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RESEARCH ARTICLE

Simulating fire frequency and urban growth in southern California coastal shrublands, USA

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Abstract Fire is an important natural disturbance in the Mediterranean-climate coastal shrublands of southern California. However, anthropogenic ignitions have increased fire frequency to the point that it threatens the persistence of some shrub species and favors the expansion of exotic annual grasses. Because human settlement is a primary driver of increased ignitions, we integrated a landscape model of disturbance and succession (LANDIS) with an urban growth model (UGM) to simulate the combined effects of urban development and high fire frequency on the distribution of coastal shrublands. We tested whether urban development would contribute to an expansion of the wildland-urban interface (WUI) and/or change in average fire return intervals and compared the relative impacts of direct habitat loss and altered fire regimes on functional vegetation types. We also evaluated two methods of integrating the simulation models. The development pattern predicted by the UGM was predominantly aggregated, which minimized the expansion of the WUI and increase in fire frequency, suggesting that fire risk may be higher at intermediate levels of urbanization due to the spatial arrangement of ignition sources and fuel. The comparison of model coupling methods illustrated how cumulative effects of repeated fires may occur gradually as urban development expands across the landscape. Coastal sage scrub species and resprouting chaparral were more susceptible to direct habitat loss, but increased fire frequency was more of a concern to obligate seeder species that germinate from a persistent seed bank. Simulating different scenarios of fire frequency and urban growth within one modeling framework can help managers locate areas of highest risk and determine which vegetation types are most vulnerable to direct habitat loss, altered fire regimes, or both.

Keywords Chaparral · Coastal sage scrub · Exotic grass · Fire · LANDIS · Landscape model · Model coupling · Urban growth model · Wildland urban interface

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Introduction

The California Floristic Province is notable for its endemism and species richness (Stein et al. 2000). However, massive habitat loss and fragmentation, particularly in the southern part of the state, has made this region a global hotspot of concern for declining biodiversity (Wilson 1992). Although habitat conversion and urban development are the most cited cause of species' extinctions and extirpations in southern California (Soule et al. 1992), indirect effects of human population expansion, including altered fire regimes and biological invasions, are also becoming serious threats to the region's native vegetation (Rundel and King 2001).

Fire has an important influence on the distribution of plant species in southern California. Chaparral is considered a fire-adapted vegetation type because its component species resprout or produce seedlings after fire, and communities return rapidly to their pre-fire composition (Keeley 2000). Lightning fires are uncommon in the coastal shrublands (Keeley 1982), but Native Americans were a source of ignitions for approximately 10,000 years before present (Keeley 2002). In the last century, nearly exponential human population growth has increased ignitions in these fire-prone shrublands to the point that fire frequency is also rising nearly exponentially (Keeley et al. 1999). Although chaparral is resilient to a range of fire rotation intervals (ranging from 20 to 150 years), unnaturally short time periods between fires (less than 15 years) are starting to threaten the persistence of some shrubs. The impact of these altered fire regimes varies according to different species' life history characteristics (Haidinger and Keeley 1993).

The introduction and spread of non-native species, particularly annual grasses, have also become a threat to native vegetation in southern California. Exotic grasses are successful invaders of disturbed areas and typically spread from residential areas, roads, or areas cleared for fuel breaks (Byers 2004). They sustain high fire frequencies and can even promote fire, which in turn can lead to positive feedbacks in which fire opens up the vegetative canopy and allows the introduction of the grasses that continue to facilitate more fire and canopy opening (Mack and D'Antonio 1998). Eventually fire frequency exceeds that to which native species are adapted, resulting in a type conversion from native shrubland to exotic grassland (Zedler et al.1983; Haidinger and Keeley 1993). Although they were initially introduced during European colonization, these grasses have proliferated exponentially in the last century, paralleling human population growth and increased fire frequency (Randall et al. 1998).

The interactions between human activities and natural dynamics that contribute to altered fire regimes and exotic species invasions tend to be spatially distributed around the contact zone between wildland and people (Rundel and King 2001). This interface where human development intermingles with or abuts undeveloped wildland vegetation is termed the Wildland-Urban Interface (WUI) (Radeloff et al. 2006). The WUI has received national attention recently because houses and human lives are most vulnerable to fire in these locations and because human-caused ignitions are believed to be most common there.

As more development diffuses from urban centers to chaparral shrublands, the interface between housing and this fire-prone vegetation is expected to expand (Scott 1995). In fact, the human population in the Los Angeles metropolitan region (16.7 million) is expected to double in the next 40 years (Fulton 2001). Although this inevitable growth will undoubtedly impact the region's native habitat, there is considerable uncertainty about where and how the vegetation is likely to respond (Zedler and Zammit 1989). Therefore, land managers want to know how to anticipate these changes and to design appropriate strategies to minimize impacts (NPS 2005).

Computer models are often developed as tools to better envision the consequences of alternate management scenarios. Models are designed to simplify a reality that is too difficult to predict in all its complexity, so they usually focus on specific subsets of environmental systems (Frysinger 2002). To expand the scope of analysis, model coupling has emerged as an approach to simulate more complicated interactions than may be possible using single models alone. The methods of exchanging information between models can vary, and there are trade-offs based on their degree of integration. When models are loosely coupled, the user interface for each model is separate and their frequency of interaction is low. Tight coupling provides a modeling framework with more frequent and automatic interaction (Park and Wagner 1997). Although loose coupling requires less work in terms of software development, the interface between the simulated systems may not be fully or accurately modeled if the real-world interface involves more frequent interaction and feedback. Tight coupling may provide more realism, but it also requires a larger investment with regards to time and software development. As managers face increasingly complicated issues that also require rapid decision-making, there is growing debate about how tightly models should be coupled to provide the best information with the most efficiency (Park and Wagner 1997; Frysinger 2002)

Concerns about urban development, altered fire regimes, and exotic annual grasses in southern California have been widely documented in the literature, yet most research on these issues has focused on quantifying their ecological effects separately, typically via field studies. However, all three are interrelated because urban development directly contributes to habitat loss, but it also leads to increased ignitions and introduction of exotic species, which in turn increase fire frequency and indirectly affect habitat. Our research objective was to couple two simulation models to better understand the combined effects of urban development and increased fire frequency on the distribution of southern California coastal shrublands. The simulation results will inform fire managers, conservation planners, and land use planners about which vegetation types are most susceptible to decline and where landscape change is most likely to occur.

