SIMULATING THE EFFECTS OF URBAN GROWTH AND FREQUENT FIRE ON SOUTHERN CALIFORNIA COASTAL SHRUBLANDS

A Dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy in Geography

by

Alexandra Dunya Syphard

Committee in charge:

Professor Janet Franklin, Chair
Professor Keith Clarke
Professor Molly Pohl
Professor Dar Roberts

September 2005
The dissertation of Alexandra Dunya Syphard is approved.

____________________________________________
Keith Clarke

____________________________________________
Molly Pohl

____________________________________________
Dar Roberts

____________________________________________
Janet Franklin, Committee Chair

June 2005
Simulating the effects of urban growth and frequent fire on southern California coastal shrublands

Copyright © 2005

by

Alexandra Dunya Syphard
ACKNOWLEDGEMENTS

This dissertation is dedicated to my father and biggest supporter, John O. Syphard, Jr., and to my mother, Frieda Eastmann, who is possibly the most well read human on the planet. My parents and my late grandmother, Mary Keller (who read my mother’s college textbooks for fun), taught me to believe in education for its own sake and helped me to discover that learning is a fun way to spend the afternoon. My parents are a class act, and I am proud to be their daughter.

My advisor, Janet Franklin, has been a constant source of inspiration, and I thank her for providing financial and moral support; for always being there when I needed assistance, yet also trusting me to work independently; and for introducing me to many people who have now become colleagues. I almost don’t have words to express how fortunate I feel to have had her guidance over the last six years. Regardless of how frustrated I might have become with LANDIS (all modelers will empathize), Janet had an uncanny ability of helping me feel encouraged and revitalized after every advising meeting. She is a true role model.

Thanks to Keith Clarke, who took on the role of advisor for me while I was in Santa Barbara. Our weekly meetings and exchange of ideas not only made me feel like part of his team but also taught me much of what I know about modeling.

My other committee members, Molly Pohl and Dar Roberts, have always been responsive and generous with their time, and have provided much inspiration over
the years. The time I spent with Dar in Santa Barbara exposed me to many new approaches for studying post-fire succession at a landscape scale. Molly has been a great mentor, and I learned a lot from her through several years of working together, both in the field and in the GIS lab.

I also feel grateful for the contributions of the following people:

Thanks to Charlotte Coulter and Madhura Niphadkar for help in the painstaking process of image registration and data preparation. The scientists at the Santa Monica Mountains National Recreation Area were instrumental in providing data and ideas for this research, including Robert Taylor, John Tiszler, Marti Witter, Denise Kamradt, and Ray Sauvajot. Carolyn Jones and Greg Hajic were always happy to help me find my way at the UCSB Map and Imagery Library. For helping me to understand the intricacies of LANDIS, I thank Hong He, David Mladenoff, Robert Scheller, Bo Shang, and Jian Yang. Jon Keeley and John O’Leary provided expertise and guidance on the demography of the plants in my study area, and Jon Keeley also provided a much-needed reality check on the model simulations. Thanks to Dena Apalatea for teaching me the value (and fun) of computer programming. Michael Goodchild and Daniel Sui helped me formulate the idea for Chapter 1, Jennifer Swenson provided GIS data for Chapter 2, and Bob von Elgg helped with graphics for several of the chapters. Finally, thanks to the love of my friends, especially Wayne Riker, Marjorie Adkins, and Julie Hart, who supported me when I needed it most.
Funding for this research was provided by a NASA Earth System Science Fellowship (52713) (to ADS) and a National Science Foundation grant (BCS-9818665) to JF. The Department of Geography at San Diego State also generously provided financial support and access to many other resources during my entire tenure at SDSU.
VITA OF ALEXANDRA DUNYA SYPHARD
June 2005

EDUCATION

Bachelor of Arts in English, Mary Washington College, May 1992 (with Honors)
Master of Public Health, Medical College of Virginia, December 1995
Master of Environmental Studies, Virginia Commonwealth University, December 1998
Doctor of Philosophy in Geography, San Diego State University / University of California, Santa Barbara, June 2005 (expected)

PROFESSIONAL EMPLOYMENT

2005-present: Postdoctoral research fellow, University of Wisconsin, Madison
1999-2005: Teaching Assistant, Department of Geography, San Diego State University
1997-1998: Graduate Research Assistant, Department of Urban Studies and Planning, Virginia Commonwealth University
1995-1998: Publications Writer, Alliance for the Chesapeake Bay

PUBLICATIONS


AWARDS

NASA Earth System Science Fellowship, supported for three years (2002-2005)

