type extent for every time step in the simulations. From these maps, the proportion of area occupied by each functional type was calculated over time for each fire-regime treatment. Because multiple species can exist within any one cell at a given time, maps of each functional-type's presence for years 0 and 50 were overlaid for each treatment. The cross-tabulation of these maps showed the locations of gain and loss of functional-type cover (extent) over the course of the simulations.

Fire frequency and functional-type change.—Maps of fire events for each time step were overlaid and summed to generate new maps of fire frequency, which also allowed the calculation of fire-return intervals for each simulation across the landscape. Unlike the fire rotation interval (FRI), the "fire-return interval" indicates the average number of years between two successive fire events at specific locations and can therefore reveal whether certain portions of the landscape burn more frequently than others. The fire-frequency maps were overlain with the maps of functional type gain and loss to compare the effects of fire frequency on functional-type change.

Vegetation-type conversion.—We quantified conversion of cover between functional types through spatial overlay of extent at time 0 and 50. To better understand conversion between physiognomic types, the chaparral functional types were grouped together for this analysis. Change was also quantified among the transition (mixed) classes of coastal sage scrub with grass and coastal sage scrub with chaparral (as opposed to pure stands of these functional types). Multiple species can be present within each grid cell; therefore, quantifying change between these mixtures of functional types provided additional information on simulated vegetation dynamics. Because very little overlap between grass and chaparral occurred, that combination was not considered.

RESULTS

Extent.—The two functional types with the largest differences in extent between model treatments were the obligate seeders and the facultative seeders (Figs. 3 and
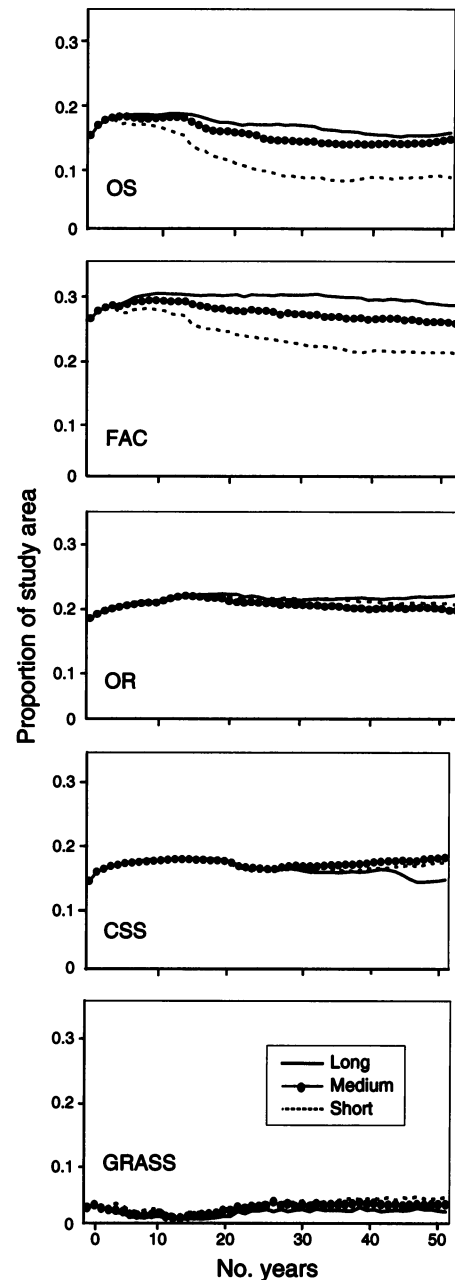

FIG. 3. Proportion of study area occupied for the five functional types under the long (60 yr), medium (30 yr), and short (15 yr) fire-regime treatments. Key to functional types: OR, obligate resprouter; OS, obligate seeder; FAC, facultative seeder; CSS, coastal sage scrub; and GRASS, annual grass. Results shown are for a single model run.