Our approach was to use a spatially explicit landscape model of fire disturbance and succession (LANDIS) for the simulation of vegetation dynamics in response to three different fire regime scenarios. To simulate direct habitat loss and indirect impacts of urbanization, we coupled LANDIS with the Clarke Urban Growth Model (UGM). We also compared two methods of integrating LANDIS with the UGM to contribute theoretically to the model coupling debate and to provide practical guidance to other ecological modelers. Loose coupling incorporated the spatial extent of the final year of urban growth predictions (2050) into the initial conditions (2000) of the LANDIS simulations, allowing the UGM's future to inform the behavior of the LANDIS model (although LANDIS did not provide feedback to the UGM). Tight coupling more realistically simulated urban expansion by annually updating the LANDIS simulations with each year of the UGM predictions from 2000 to 2050.

In addition to direct habitat loss, the UGM predictions could affect the LANDIS simulations indirectly through the changing extent and configuration of a buffer zone around urban areas and roads representing the WUI. Within these buffers, fire ignition probabilities were higher, as were the probabilities of establishment of exotic grasses. Although fire regime parameters were specified and calibrated for LANDIS using a reference landscape, the different area and spatial configuration of these WUI buffers in the coupled model runs allowed the possibility for fire to differ in frequency or spatial pattern with the change in urban development. An altered fire regime or the expansion of exotic grasses due to the changing spatial extent of these buffers could, in turn, impact the native vegetation in the simulations.

We used simulation modeling to examine three hypothesized patterns of landscape change. First, due to the substantial increase in the WUI in California during the 1990s (Hammer et al., in review), we hypothesized that the total area in WUI buffers in our simulations would expand with urban development, and we tested this by quantifying the difference in WUI area from 2000 to 2050.

The primary ecological risk to native shrublands from altered fire regimes is repeated burns in the same location (e.g. Zedler et al. 1983). The risk of repeated fires in LANDIS is not only a function of the total amount of fire on the landscape, but also results from the spatial configuration of fire-prone landtypes and from the stochasticity of the model (as with natural processes). Assuming that the total amount of fire would be greater with more urban development and that the location of fires would be concentrated in the vicinity of the WUI buffers, our second hypothesis was that urban development would increase the risk of repeated fire on certain parts of the landscape, and we tested this by comparing fire return intervals in the coupled model runs to a reference landscape that had no urban growth.

While direct habitat loss has affected all native vegetation types in southern California, coastal sage scrub species have been disproportionately impacted due to their spatial coexistence with urban development patterns (O'Leary 1995). Altered fire regimes can also differentially impact chaparral species based on their functional type (Haidinger and Keeley 1993). Our third hypothesis was that functional vegetation types would respond differentially to urban development and increased fire, particularly that coastal sage scrub and resprouting chaparral would be more susceptible to direct habitat loss, but that shrubs dependent on fire-cued seed germination would be more susceptible to repeated fire. To test this, we calculated the area of cover for these vegetation types over time and at the end of the simulations. Finally, we compared the results of our hypothesis tests to determine if they differed depending upon whether the models were loosely or tightly coupled.

Methods

Study area

The Santa Monica Mountains National Recreation Area (SMMNRA) is an administrative unit that extends across approximately 60,000 ha of Mediterranean habitat, characterized by steep, coastal mountains that form the southernmost range in the Transverse Ranges of southern California (Fig. 1). Slightly more than half of the land is protected through public ownership (including the National Park Service); however, the majority of the privately owned land is available for development (NPS 2005). The SMMNRA exemplifies issues related to the expanding WUI in southern California because of its proximity to the highly developed, rapidly expanding Los Angeles metropolitan area and because the region is characterized by frequent fires. Ninety-eight percent of the fire starts have been of human origin, and some locations have burned up to 10 times in the last 75 years (NPS 2005). The region is biologically rich, supporting approximately 1,000 plant species, 50 mammal species, 40 bird species, and 35 species of reptiles and amphibians. The primary vegetation types are chaparral (approximately 60%) and coastal sage scrub vegetation (25%); the remaining 15% include oak woodland, (primarily exotic) grasslands, and riparian vegetation. Vegetation type conversion has been observed in several locations that experienced repeated fires in short succession (NPS 2005).

LANDIS model description and simulations

LANDIS is a spatially explicit, raster-based model that simulates forest dynamics on a heterogeneous landscape, including stochastically driven interactions among fire regimes, plant life history strategies, and site conditions. Successional dynamics, simulated over broad temporal and spatial scales, are driven by life history parameters for each species included in the simulations (longevity, maturity, dispersal distance, relative shade and fire tolerance, and the ability to resprout following fire). General information on LANDIS and its recent developments can be found in a special issue of Ecological Modelling (Volume 180, 2004); descriptions of how we calibrated LANDIS for another landscape in southern California are provided in Franklin et al. (2001), Syphard and Franklin (2004), and Franklin et al. (2005); and detailed information on the calibration process from using LANDIS in the SMMNRA can be found in Syphard et al. (2005). We used LANDIS 4.0, which is publicly available (He et al. 2005).

The landscape in LANDIS is described by the species-age map, which contains information about the presence of each species by age class within every grid cell. Multiple plant species and age cohorts may be present within one cell. For the SMMNRA, we selected 19 dominant species to use in the simulations based on a literature review and consultation with National Park Service

Fig. 1 The Santa Monica Mountains in southern California

vegetation scientists. The values for the species life history attributes were also derived from the literature, and the species were classified into functional types that reflected the differences in post-fire response strategies characteristic of the vegetation in the region. Analysis of these species as groups provided a framework for understanding the fundamental mechanisms driving vegetation response. The species-age map was developed using a digital map with species-level distribution information from the 1930s (Wieslander 1935) combined with a contemporary map of vegetation types. A majority of fires are stand replacing in California shrublands, so a current fire history GIS map was used to determine the age of the vegetation by subtracting the time of last fire from the current year.