McFarland Scholarship, San Diego State University (2002)

Full-tuition scholarship, Center for Environmental Studies, Virginia Commonwealth University (1997-1998)

Grant recipient ($7,500) Virginia Environmental Endowment, VA (1997-1998)

FIELDS OF STUDY

Landscape Ecology, GIS, Environmental Modelling, Fire Ecology, Mediterranean-type ecosystems
ABSTRACT

Simulating the effects of urban growth and frequent fire on southern California coastal shrublands

by

Alexandra Dunya Syphard

The foothills and mountains of southern California support fire-prone shrublands that are adapted to the summer drought and winter rains of the Mediterranean-type climate. Humans have altered the region’s natural fire regime through increased ignitions and fire suppression, and the magnitude and direction of those effects varies across the landscape. In low-elevation coastal areas, ignitions at the wildland urban interface have increased fire frequency beyond its natural range of variability. Also, urban growth threatens the high biodiversity in the region through habitat loss and fragmentation. This research used an integrated simulation modeling strategy to evaluate the long-term consequences of altered fire regimes and urban growth on the composition and distribution of native shrublands in a study area administered by the National Park Service. First, an urban growth model (UGM) was calibrated to predict the effects of future development on habitat loss and spatial pattern from 2000 – 2050. Due to the steep terrain in the region, three scenarios were compared
with development prohibited beyond 25%, 30%, and 60% slope. Next, a spatially explicit simulation model of landscape disturbance and succession (LANDIS) was used to predict the effects of high fire frequency on dominant plant functional types. Because human settlement is the primary driver of increased ignitions, the UGM was integrated with LANDIS to evaluate the combined effects of urban development and high fire frequency. The UGM predicted that urban area would increase from 11% of the landscape in 2000 to 26%, 35%, and 47% in 2050, respectively, for the three management scenarios. The spatial pattern of the vegetation became highly disconnected when development was allowed up to 60% slope. The LANDIS simulations predicted that shrubs dependent on fire-cued seed germination were most sensitive to high fire frequency and could potentially convert to other vegetation types under short fire return intervals. In the integrated model runs, fire frequency did not increase as expected because development patterns were aggregated and thus did not substantially increase the wildland urban interface where ignitions were more likely to occur. However, integrating the models contributed to more realism in the simulations than using the models separately.
# TABLE OF CONTENTS

Acknowledgements........................................................................................................iv
Vita..............................................................................................................................vii
Abstract.....................................................................................................................ix
Preface.........................................................................................................................xxviii
Contributions...............................................................................................................xxxii

Chapter I. Spatial aggregation effects on the simulation of landscape pattern and ecological processes in southern California plant communities................. 1

1.0 Abstract............................................................................................................... 1
1.1 Introduction......................................................................................................... 2
1.2 Methods............................................................................................................. 7
  1.2.1 The LANDIS Model..................................................................................... 7
  1.2.2 Landscapes.................................................................................................. 9
  1.2.3 Species analyzed......................................................................................... 12
  1.2.4 Spatial aggregation..................................................................................... 13
  1.2.5 Analysis of process: fire........................................................................... 13
  1.2.6 Analysis of landscape pattern................................................................. 15
1.3 Results.............................................................................................................. 17
  1.3.1 Fire............................................................................................................ 17
  1.3.2 Extent of Species....................................................................................... 17
  1.3.3 Landscape Pattern and spatial distribution of species......................... 19
1.4 Discussion .................................................................................. 21
1.5 Conclusion ............................................................................... 27
1.6 References .............................................................................. 29

Chapter II. Using a cellular automaton model to forecast the effects of urban growth on habitat pattern in southern California ........................................ 47

2.0 Abstract ............................................................................... 47
2.1 Introduction ........................................................................... 48
2.2 Methods ............................................................................... 53
   2.2.1 The study area .................................................................. 53
   2.2.2 The Urban Growth Model (UGM) ....................................... 55
   2.2.3 UGM data preparation ....................................................... 57
   2.2.4 UGM calibration and predictions ....................................... 59
   2.2.5 Landscape pattern analysis ............................................... 61
   2.2.6 Comparison with the GIS overlay model ............................. 64
2.3 Results .................................................................................. 65
   2.3.1 UGM calibration and predictions ....................................... 65
   2.3.2 Comparison to GIS overlay model ..................................... 68
2.4 Discussion ............................................................................ 69
2.5 Conclusion ............................................................................ 74
2.6 References ............................................................................ 76

Chapter III. Calibrating a forest landscape model to simulate high fire frequency in Mediterranean-type shrublands ............................................ 94
5.5 Conclusion