4). Both functional types declined as the fire rotation interval got shorter, but lost proportionally more cover between the medium and short treatments than between the long and medium treatments. The obligate resprouters were slightly favored by the long and short treatments; the coastal sage scrub species were slightly favored by the medium and short treatments; and grass
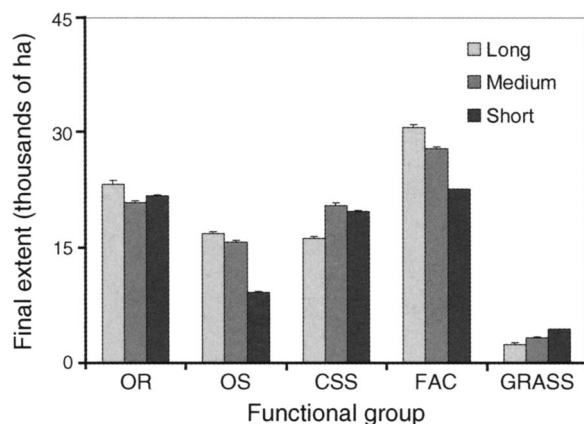
FIG. 4. Extent (area) of functional-type cover at the end of 10 replicates of 50-year model simulations (mean and SE shown) for the long, medium, and short fire-regime treatments. The functional-type key is as in Fig. 3.

cover steadily expanded as the fire frequency increased (Figs. 3 and 4).

Fire frequency and functional-type change.—The maximum number of fires anywhere on the landscape was five fires in the long (60-yr) treatment (fire-return interval of 10 years), seven fires in the medium (30-yr) treatment (fire-return interval of 7 years), and 11 fires in the short (15-yr) treatment (fire-return interval of 4 years), although <1% of the landscape burned more than eight times (Fig. 5). The land types that experienced the highest simulated fire frequencies generally captured the spatial patterns of fire in the actual fire history of the

region (Fig. 5). The lower-elevation coastal land types burned at higher fire frequencies than the inland, higher-elevation land types, and the western portion of the study area burned more frequently than the eastern side. The tendency for high fire frequency to occur in the canyon running south to north toward the northern peninsula in the study area (Malibu Canyon) was also captured in the simulations. The primary difference between the simulated fire-frequency patterns vs. historical patterns is that high-frequency fire occurred more extensively along the length of the coast in the simulations.

In the long and medium treatments, the obligate seeders expanded the most in the northwest portion of the landscape where fire frequencies were intermediate (fire-return intervals of 50 and 25 years) (Fig. 6). However, they also declined in the northeast where no fires occurred. In the medium and short treatments, the obligate seeders declined when fire-return intervals were 17 years or shorter (≥3 fires), primarily in the coastal land types where fire frequency was highest (Figs. 5 and 6).

In the long treatment, the facultative seeders increased in locations where the fire-return intervals were 50 and 25 years, and they persisted better than the obligate seeders when no fires occurred (Fig. 6). Like the obligate seeders, the facultative seeders declined at fire-return intervals of 17 years or shorter in the medium and short treatments in locations where fire frequency was highest.

The patterns of expansion and decline for the obligate resprouters were more evenly distributed than those of the obligate and facultative seeders, particularly in the long treatment (Fig. 6). In the medium and short
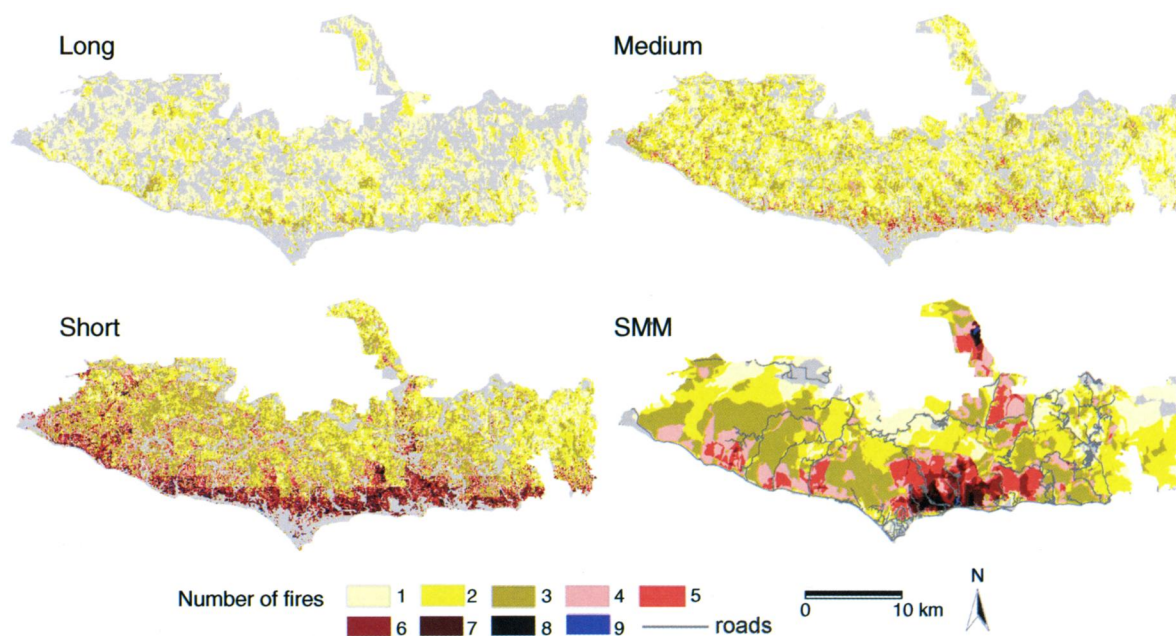