The other spatial input to the model is the landtype map, which is used to stratify the landscape into discrete ecological units that represent relatively homogenous site conditions across the landscape. Derived from climate and terrain variables associated with the spatial distribution of vegetation in the landscape, the landtype map reflects the environmental conditions affecting potential establishment and growth of vegetation. Each landtype is parameterized with uniform species establishment coefficients, fuel accumulation curves representing rates of biomass accumulation and potential fire severity over time, and other fire regime characteristics such as mean fire rotation intervals and probabilities of ignition (He and Mladenoff 1999). A fire rotation interval is defined as the time required to burn an area equivalent to the area in question. The landtype map for the SMMNRA consisted of seven vegetated classes that stratified the landscape according to slope-aspect, elevation, and distance to the coast (Fig. 2).

In LANDIS simulations, fire is spatially explicit in that its spread is contagious, with higher probabilities of spread occurring in neighboring cells with longer time since last fire (greater fuel load). Fire ignition is stochastic, but occurs with increased probability with the time since last fire as well as through the ignition probability coefficients specified for each landtype. Fire size is also stochastic, but small fires are more likely to occur than large fires, following a lognormal distribution and mean fire size as specified in the input parameters. Groups of individual fires can occur within one time step.

We developed three fire regime scenarios to evaluate the relative effects of increased fire frequency on the distribution of functional vegetation types. Using a reference landscape, we calibrated LANDIS to simulate different fire

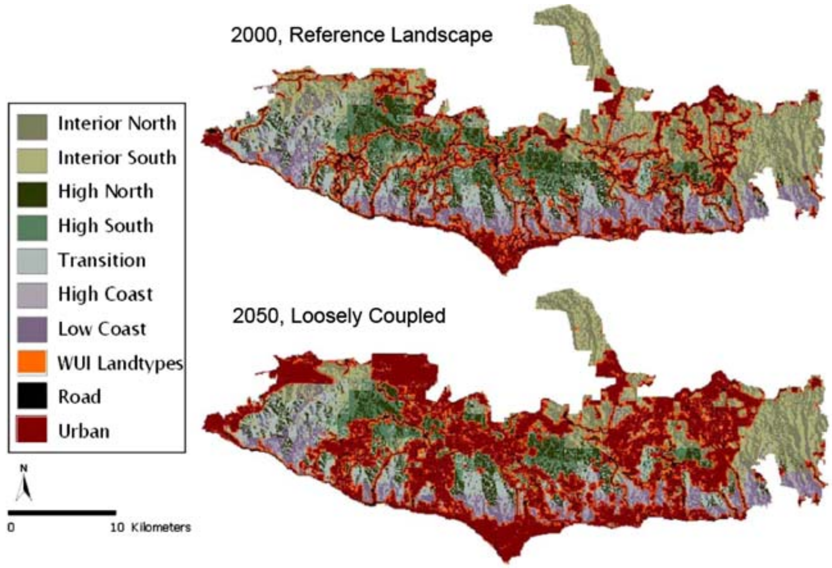

Fig. 2 Landtype maps for the Santa Monica Mountains depicting urban land and wildland urban interface (WUI) in 2000 (Reference landscape) and urban growth predictions and WUI in 2050 (loosely coupled). The tightly coupled approach uses the 2000 landtype map in the initial conditions of the LANDIS simulations, but ends with the 2050 landtype map

rotation intervals for the three scenarios (Syphard et al. in press). The ''long'' scenario (average landscape fire rotation interval of 60 years) was designed to approximate the historic fire rotation intervals that maintained species' distribution patterns over the last century. The ''medium'' scenario (average landscape fire rotation interval of 30 years) reflected the shorter fire rotation intervals that have been occurring since 1951; and the ''short'' scenario (average landscape fire rotation interval of 15 years) applied fire rotation intervals observed in parts of the landscape that are burning at the highest fire frequencies. These fire rotation intervals, calibrated for the reference landscape, represent mean values for the amount of time it would take for the entire landscape to burn, assuming all landscape components were held constant. In the coupled model runs, however, the distribution of burnable areas changed, allowing for the observed fire rotation intervals to differ from those of the reference landscape.

UGM model and simulations

The Clarke Urban Growth Model (UGM) (Clarke and Gaydos 1998) was linked with LANDIS because it is a spatially and temporally explicit model with compatible scales. UGM is a cellular automaton (CA) model that predicts the spatial extent of urban expansion based on repeated application of growth rules and weighted probabilities that encourage or inhibit growth. Broad-scale patterns of development emerge as a result of local interactions between individual cells and their neighbors, and growth is more likely to occur on gentler slopes, near existing settlements, and along transportation corridors. The model also simulates growth of isolated clusters of new urban development.

The predictive strength of the model results from the calibration process that statistically and spatially associates future urban growth with historic growth patterns in the study area using a combination of hindcasting and Monte Carlo techniques. Hindcasting is a method used to explain dynamics observed up to the time and place where the original data were gathered. In the UGM, hindcasting fits simulated data to historical data, assuming that growth patterns in the past can be captured to reasonably forecast into that regions' future. This is done by finding the best combination of five calibration coefficients that affect the application of growth rules in the model. Monte Carlo techniques are used in this calibration process to run through thousands of simulations using different combinations of these coefficients. Every time the model simulations reach a date for which there are historic data, various measures of fit are calculated to compare, for example, the actual versus simulated number of urban pixels, number of edges (urban adjacent to non-urban), and number of separate clusters. Spatial correspondence is determined through a modified Lee-Sallee shape index (a ratio of the intersection over the union). The calibration coefficient combination that produces the best fit (highest r-squared values) between the simulations and the historic data is then used to seed the model to predict into the future. We calibrated the UGM for the SMMNRA using four dates of historic urban extent (1947, 1976/1977, 1989, and 2000) and two dates of transportation maps (1947 and 2000). We predicted urban growth from 2000–2050 using 100 Monte Carlo iterations, then converted the annual probabilistic images to binary maps at 95% or greater likelihood of development for input into the LANDIS model.