5.6 References

Appendix 1. AML used to update landtype maps with annual urban growth predictions
LIST OF FIGURES

Figure 1-1. The foothills and mountains of the Peninsular Ranges, southern California

Figure 1-2. Simulated mean fire return interval and mean fire size for unreplicated 500-year model runs in the Simplified and Foothills landscapes

Figure 1-3. Fire severity class for all fires during 500-year model runs at the finest, intermediate, and coarsest cell sizes, Simplified and Foothills landscapes

Figure 1-4. Initial extent of plant species cover at the finest, intermediate, and coarsest cell sizes, Simplified and Foothills landscapes. JP, AG, QB, and AF correspond to *Pinus jeffreyi, Arctostaphylos glauca, Quercus berberidifolia, and Adenostoma fasciculatum*, respectively

Figure 1-5. Proportion of initial landscape cover for each species at the finest, intermediate, and coarsest cell sizes, Simplified landscape

Figure 1-6. Proportion of initial landscape cover for each species at the finest, intermediate, and coarsest cell sizes, Foothills landscape

Figure 1-7. Map of *Adenostoma fasciculatum* at model years 1, 250, and 500 for the finest, intermediate, and coarsest cell sizes, Simplified landscape

Figure 1-8. Map of *Adenostoma fasciculatum* at model years 1, 250, and 500 for the finest, intermediate, and coarsest cell sizes, Foothills landscape

Figure 1-9. Lacunarity values for five box sizes (1, 2, 4, 8, 16) at the finest, intermediate, and coarsest cell sizes over 500-year model runs, Simplified
landscape. Particularly high lacunarity values for *A. glauca* reflect the rapid decline of this species on the landscape. *A. glauca* can only regenerate from a fire-cued seedbank, is relatively short-lived and shade intolerant, and thus fared poorly with long intervals between fires. The lacunarity trajectories end when this species disappeared from the landscape .................................................... 45

Figure 1-10. Lacunarity values for five box sizes (1,2,4,8,16) at the finest, intermediate, and coarsest cell sizes over 500-year model runs, Foothills landscape .......................................................................................................... 46

Figure 2-1. The Santa Monica Mountains in southern California......................... 86
Figure 2-2. Input data layers for the Urban Growth Model: urban development and road networks in 1947 and 2000, and land excluded from development (in black)................................................................................................................ 87
Figure 2-3. UGM self-modification of growth coefficients (range 0 – 100) from 2000 – 2050 with development prohibited beyond 25%, 30%, and 60% slope........ 88
Figure 2-4. Predicted growth rate of urbanization in the Santa Monica Mountains from 2000 – 2050 with development prohibited beyond 25%, 30%, and 60% slope ................................................................................................................. 89
Figure 2-5. Predicted urban development in the Santa Monica Mountains in 2025 and 2050 with development prohibited beyond 25%, 30%, and 60% slope............ 90
Figure 2-6. Landscape metrics (see Table 3) calculated for urban growth predictions with development prohibited beyond 25%, 30%, and 60% slope: (A) total core
area, (B) number of distinct core patches, (C) mean core patch area, (D) total edge, (E) number of patches, and (F) largest patch index ................................ 91

Figure 2-7 Landscape metric values (Table 3) calculated for the Standard Development and Maximum Development scenarios of the GIS overlay model and the for dates with the closest corresponding total class area from the Urban Growth Model predictions when growth was prohibited beyond 25%, 30%, and 60% slope. Number of patches and total edge have been divided by 10 ....... 92

Figure 2-8. Overlay of the Standard Development and Maximum Development scenarios of the GIS overlay model with the Urban Growth Model predictions that had the closest total area of remaining vegetation ........................................ 93

Figure 3-1. The Santa Monica Mountains in southern California................. 148

Figure 3-2. Map of seven landtypes overlaid with roads, urban areas, and wildland urban interface in the Santa Monica Mountains, CA ........................... 149

Figure 3-3. Distribution of Ceanothus megacarpus before (A) and after (B) classification into species-age classes for the LANDIS model ................ 150

Figure 3-4. 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………………151

Figure 3-5. Hypothetical resilience of obligate resprouters and obligate seeders across a range of fire return intervals in California chaparral (modified from Keeley 1986) ................................ 152
Figure 3-6. 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.................................153

Figure 3-7. 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........................................154

Figure 3-8. Proportions of study area occupied by obligate seeders (A) and obligate resprouters (B) with dispersal distances of obligate seeders at 5m, 50m, 75m, and 100m 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 5m; OR OS 50 in the legend corresponds to obligate resprouter extent with obligate seeder dispersal distance set to 50 m, etc..........................155

Figure 3-9. Maps illustrating presence of obligate resprouters and obligate seeders at year 0 and at year 50 for the short, medium, and long model treatments......156

Figure 3-10. Simulated resilience of obligate resprouters and obligate seeders across a range of fire intervals in the Santa Monica Mountains, CA..................157

Figure 3-11. 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.