FIG. 5. Maps for the long, medium, and short fire-regime treatments illustrating fire frequency in the Santa Monica Mountains (California, USA) over 50-year model simulations, and map of 1925–2003 fire frequency using the Santa Monica Mountains (SMM) fire-history data from the National Park Service.
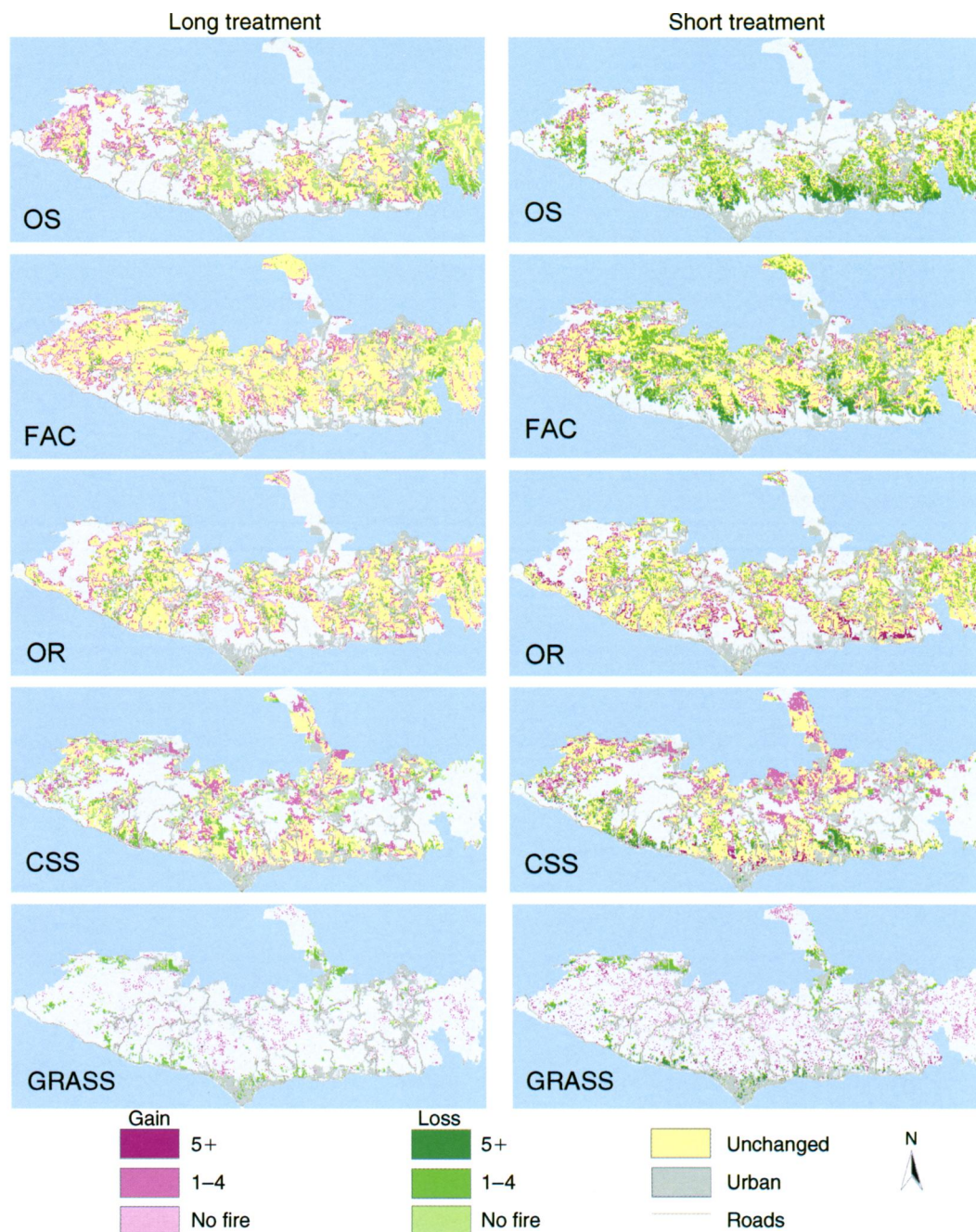
Fig. 6. Map showing the distribution of areas lost and areas gained by the five functional types for the long and short fire-regime treatments over three categories of fire frequency (5+, gain or loss at five or more fires; 1–4, gain or loss at one to four fires; no fire, gain or loss with no fires) that occurred during the course of the simulations from year 0 to 50. The functional-type key is as in Fig. 3.