Model integration

We assimilated the urban growth predictions into LANDIS by manipulating the landtype map. Although the primary function of the landtype map is to partition the landscape into homogenous ecological units that differentially affect vegetation response, the LANDIS model also allows special landtypes, such as waterways or urban areas, which can be designated as ‘‘non-active’’ and excluded from vegetation simulation. LANDIS ignores non-active landtypes so that no species can establish on them and fire cannot spread on or across them. Therefore, we overlaid all urban land (current urban areas and areas predicted to become urban) on the reference landtype map and created a new, non-active landtype designated as ‘‘urban core.’’ We also overlaid a map of roads in 2000 on the reference landtype map to create another new landtype. Although roads may act as fire breaks in some circumstances (Radtke et al. 1982), fires have jumped roads, even major highways, in the chaparral under high wind conditions (Halsey 2004). Therefore, we kept roads as active landtypes so that fire could potentially spread across them, but only at a low probability. We set the species' establishment probabilities on roads to zero.

We also created WUI landtypes to capture the spatial pattern of human influence on the fire regime through increased probability of ignition and establishment of exotic grass. According to the Federal Register definition, there are two types of WUI (USDA and USDI 2001). Intermix WUI is where housing development intermingles with wildland vegetation; and Interface WUI is where housing development abuts wildland vegetation. Both types of WUI are a function of housing density, which is not predicted by the UGM. In the Santa Monica Mountains, almost all ignitions are anthropogenic, and most originate along roadsides and other areas of human activity (NPS 2005). Without empirical data to construct a sophisticated gradient of effects on the landscape, we created 90 m buffers (one pixel) around roads and urban areas, approximating an Interface WUI, under the assumption that most human-caused ignitions occur within close proximity to these areas. This distance also corresponds closely to a 100 m buffer distance around roads to specify higher risk of human-caused ignitions in Colorado (CSFS 2002). To maintain the distinctive ecological conditions of the original landtypes, however, the WUI was subdivided to create a WUI variant of each of the seven original landtypes. Because we lack data to quantify the exact effect of more ignitions on fire frequency, we parameterized the ignition probabilities in the WUI landtypes so that the fire rotation intervals would be 25% shorter than those in their respective non-WUI landtypes, based on the degree of change that has been observed in fire frequency in the last century (Keeley et al. 1999). We increased the probabilities of establishment for exotic grasses to 100% for all WUI landtypes because these species are very likely to invade from developed areas (Sauvajot 1995). The probabilities of establishment for all of the other species, however, remained the same as the original landtype.

Simulation experiments

Loose coupling involved running the LANDIS simulations with the final urban extent prediction (2050) incorporated into the first time step (2000). We overlaid the 2050 urban extent on the 2000 landtype map and gave the predicted urban core areas and WUI buffers precedence over the old landtypes, including the roads. The landtype map remained the same for the duration of the simulations. The simulations were run for 50 years for the three fire regime scenarios and were each replicated 10 times.

We accounted for incremental urban expansion over time in the tightly coupled approach by updating the landtype maps with the urban growth predictions (e.g., using a new landtype map) for every annual time step. Because the urban core landtypes were non-active, any vegetated areas that became urbanized during the simulations were excluded in future time steps, thereby simulating the direct loss of habitat.

Analysis

To test our hypotheses, we calculated the change in area of the WUI and non-WUI landtypes for years 2000 and 2050 and compared the loosely and tightly coupled model runs to a reference landscape for the three fire regime scenarios. To test the risk of repeated fires on the landscape, we compared spatially-explicit fire return intervals using overlaid GIS maps of fire events for all 50 years in the simulations and then averaged the number of years between successive fire events for all pixels in each landtype. To analyze the effect of the simulations on vegetation, we compared the extent and spatial pattern of three functional vegetation types: two that represent the primary post-fire response strategies characteristic of chaparral (obligate seeders and obligate resprouters), and one was the sub-shrub vegetation type, coastal sage scrub.

Obligate seeders (e.g. *Ceanothus megacarpus*) recruit from long-lived dormant seed banks that are cued by fire to germinate and rarely recruit new individuals in the absence of fire (Keeley 2000). As it takes 5–25 years for obligate seeders to replenish their seed banks following fire, they are susceptible to decline and type conversion under high fire frequencies (Keeley 1986). On the other hand, obligate resprouters (e.g. *Quercus berberidifolia*) do not produce new individuals following fire; instead, these species vigorously resprout. Obligate resprouters are longer-lived and more shade tolerant than obligate seeders, so they are consequently resilient to a wider range of fire rotation intervals (Keeley 1986).

Coastal sage scrub species (CSS) (e.g. *Salvia* spp.) are drought-deciduous subshrubs that occupy lower-elevations than chaparral on coastal mountains and inland valleys. CSS species are shorter-lived and less shade tolerant than chaparral, but also mature early and recruit continuously between fires (Westman 1982). Although they don’t have a fire-cued seed bank, all of the CSS species we simulated resprout following fire, but with different probabilities (Malanson and O’Leary 1982). These species can often persist under fire frequencies that eliminate chaparral (O’Leary 1995) and may replace chaparral at fire rotation intervals of 5–10 years (Keeley 2000). However, under extremely frequent fire, CSS can also start to decline (Haidinger and Keeley 1993).

Results

The total edge calculated between urban land and natural habitat increased by 80% over the course of the simulations, but there was no net increase in WUI area from 2000 to 2050. Non-WUI vegetated landtypes experienced a 30% decrease in area. Substantial change in WUI occurred, but it was disproportionate among landtypes (Fig. 3). Whereas the two high-elevation landtypes and the high coast landtype gained substantial WUI area, the two interior landtypes and the low coast landtype lost WUI over time. The WUI area in the transition landtype between the coast and the mountains only increased slightly.