Figure 4-1. The Santa Monica Mountains in southern California.

Figure 4-2. Expected and mean simulated fire return intervals (FRI, by year) by landtype for the long (upper), medium (middle), and short (lower) fire regime treatments. Only one label is used when the expected and simulated values are the same.

Figure 4-3. Proportion of study area occupied and aggregation index values for the five functional groups under the long, medium, and short fire regime treatments. OR = obligate resprouter; OS = obligate seeder; FAC = facultative seeder; CSS = coastal sage scrub; GRASS = annual grass.

Figure 4-4. Mean extent (area) of functional type cover at the end of 10 replicates of 50-year model simulations (with standard errors shown) for the long, medium, and short fire regime treatments. OR = obligate resprouter; OS = obligate seeder; FAC = facultative seeder; CSS = coastal sage scrub; GRASS = annual grass.

Figure 4-5. Maps for the long, medium, and short fire regime treatments illustrating fire frequency in the Santa Monica Mountains over 50-year model simulations.

Figure 4-6. Map produced by the National Park Service illustrating fire frequency in the Santa Monica Mountains from 1925 – 1997.
Figure 4-7. Distribution of net gain and/or net loss of functional type extent in the three treatments over the number of fires that occurred in those areas for 50-year model simulations. Fire frequency was translated into fire return intervals. Note that the scale of the long treatment differs from the medium and short treatments.

Figure 4-8. Map showing the distribution of areas lost and areas gained by the obligate seeder functional group over a range of fire frequencies from year 0 to year 50 in the simulations. H = high fire frequency (5 or more fires); M = medium fire frequency (3-4 fires); L = low fire frequency (1–2 fires); NF = no fires occurred; PB = functional type present in year 0 and year 50 (no loss or gain); AB = functional type absent in year 0 and year 50.

Figure 4-9. Map showing the distribution of areas lost and areas gained by the facultative seeder functional group over a range of fire frequencies from year 0 to year 50 in the simulations. H = high fire frequency (5 or more fires); M = medium fire frequency (3-4 fires); L = low fire frequency (1–2 fires); NF = no fires occurred; PB = functional type present in year 0 and year 50 (no loss or gain); AB = functional type absent in year 0 and year 50.

Figure 4-10. Map showing the distribution of areas lost and areas gained by the obligate resprouter functional group over a range of fire frequencies from year 0 to year 50 in the simulations. H = high fire frequency (5 or more fires); M = medium fire frequency (3-4 fires); L = low fire frequency (1–2 fires); NF = no
fires occurred; PB = functional type present in year 0 and year 50 (no loss or gain); AB = functional type absent in year 0 and year 50 .............................. 213

Figure 4-11. Map showing the distribution of areas lost and areas gained by the coastal sage scrub functional group over a range of fire frequencies from year 0 to year 50 in the simulations. H = high fire frequency (5 or more fires); M = medium fire frequency (3-4 fires); L = low fire frequency (1 –2 fires); NF = no fires occurred; PB = functional type present in year 0 and year 50 (no loss or gain); AB = functional type absent in year 0 and year 50 .............................. 214

Figure 4-12. Map showing the distribution of areas lost and areas gained by the annual grass functional group over a range of fire frequencies from year 0 to year 50 in the simulations. H = high fire frequency (5 or more fires); M = medium fire frequency (3-4 fires); L = low fire frequency (1 –2 fires); NF = no fires occurred; PB = functional type present in year 0 and year 50 (no loss or gain); AB = functional type absent in year 0 and year 50 .............................. 215

Figure 4-13. Vegetation type conversion represented by net area gain or loss for the long, medium, and short fire regime treatments. 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.........................................................216-217

Figure 5-1. The Santa Monica Mountains in southern California.......................... 259
Figure 5-2. Landtype maps for the Santa Monica Mountains depicting urban land and
WUI in 2000 (LANDIS alone) 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 ................................................................. 260

Figure 5-3. Percent change in area of landtypes and their respective WUIs from 2000
– 2050 ............................................................................................................. 261