treatments, they expanded substantially in fire-prone land types where the obligate and facultative seeders declined.

In all three treatments, the coastal sage scrub species declined where no fires occurred, and they expanded in the middle and northern regions of the landscape under intermediate to high fire frequencies (from 50- to 13-year fire-return intervals) (Fig. 6). Although they also

expanded in some portions of the fire-prone coastal land types, they declined where the fire frequencies were the highest.

In all three treatments, grass declined when there was no fire, but expanded when the fire-return intervals were ≤25 years. The ephemeral spatial pattern of grass is apparent in the aggregated patches representing their decline on the landscape (Fig. 6). The primary difference
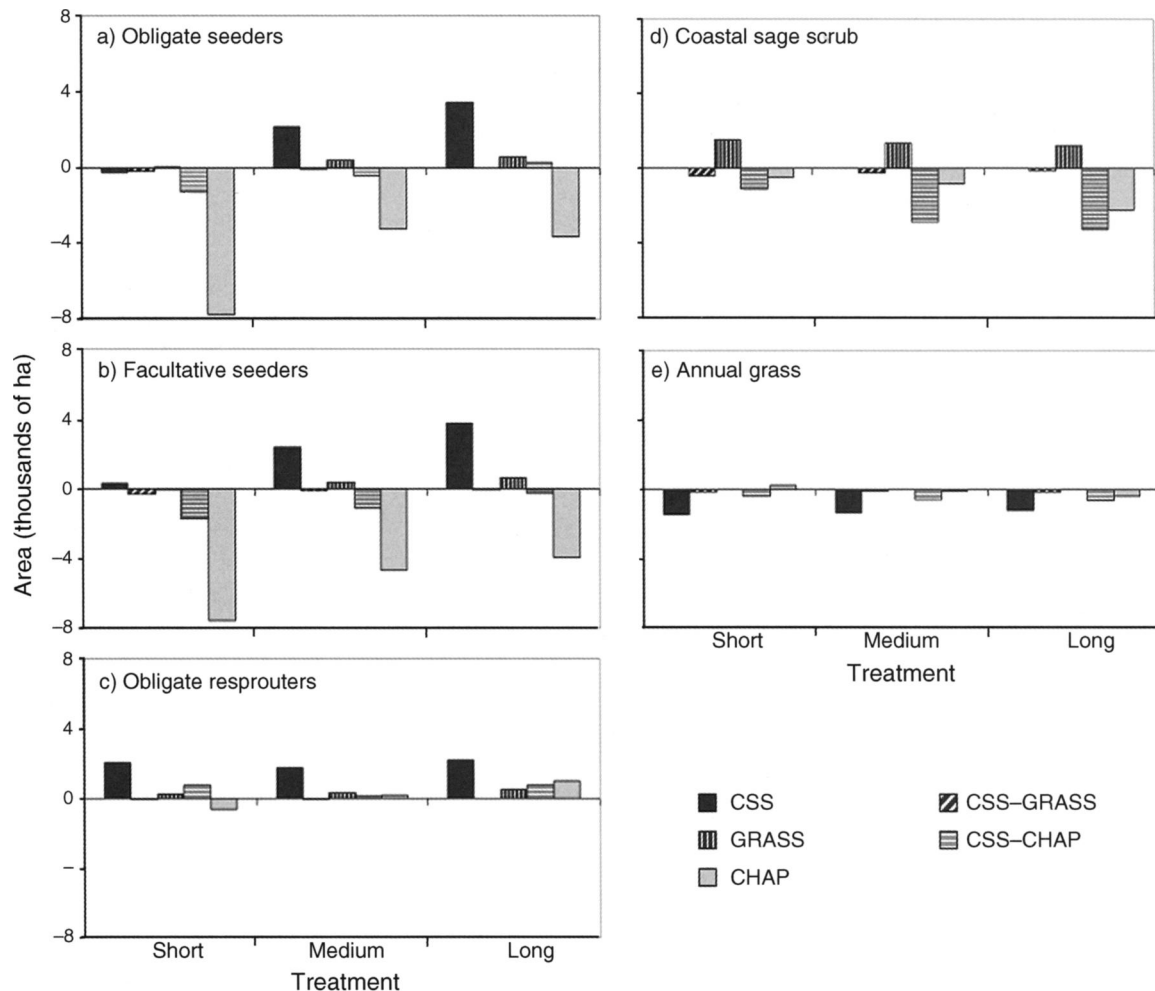
FIG. 7. Vegetation-type conversion represented by net area gained or lost for the long, medium, and short fire-regime treatments, and the vegetation type in which this gain or loss occurred. Functional types: CSS, coastal sage scrub; CSS–GRASS, mix of coastal sage scrub and annual grass; GRASS, annual grass; CSS–CHAP, mix of coastal sage scrub with chaparral; CHAP, any combination of the chaparral functional types (obligate resprouters, obligate seeders, and/or facultative seeders).