The total area burned on the landscape for the non-WUI and WUI landtypes, for all three fire regime scenarios, differed only slightly when LANDIS was coupled with the UGM (compared to the reference landscape); but the average fire return intervals differed between the coupled model runs and the reference landscape (Fig. 4). The mean fire return interval was longer in the reference landscape than in the loosely coupled model runs, but the tightly coupled model runs had a longer mean fire return interval than the loosely coupled runs and the reference landscape. At a larger scale, the spatial pattern of high fire frequency was similar across the model runs, with most fires occurring along the coast and in the western portion of the landscape (Fig. 5).

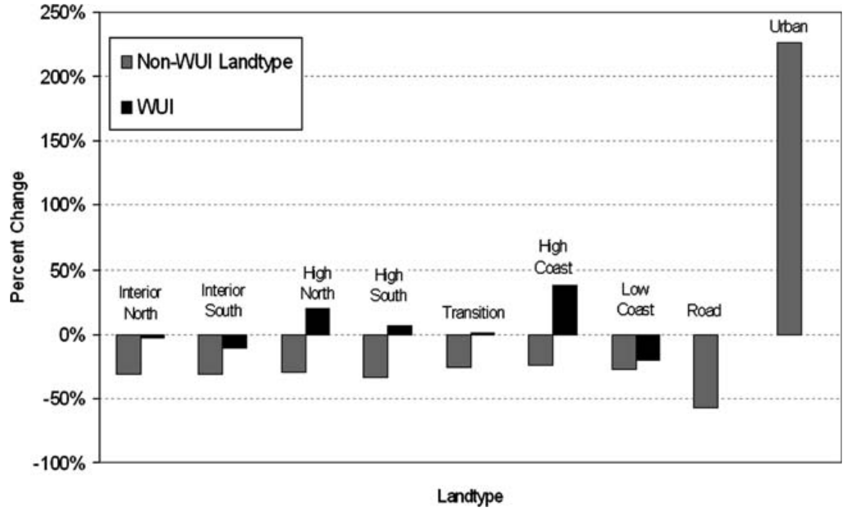

Fig. 3 Percent change in area of landtypes and their respective WUIs from 2000–2050

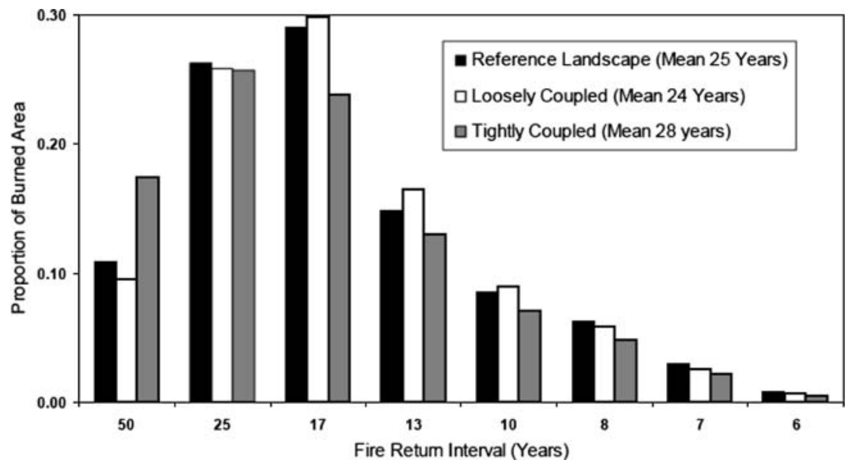

Fig. 4 Distribution of total area burned by fire return interval classes for the short fire regime scenario of the reference landscape, loosely coupled, and tightly coupled model runs

Although the final extent (i.e. total area of cover) of the plant functional types was substantially lower in the coupled runs than in the reference landscape, there was little difference between the loosely and tightly coupled runs for all three of the fire regime scenarios (Fig. 6). However, there was a distinct difference in the functional types' dynamics over the course of the simulations. The extent in the tightly coupled runs declined in proportion to the landscape becoming urbanized until the cover became similar to that in the loosely coupled runs, which happened after approximately 30 years for all runs.

Although there were many localized differences, the general spatial pattern of the functional types' extent was similar between the reference landscape and both of the coupled model runs (Fig. 7). In all of the runs, the obligate seeders gained the most cover in the west and lost in the southeast in the long scenario, and they lost substantial area along the coast in the short scenario, where the fire frequency was highest.

The extent of the obligate resprouters changed less than the obligate seeders, and the locations of gain and loss of cover were patchier. Across all scenarios and runs, most of the gain occurred around the perimeter of the original distribution and expanded into the coastal areas with high fire frequency in the short scenario. Most of the loss occurred in the interior portions of the study area in locations that favored other functional types.

For the CSS species, much of the area that was converted through urbanization in the coupled model runs also declined in the reference