Figure 5-4. Average simulated fire rotation intervals in the non-WUI and WUI
landtypes for the long, medium, and short fire regime treatments of the LANDIS
alone, loosely coupled, and tightly coupled model runs. The expected fire
rotation intervals for the non-WUI and WUI landtypes were 60 and 45 for the
long treatment, 30 and 22 for the medium treatment, and 15 and 11 for the short
treatment ......................................................................................................... 262

Figure 5-5. Distribution of total area burned across fire return interval classes for the
short fire regime treatment of the LANDIS alone, loosely coupled, and tightly
coupled model runs ...................................................................................... 263

Figure 5-6. Maps illustrating locations that burned five times or more (black) for the
short fire regime treatment treatment of the LANDIS alone, loosely coupled, and tightly
coupled model runs. White represents urban area at year 2000, and
gray represents areas that burned fewer than five times............................... 264

Figure 5-7. Final extent (ha) of functional types after 50 years of simulation for the
long, medium, and short fire regime treatments of the LANDIS alone, loosely
coupled, and tightly coupled model runs. OR = obligate resprouters; OS = obligate seeders; FAC = facultative seeders; CSS = coastal sage scrub species; GRASS = non-native annual grass...265

Figure 5-8. 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 treatments of the LANDIS alone (NC), loosely coupled (LC), and tightly coupled (TC) model runs...266

Figure 5-9. Map showing the distribution of areas lost, areas gained, and areas that maintained cover by the obligate seeders from 2000 – 2050 for the long and short fire regime treatments in the LANDIS alone, loosely coupled, and tightly coupled model runs...267

Figure 5-10. Map showing the distribution of areas lost, areas gained, and areas that maintained cover by the obligate resprouters from 2000 – 2050 for the long and short fire regime treatments in the LANDIS alone, loosely coupled, and tightly coupled model runs...268

Figure 5-11. Map showing the distribution of areas lost, areas gained, and areas that maintained cover by the coastal sage scrub species from 2000 – 2050 for the long and short fire regime treatments in the LANDIS alone, loosely coupled, and tightly coupled model runs...269
LIST OF TABLES

Table 1-1. Species life history parameters used in LANDIS for the Simplified and the Foothills landscapes ................................................................. 33

Table 1-2. Specified and simulated fire rotation intervals (FRI, by year by landtype for the Simplified and the Foothills landscapes ................................. 34

Table 1-3. Species initial and final values for calibration by landtype ................. 35

Table 1-4. Average simulated fire rotation intervals (FRI) and number of fires for the Simplified and Foothills landscapes at fine, intermediate, and coarse cell sizes .......................................................................................................................... 36

Table 2-1. Sequential growth types and controlling coefficients in the UGM, after Jantz et al. (2003) ............................................................................................. 81

Table 2-2. Spatial data used to calibrate the UGM .................................................. 82

Table 2-3. Landscape pattern metrics used in the analysis................................. 83

Table 2-4. Coefficients used for UGM calibration and prediction in the Santa Monica Mountains.............................................................................................................. 84

Table 2-5. Land available for development (hectares, percent of landscape) and land urbanized in 2000 .............................................................................................................. 85

Table 3-1. Variables used to create landtype classes in the SMMNRA............... 143

Table 3-2. Final species life history attributes and parameters used in LANDIS for seven functional groups .................................................................................. 144
Table 3-3. Targeted and mean fire rotation 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 replicate runs) ................................................................. 145

Table 3-4. Probabilities of species establishment on landtypes for 19 species under two scenarios ........................................................................................................................................................................ 146

Table 3-5. Parameter scenarios listed in the order they were evaluated ........................................ 147

Table 4-1. Final species life history attributes and parameters used in LANDIS for seven functional groups ...................................................................................................................... 203
Preface

Feedbacks between human-induced global change and natural disturbance regimes profoundly affect land cover condition and community dynamics in many ecosystems. In southern California Mediterranean-type shrublands, fire disturbance is a necessary agent of change, shaping the distribution, composition, and structure of most plant communities in the region. However, humans have altered the natural fire regime beyond the historic range of variability starting in the 20th century. Despite a policy of fire suppression, population growth and urban expansion in the coastal shrublands has resulted in increased ignitions and fire frequency at the wildland urban interface.

Local fire regimes influence the distribution of plant communities due to species’ differences in post-fire regeneration strategies. Although chaparral vegetation is resilient to a range of fire frequencies, extremely short time intervals between burns are beginning to threaten the persistence of these shrublands. In fact, some species are likely to be converted to other vegetation types, particularly exotic annual grasses that can tolerate (and even promote) repeated burns. Evidence suggests that this “vegetation type conversion” may differentially affect species based on their life history strategies.