between the treatments was the overall expansion of grass at higher fire frequencies.

Vegetation-type conversion.—In the long treatment, the obligate seeders gained approximately the same amount of cover from coastal sage scrub species as they lost to other chaparral functional types in different locations (Fig. 7a). They also gained some area from grass and coastal sage scrub–chaparral mix. In the medium treatment, the obligate seeders gained the most area from coastal sage scrub and lost the most to other chaparral types, but they also lost some cover to coastal sage scrub–chaparral mix. In the short treatment, the obligate seeders lost more cover to coastal sage scrub–chaparral mix than in the other treatments. They also lost cover to coastal sage scrub species and to coastal sage scrub–grass mix. The relative proportions of net gain and loss to other functional types for the facultative seeders were very similar to those of the obligate seeders (Fig. 7b).

In all three treatments, the obligate resprouters replaced coastal sage scrub in similar proportions, representing the largest net gain in area across the landscape (Fig. 7c). In both the short and long treatments the obligate resprouters also gained from coastal sage scrub–chaparral mix and from grass. Whereas some area was gained from other chaparral functional types in the long treatment, a similar amount of area was lost to other chaparral functional types in the short treatment.

The entire amount of area gained by the coastal sage scrub species was originally grass in all three of the treatments (Fig. 7d). The amount of net loss to other functional types systematically changed in proportion to the fire frequencies of the treatments. Specifically, coastal sage scrub lost increasingly less cover to chaparral and to coastal sage scrub–chaparral mix from the long treatment to the short treatment and lost

increasingly more cover to coastal sage scrub–grass mix as the fire frequency increased across treatments.

Not surprisingly, the area of net loss of grass to coastal sage scrub in all three treatments is approximately the same as the net gain from grass to coastal sage scrub (Fig. 7e). Grass was also converted to coastal sage scrub–chaparral mix in all three treatments. The type of net gain for grass was a conversion from chaparral in the short treatment. However, grass was lost to chaparral in the long treatment.

DISCUSSION

We were able to use LANDIS, a landscape-scale simulation model of fire disturbance and succession, to simulate potential effects of frequent fire on the distribution of dominant plant functional types in southern California, USA. Although direct observation and experimentation is important for understanding species' life-history strategies and post-fire response mechanisms, using a simulation model offered advantages for evaluating research questions related to broad-scale vegetation change due to altered fire regimes. Cumulative impacts are difficult to detect over short time periods, and Zedler and Zammit (1989) gave the example that if a species declined in abundance 20% after each fire, it would require three fires to see a 50% reduction in the species. Whereas long-term, broad-scale field research is costly, time-consuming, logistically difficult, and requires decades to produce answers, simulation models that are parameterized with biologically realistic input data can relatively quickly simulate complex interactions and multiple ecosystem processes over broad time and space scales. Furthermore, models are effective tools for evaluating potential consequences under alternate management scenarios, mimicking an experimental design without having to directly manipulate the environment.