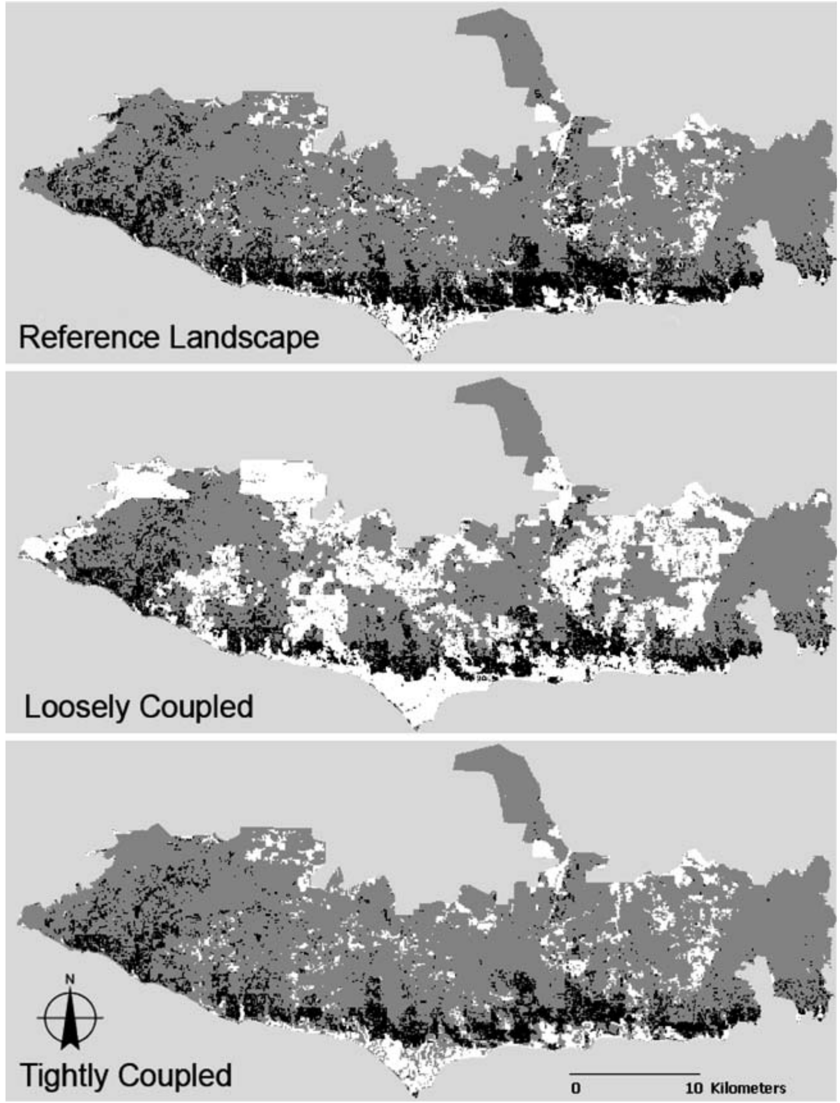

Fig. 5 Maps illustrating locations that burned five times or more (black) for the short fire regime scenario of the reference landscape, loosely coupled, and tightly coupled model runs. White represents urban area at year 2000, and gray represents areas that burned fewer than five times

landscape for the long scenario (in the interior and northwest), but CSS gained several patches in the middle of the landscape in the coupled model runs that were not gained in the reference landscape. In the short scenario, the areas that were lost to urbanization in the coupled model runs remained on the reference landscape.

Discussion

Based on the substantial expansion of the WUI in the recent past, and the expectation for urban growth to continue in a sprawling pattern (Scott 1995), our first hypothesis was that increased urban development would contribute to an increase in the extent of the WUI. Although it was surprising that there was no net increase in the WUI, recent trends have indicated that Intermix WUI is increasing far more than Interface WUI (Hammer et al. in press), and our buffers were designed to approximate Interface WUI. The lack of WUI increase can be explained by the clustered spatial pattern of urban development in the simulations, with high rates of infill that converted the vegetated WUI into urban core. The low net WUI change, however, masked more substantial gains and losses that occurred disproportionately

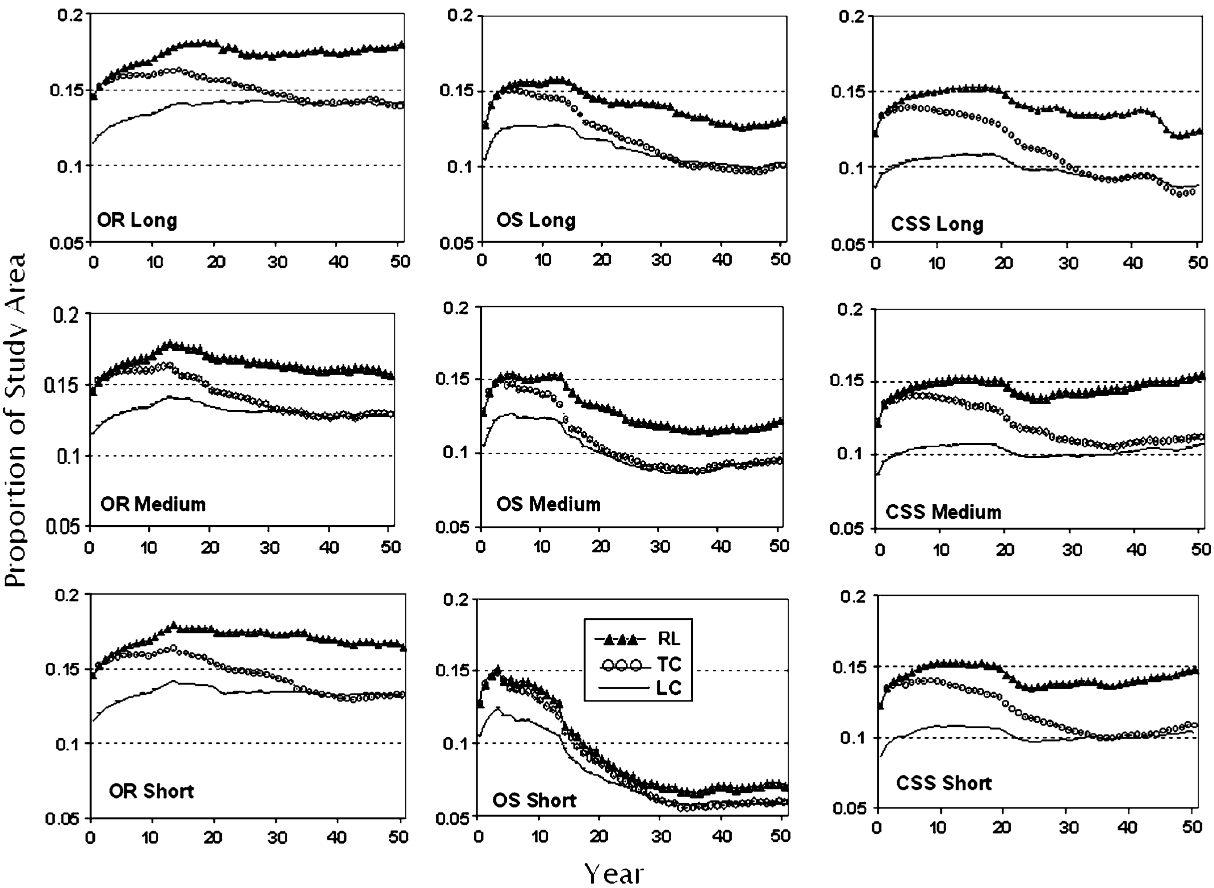

Fig. 6 Proportion of study area occupied by the obligate resprouters (OR), obligate seeders (OS), and coastal sage scrub species (CSS) over 50-year simulations for the long, medium, and short fire regime scenarios of the reference landscape (RL), loosely coupled (LC), and tightly coupled (TC) model runs