Although much is known about the immediate post-fire response of many chaparral species, little is understood about the long-term dynamics of shrubland ecosystems, especially in future scenarios with increasing urbanization and altered fire regimes. Therefore, the objective of this dissertation was to use two simulation
models to forecast potential scenarios of landscape change in the next 50 years in southern California and to evaluate what impacts that change, in combination with altered fire regimes, might have on the distribution of the native shrublands.

**Organization of dissertation**

To examine the effects of high frequency fire on native vegetation, a landscape-scale simulation model of fire disturbance and succession (LANDIS) was selected to predict where and when vegetation changes could occur. Chapter 1 describes an experiment used to evaluate the sensitivity of LANDIS to change in spatial resolution. The model was robust to variations in cell size, but spatial aggregation produced unpredictable model results beyond certain thresholds.

Human settlement is the primary driver of increased ignitions in the coastal shrublands, so an urban growth model (UGM) was selected to integrate with LANDIS to evaluate the combined impacts of high fire frequency and urban development on the landscape. Because urban development is also cited as the top contributor to habitat degradation and species extinctions in southern California, Chapter 2 presents results from using the UGM to predict the effects of future development on habitat loss and spatial pattern for the years 2000 – 2050. Due to the steep terrain in the region, three alternative management scenarios were compared with development prohibited beyond 25%, 30%, and 60% slope. Urban area was predicted to increase from 11% of the landscape in 2000 to 26%, 35%, and 47% in 2050, respectively, for the three management scenarios, and the natural habitat became highly disconnected when development was allowed up to 60% slope.
LANDIS was initially developed for northern hardwood forests, so substantial modification was required to adapt the model to simulate the fire regimes and post-fire regeneration strategies characteristic of southern California and other Mediterranean-type shrublands. Chapter 3 details the methods used to assemble the spatial and non-spatial input to LANDIS; to calibrate the model to simulate three fire regime treatments; and to evaluate the realism of model results based on several parameter scenarios. The model results reasonably reflected how dominant plant species functional groups are expected to respond under a range of fire frequencies in the study area.

Chapter 4 provides a more detailed evaluation of the LANDIS results with emphasis on how five plant functional types responded to increasing fire frequency on the landscape. As expected, shrubs dependent on fire-cued seed germination were most sensitive to very high fire frequency, but those species that produce seedlings and resprout following fire also declined substantially in those treatments. Species that resprout vigorously following fire, coastal sage scrub species, and alien grasses all expanded with more fire on the landscape. If fire frequency continues to increase, the simulations suggested that parts of the landscape may shift from chaparral to coastal sage scrub.

The results of coupling LANDIS with the UGM are presented in chapter 5 along with an analysis of how different the projections were based on two levels of model integration. Because the type of urban development predicted by the UGM was more clustered than dispersed, the wildland urban interface (where increased ignitions
were expected to occur) did not increase to the extent that was expected. Therefore, the fire regime changed little with model integration. Habitat loss occurred more gradually over time when the urban growth predictions were incorporated annually into the LANDIS simulations. However, the overall cover of the dominant plant functional types at the end of the simulations was similar to that from the model runs that incorporated the final urban growth prediction in the initial conditions of the LANDIS simulations.
Contributions

The work in this dissertation is predominantly my own and is presented as five interrelated but self-contained chapters that have either been published, accepted for publication, or prepared to submit to a scientific journal.

Contributions from coauthors are described below for each chapter:

Chapter 1 is primarily based on work presented in:


Janet Franklin provided feedback on the text in the manuscript and helped with the development of ideas regarding model behavior in response to spatial aggregation.

Chapter 2 is primarily based on work presented in:

Syphard, A.D., Clarke, K.C., and Franklin, J. In press. Using a cellular automaton model to forecast the effects of urban growth on habitat pattern in southern California. Ecological Complexity.

Keith Clarke worked with me to implement the urban growth model (UGM) and provided guidance with regards to model calibration. Keith also helped me in the
initial decision-making process when I selected the UGM as the model to use for my research. Janet Franklin helped me develop ideas on how to compare the results of the urban growth model to those of a GIS overlay model. Both coauthors provided editorial feedback on the text in the manuscript.

Chapter 3 is primarily based on work presented in:


Jian Yang and Hong He (from the University of Missouri, Columbia) provided assistance with computer programming and developing an annual time step version of LANDIS. They also worked with me to develop a method to update one of the model’s spatial inputs every time step. Janet Franklin helped me review and organize results from the innumerable model runs that were involved in the calibration process and worked with me to develop a methodology for selecting the best parameter combinations. Jon Keeley provided input with regards to the biological realism of model results.