Using a spatially explicit model was also necessary for us to identify locations where repeated fires and sensitive species were most likely to co-occur. Therefore, it was important that we effectively simulated the specified fire rotation intervals of the three treatments and that the modeled fire patterns were generally consistent with those expected in the study area. Although our simulations predicted high-frequency fire more extensively along the coast than the historic pattern, these coastal areas are generally expected to experience the highest fire frequency in the Santa Monica Mountains (Radtke 1981).

Our expectations for the model results were based on field observations of differential impacts to plant functional types of repeated fires. Species within functional types share similar life-history traits and responses to disturbance. Therefore, using functional types to simulate vegetation dynamics has been an effective approach for analyzing vegetation change in disturbance-prone ecosystems (Pausas 1999, 2003, Franklin et al. 2001, Rusch et al. 2003).

The changes predicted by the model agreed with our expectations that the obligate seeders would be most susceptible to type conversion, but that the facultative seeders would also decline under repeated fires. Although facultative species can resprout after fire, repeated disturbances have reduced populations of these plants due to high mortality of lignotubers and by killing seedlings recovering from previous fires (Zedler et al. 1983, Haidinger and Keeley 1993). While the ability to resprout gave the facultative seeders an advantage over the obligate seeders, the probability of these species resprouting was lower than that of the obligate resprouters. The facultative seeders also had lower shade tolerance and shorter dispersal distances than obligate resprouters. Therefore, the obligate resprouters increased in the short treatment as we expected, but they also experienced a net gain under all three treatments, likely because they were more shade tolerant than the other functional types and could compete better in fire-free conditions.

Although the obligate and facultative seeders declined with repeat fires, they both needed some fire on the landscape (fire-return intervals between 25 and 50 years), which would be expected because both functional types are disturbance dependent (Keeley 1998). In fact, the obligate seeders declined in locations where no fires burned.

One of the primary reasons for the simulated decline of both the obligate seeders and the facultative seeders was that the age of maturity was set to 10 and 15 years, respectively, to reflect the amount of time these species require to replenish their seed banks. Estimates for the time required to replenish seed banks range between 5 and 25 years (Keeley 1977, Zedler 1995b). This time lag between fire-cued germination and subsequent replenishment of a seed bank has also been proposed in the literature as an explanation for the greater susceptibility of these functional types to repeated fires (e.g., Zedler et al. 1983, Haidinger and Keeley 1993, NPS 2004). The species in these functional types rarely recruit seedlings in the absence of fire; therefore, if fire recurs before a seed bank is replenished (or the species reached maturity in the simulations), there would be no opportunity for fire-cued germination. Because only one age of maturity can be specified for each species in the simulations, we erred on the conservative side in assigning this parameter. The implication is that, if these species do require longer than 10 or 15 years for the replenishment of a seed bank, the consequences under high fire frequency could be even graver than the simulations suggest.

In addition to expecting that obligate and facultative seeders would decline with repeated fire, we also anticipated that parts of the landscape would shift from chaparral shrubland to coastal sage scrub or annual grass at high fire frequencies. Vegetation type conversion has already been observed in localized field studies in the Santa Monica Mountains National

Recreation Area (NPS 2004; A. L. Jacobsen, S. D. Davis, and S. L. Fabritus, *unpublished manuscript*). In one study, nonnative annuals completely replaced an obligate seeder and mostly replaced a facultative seeder after an area burned three times in 11 years (S. L. Fabritus and S. D. Davis, *unpublished manuscript*). The obligate resprouter persisted throughout these fire events. In another study, four sites with fire-return intervals of ≤6 years and two sites with fire-return intervals of 7–12 years were compared to nearby control sites of similar slope, aspect and elevation, but fire-return interval of ≥12 years (A. L. Jacobsen, S. D. Davis, and S. L. Fabritus, *unpublished manuscript*). The obligate seeders declined in all sites with short fire-return intervals, particularly those with the highest fire frequencies, and there was a corresponding increase in coastal sage scrub and alien grasses.