among landtypes, which also reflected the different types and amounts of urban growth across the landscape. For example, although the low coast landtype lost the greatest proportion of WUI, much of this landtype was already developed at the beginning of the simulations. Therefore, most of the predicted urban growth in this landtype occurred as infill between the developed areas. On the other hand, the high coast landtype, with the highest increase in WUI, experienced more sprawling development from the expansion of the developed areas in the low coast; therefore, less infill occurred because this area was sparsely developed in 2000.

Because the WUI did not increase as much as we expected, the total area burned was similar between the coupled model runs and the reference landscape. Regardless, there was a difference in fire return intervals, which partly supported our second hypothesis that urban development would increase the risk of repeated fire on certain parts of the landscape. However, the shorter fire return intervals were not solely a function of urban growth as we expected. While the average fire return intervals were shorter in the loosely coupled runs than the reference landscape, the fact that the fire return intervals were longest in the tightly coupled model runs demonstrated that change to average fire return intervals is a function of time. With the reference landscape and the loosely coupled simulations, the location of urban extent and WUI were static for all 50 years, leaving more time for fires to recur in the same locations; but with the tightly coupled model runs, the configuration of the most fire-prone landtypes changed dynamically, the way new urban devel-

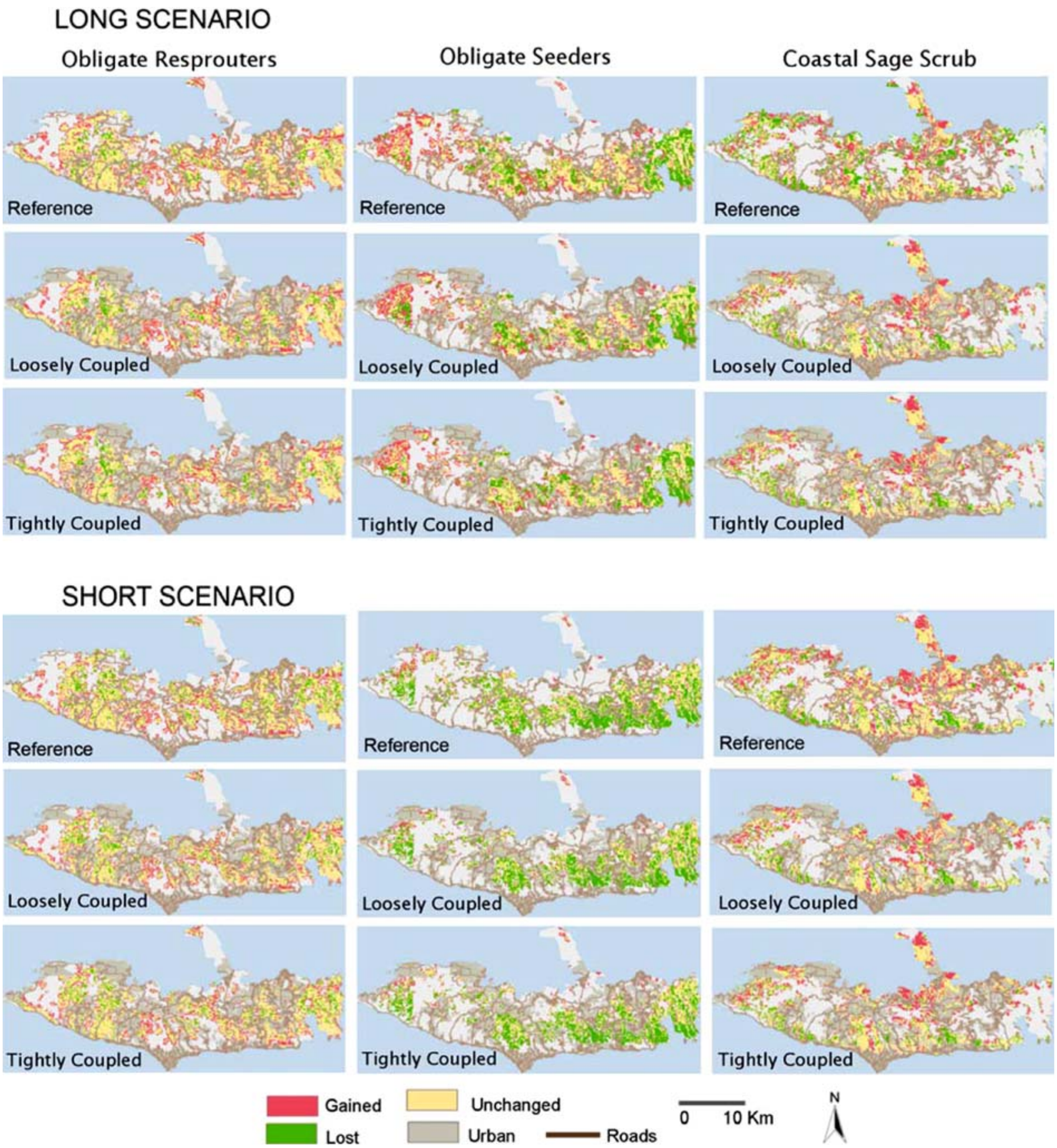

Fig. 7 Map showing the distribution of areas lost, areas gained, and areas that maintained cover by the obligate resprouters, obligate seeders, and coastal sage scrub species from 2000 to 2050 for the long fire regime (Top) and the short fire regime scenario (Bottom) in the reference landscape, loosely coupled, and tightly coupled model runs

opment would also shift the location of ignitions across the landscape. An important management implication of these results is that, as human activities expand into the landscape, the spatial pattern of ignition sources can also shift, and there may be a lag time before cumulative ecological impacts, such as the response to repeated fires in those locations, become apparent.