Chapter 4 is primarily based on work presented in:

Both Janet Franklin and Jon Keeley provided guidance and interpretation with regards to the biological realism of model results. Jon Keeley assisted with ideas on how to improve the model code and parameterization for future simulations in Mediterranean-type ecosystems.

Chapter 5 is primarily based on work presented in:

Syphard, A.D., Clarke, K.C. and Franklin, J. Coupling two landscape models to simulate frequent fire and urban growth on southern California coastal shrublands. Manuscript in preparation.

Keith Clarke introduced me to the issues involved with “loose coupling” vs. “tight coupling” and thus provided inspiration for the experimental design. Janet Franklin helped with discussion of ideas for all aspects of the paper.
Chapter I. Spatial aggregation effects on the simulation of landscape pattern and ecological processes in southern California plant communities

1.0 Abstract

Accurate representation of the processes and components of natural systems is necessary for reliable ecological models, yet data generalization is often needed to reduce unneeded detail and to increase model efficiency. A spatially explicit, raster-based simulation model of disturbance and succession (LANDIS) was used to examine the effects of spatial aggregation on modeled pattern (species composition) and process (fire disturbance). At systematically increased levels of data aggregation, the model was tested on two landscapes, one based on species patterns that were initially random and one based on more realistic distributions, over 500-year time periods for a southern California (Mediterranean-climate) landscape. In both landscapes, spatial aggregation resulted in less frequent, more unpredictable, yet higher-severity fires, and plant species cover became more variable over time in response to infrequent, high-severity fire. The systematic effects of aggregation on pattern, process, and species response suggest that modelers can detect ranges of resolutions for which parameters hold, helping to identify appropriate levels of spatial generalization for their research.
1.1 Introduction

Ecological research traditionally involves observation and description of complex natural systems in small study plots (Shugart, 1998). However, as scientists seek to understand how the earth’s surface processes respond to broad-scale environmental changes (e.g., climate, land use, and disturbance), increasingly sophisticated tools are being developed to understand system dynamics over large areas and long time spans. In particular, ecological models that simulate spatial patterns and interactions over time are becoming more widely used to assess the long-term, broad-scale impacts of different management scenarios (Hunsaker et al., 1993; Mladenoff and Baker, 1999; Waters, 2002). One of the biggest challenges in developing these models is determining appropriate levels of abstraction to accurately, yet efficiently represent the processes and components of natural systems. In other words, to work with the increased data demands of studying large areas over long time periods, it is important to determine how to generalize some information without losing essential detail.

One of the difficulties with identifying appropriate levels of generalization for ecosystem modeling research is that processes such as disturbance and plant dispersal operate at a range of space and time scales (Shugart, 1998; Nathan and Muller-Landau, 2000). Also, space and time scales often differ between observable patterns on the landscape and the mechanisms that create those patterns (Meentemeyer, 1989). The variability of patterns in surface processes and landscape features also depends upon the scale of measurement, so that a phenomenon may
appear heterogeneous at finer-scale (high detail) and homogeneous at coarser-scale (less detail) (Davis et al.; 1991, Levin, 1992; Constanza and Maxwell, 1994). Quantifying heterogeneity and landscape patchiness is fundamental to understanding ecological processes such as succession and species persistence (Levin, 1992). However, although many processes have characteristic scales (space and time intervals for which the process can be detected), the scale dependencies of these processes are often poorly understood because of regional or temporal variation (Davis et al., 1991).

Because of the scale dependency of ecological pattern and process, an important component to landscape-level ecological modeling is specification of an appropriate scale of analysis. Although the representative fraction is typically used to represent spatial scale in cartography (Goodchild and Proctor, 1997), it is logical to consider spatial and temporal scale in ecological modeling in terms of grain and extent (Turner et al., 1989). Grain is a measure of data resolution, where each data unit represents an area on the ground (spatial) or a length of time (temporal). Extent refers to the overall area or duration of analysis. Spatial input to ecological models is frequently derived from remotely sensed imagery, with the grid data structure forming the basis for data layers. Although the initial grain of the grids often matches the spatial resolution of the raw data, exponential increases in computation time and disk space in high-resolution landscapes often require spatial data to be aggregated to coarser resolutions (He and Mladenoff, 1999a).
Although this data generalization may reduce computation time, issues of scale dependency make it necessary to determine critical thresholds of aggregation to capture the appropriate level of abstraction to represent the ecosystem processes and components in the analysis. A number of studies document information loss and distortion when coarsening the resolution of landscape data. In particular, more dominant map classes tend to increase in abundance while rare map classes can diminish in cover or even disappear from the map (e.g. Turner et al., 1989). Reducing the number of cells in dynamic environmental models has also been shown to reduce predicted plant species diversity (Malanson and Armstrong, 1997) as well as change the apparent configuration of forest structural patterns and observed equilibrium (Smith and Urban, 1988). Although data aggregation reduces descriptive detail, certain levels of generalization can also increase predictability and regularity of spatial pattern (Costanza and Maxwell, 1994).