The general pattern of change between vegetation types in the simulations fit these expectations in that relatively greater extents of the landscape shifted from obligate and facultative seeders to coastal sage scrub and coastal sage scrub–transition at higher fire frequencies. Also, the only time the alien grasses experienced a net gain in extent was in the short treatment, and that net gain was from chaparral.

Coastal sage scrub species can often persist under fire frequencies that eliminate chaparral, and they may replace chaparral at fire-return intervals of 5–10 years (O'Leary 1995). Some researchers also believe that high fire frequencies in coastal areas, in addition to grazing, have expanded the distribution of coastal sage scrub (Radtke 1981). One advantage the coastal sage scrub species have over chaparral is that they mature early and continually recruit between fires (Westman 1982, Minnich and Dezzani 1998). Additional advantages in the simulations were that they had relatively higher probabilities of establishment on their preferred land types (coastal areas and interior valleys) and they could resprout with varying success after fire.

Despite greater resilience to repeated fire, there is evidence that coastal sage scrub may also decline and convert to grasslands when the fire frequency becomes extremely high (Freudenberger et al. 1987, Callaway and Davis 1993, Minnich and Dezzani 1998). One of the advantages of using a spatially explicit model was that, although the coastal sage scrub species experienced an overall net gain in the short treatment, the maps of gain and loss revealed that they actually declined in the areas that experienced the very highest fire frequencies.

Although alien grass and coastal sage scrub do tend to intermix on this landscape, the most questionable simulation results were those in which large patches of the original grassland area converted to coastal sage scrub. This was unrealistic because it happened under the medium and short treatments in which the high fire frequencies should have favored grass. The fact that the grasses did increase steadily in extent at higher fire frequencies fit expectations. However, the distributional

pattern was improbable because grass is likely to persist on the landscape over time, and has even been shown to inhibit post-disturbance establishment of other species (Eliason and Allen 1997). Therefore, the impact of alien grass on system dynamics is probably more substantial than we simulated because of its ability to persist once established.

The area that obligate seeders and facultative seeders gained from coastal sage scrub and lost to other chaparral types was likely greater in our simulations than would be expected because chaparral species have short dispersal distances and the community typically returns to its pre-fire composition with little invasion by other species (Keeley 1986). Regardless, there was no substantial change in the location of any functional type on the landscape during the simulations, so the overall species distributions remained realistic. Therefore, some of the compositional change was likely the result of localized, subtle shifts in mixed stands due to differences in species' shade-tolerance values.

CONCLUSION

Our simulations predicted broad-scale differential impacts of repeated fire similar in nature to those that have been observed in localized field studies, strongly suggesting that there may be serious ecological consequences from altered fire regimes in southern California. In particular, obligate and facultative seeders could experience substantial declines and may be replaced with coastal sage scrub or nonnative grass. Type conversion to nonnative grass is often considered the most substantial ecological threat related to high fire frequency (e.g., NPS 2004), in part because coastal sage scrub is an ecologically important vegetation community and provides habitat for a number of endangered species (Davis et al. 1994).

Considering the conservative estimates of our maturity parameters for the seeders and the ephemeral distribution of grass in the simulations, type conversion from chaparral to grass is likely to be even more of a concern than our simulations suggest. In fact, the invasion of grasses in fire-prone ecosystems has been shown to alter disturbance regimes in a number of plant communities (Bond and van Wilgen 1996, Mack and D'Antonio 1998). Grasslands facilitate fire spread, and they recover quickly following fire, thus helping to increase their dominance (Barro and Conard 1987). With lower heat requirements for ignition, grasslands also have the longest fire season of any southern California vegetation type and have been shown to support fire-return intervals of one or two years (Minnich and Dezzani 1998).

Despite overwhelming evidence that fire frequency is continuing to increase in coastal southern California (Keeley et al. 1999, Moritz et al. 2004, NPS 2004), the current fire- management program subscribes to the paradigm that fire suppression has led to fewer, larger

fires, and that landscape-scale prescribed fire should be used to create a fine-scaled age mosaic. Considering the results of our simulations, we believe that adding more fire to the landscape through broad-scale prescribed burning may have negative ecological effects. Instead, our results are consistent with recent recommendations from the U.S. National Park Service to change the fire-management program to focus fuel-reduction efforts and prescribed fire on strategic locations such as the wildland–urban interface (NPS 2004).

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