The fact that aggregated patterns of predicted urban growth resulted in minimal increase of the WUI with no subsequent increase in fire suggests that the highest fire risk may occur at intermediate levels of urbanization due to the spatial arrangement between ignition sources and continuous vegetation. In other words, there may be a threshold at which fire frequency from increased ignitions is offset because urban infilling reduces available fuel. Fire suppression efforts are often more effective in accessible areas with fragmented fuels (Radtke et al. 1982; Cardille et al. 2001). This phenomenon, in which increased fire frequency levels off, was observed in the East Bay region near San Francisco, CA, which also has an anthropogenic fire regime with few lightning-ignited fires. In this region, increasing fire frequency paralleled human population growth until the latter part of the 20th century, when the number of fires began to level off, despite the fact that the population was still growing (Keeley 2005).

The hypothesis that intermediate levels of urbanization may create the greatest fire risk may also be a function of scale. Percolation theory describes how a landscape's connectivity undergoes an abrupt transition from connected to unconnected at critical thresholds, which affect the flow of disturbance or other processes across the landscape (Turner et al. 2001). Disturbance is expected to percolate best across a random landscape that is approximately 60% cover; below 30% cover, connectivity is lost and the spread of disturbance is limited. Based on this theory, the overall proportion of a landscape that becomes urbanized may exceed a certain level at which fire disturbance is reduced due to the interruption of continuous burnable land.

Using three scenarios of fire frequency, we were able to compare the impacts of direct habitat loss with the impacts of altered fire regimes on the native vegetation in the simulations. Our third hypothesis was that functional vegetation types would respond differentially to urban development and increased fire, particularly that CSS and resprouting chaparral species would be more susceptible to direct habitat loss, but that shrubs dependent on fire-cued seed germination would be more susceptible to repeated fire.

As we expected, CSS was most affected by direct habitat loss, primarily because much of its distribution occurs in locations that are favorable for development (e.g. along the coast or in low-slope areas), which is also why this plant community has already lost a substantial proportion of its original extent (O'Leary 1995). Although CSS can be sensitive to extremely short fire return intervals, the most effective way to protect these species would be through direct acquisition or land use planning to prevent conversion to development. The obligate resprouters were also more susceptible to direct habitat loss than to altered fire regimes, as expected, but this was because these species are very resilient to high frequency (Keeley 1986).

Also as we predicted, the obligate seeders were most sensitive to short fire return intervals, and they lost proportionally less area directly to urbanization than the other two functional vegetation types. There is already growing concern over loss of obligate seeders in the Santa Monica Mountains (NPS 2005), and our simulations agree that increased fire frequency appears to be their primary threat. Furthermore, the future scenario in the Santa Monica Mountains will probably resemble that of the short fire regime scenario based on current and projected fire frequencies on the landscape (Keeley et al. 1999; NPS 2005). The current fire management program in southern California advocates landscape-scale prescribed fire. Considering the potential negative ecological effects that could result from adding even more fire to this region, our results support the recent recommendations of the U.S. National Park Service to change the fire management program to focus fuel reduction and prescribed fire on strategic locations such as the WUI (NPS 2005).

The benefits of coupling LANDIS with the UGM were that the combined impacts of direct habitat loss and frequent fire could be evaluated within the same modeling framework. Although the coupled simulations only included feedbacks in one direction, the integrated results nevertheless informed the UGM predictions as well as the LANDIS predictions by providing a dynamic context for the landtype properties, fire regimes, and vegetation types that were being urbanized. Model coupling is becoming a more common approach for testing hypotheses about interacting systems, and decision-makers must consequently deal with trade-offs between realism and efficiency when considering how tightly the models should be integrated (Park and Wagner 1997; Frysinger 2002). The ideal approach would involve only as much effort as necessary to adequately answer the research questions, but the costs of sacrificing realism for efficiency are difficult to determine a priori due to the complex and stochastic properties inherent in many spatially explicit models (Clarke 2004).

Although the loose and tight coupling approaches provided similar answers to our hypotheses in this study, the differences in fire return intervals and rate of vegetation change over time are important to consider from an ecological and management perspective. While the longer fire return intervals in the tight coupling may underestimate the cumulative risk of repeated fires near urban areas (compared to the loose coupling), these simulations do capture the reality of lag effects and delayed response, and also suggest that the risk of local extirpations of obligate seeders is probably increasing over time. The comparison of loose and tight coupling helped to highlight the importance of these cumulative effects.

The other important difference between modeling approaches was the temporal pattern of vegetation change. While the loose and tight coupling approaches both reached similar endpoints, managers may need to consider vegetation change at a finer temporal scale and to estimate which parts of the landscape are likely to be impacted first. Nevertheless, the rate of urban development over time could vary based on a number of factors that cannot be accounted for in the simulations. For example, we assumed that the land currently protected in reserves (approximately 50% of the landscape) would remain excluded from development. However, a policy change could open up that land to future growth. On the other hand, the NPS is looking to acquire more land to purchase for preservation. Therefore, the actual rate of growth might be faster or slower than what was predicted by the model.

In conclusion, the extra effort in time and programming involved with the tight coupling would not have been necessary for us to determine the relative impacts of direct habitat loss and altered fire regimes on the functional vegetation types. However, the finer-scaled detail was important in revealing differences in fire return intervals and rates of vegetation change. Although this comparison is most relevant to coupling LANDIS and UGM, the differences help to illustrate the types of trade-offs to consider when coupling any two spatially explicit, predictive models.

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