These previous studies provide a context for understanding how data aggregation affects spatial pattern. However, because the scale of process may differ from that of the resulting spatial patterns, it is important to understand the relationship between data representation and interactions between pattern and process (over time) when working with spatially explicit landscape models. Therefore, the objective of this study was to test the sensitivity of a stochastic, spatially explicit, raster-based simulation model of disturbance and plant succession (LANDIS) to systematic levels of data aggregation. The model was tested on two different landscapes in southern California, one (the Simplified landscape) based on simulated species and landscape
patterns and one (the Foothills landscape) based on more realistic species distributions, over 500-year time periods to answer these research questions:

a). Does spatial aggregation affect the dynamics of model process, specifically fire disturbance, and are these effects similar in two different landscapes?

As indicated, coarsening the resolution of landscape data can alter landscape pattern in static maps, typically by reducing landscape heterogeneity, or number of different cover types (Turner et al., 2001). Also, landscape heterogeneity can enhance or retard the spread of disturbance, depending on the likelihood of the disturbance propagating within or between habitat types (Turner, 1989). Therefore, systematic change in initial spatial pattern was expected to affect the occurrence of disturbance across the landscape, and in turn, simulated plant species composition, with effects becoming more magnified at each level of aggregation over time.

Assuming aggregation increasingly homogenized landscape pattern, it was also hypothesized that the Simplified landscape would respond more dramatically than the Foothills landscape because the Simplified landscape was populated with fewer landscape elements to begin with. However, because the target fire regime parameters and life history responses of plant species were similar between landscapes, the direction of change (e.g., rate of disturbance response to aggregation) was expected to be similar. In an increasingly homogenized landscape, fire disturbance might be expected to increase due to reduced spatial barriers to spread, such as younger age cohorts or patches of more flammable vegetation. However, even if a landscape becomes increasingly homogenized by reducing the number of
cover types, the configuration of and contrast between landscape elements may vary, indicating the degree of difference and abruptness of transition between landscape elements (Forman and Godron 1986). Therefore, a lacunarity index was used to determine the effects of aggregation on landscape texture.

b). Does aggregation produce different effects for different plant species?

The two landscapes were each initially developed to analyze the effect of altered fire regimes on the distribution of native plants in southern California. Because succession is driven by life history traits in LANDIS, and because plant demographics are keyed to fire in the chaparral shrublands of southern California (Zedler 1995), aggregation was expected to differentially affect plant functional groups. Specifically, by changing the rate of disturbance across the landscape, aggregation was expected to produce more dramatic changes in extent of fire-sensitive shrub species than for fire-tolerant tree species.

c). Is there a temporal pattern to the effects of this change in resolution?

Change in vegetation pattern occurs at a scale equal to the time interval required to record their dynamics (Turner et al., 2001). In other words, gradual changes that result from cumulative effects are difficult to detect over a short time period, and different ecological systems have unique temporal signatures, depending on rates of disturbance and/or longevities of species on the landscape. Zedler and Zammit (1983) give the example that if a species were declining in abundance 20% after each fire, it would require three fires to see a 50% reduction in the species cover.
Therefore, it was assumed that aggregation would produce feedbacks between pattern and process, with the effects becoming more pronounced over the course of the simulations.

1.2 Methods

1.2.1 The LANDIS Model

LANDIS is a raster-based model that simulates forest landscape dynamics, including stochastically driven interactions between fire regimes, plant life history behaviors, and site conditions. Successional dynamics are simulated over broad spatial extents and long time periods, using a 10-year time step. The cell size for the model is user-specified, and each cell in the model represents a ‘site’ that tracks the presence or absence of 10-year age cohorts of individual plant species. Multiple plant species and age cohorts may be present within one site. Detailed descriptions of the LANDIS model can be found elsewhere (e.g. Mladenoff et al., 1996; He and Mladenoff, 1999b; He et al., 1999) but will be summarized here.

Two spatial data layers, in addition to other non-spatial parameters, are needed as model inputs to LANDIS. The first is a ‘landtype map’ that characterizes homogenous units within a heterogeneous landscape. The ecological units, or landtypes, can be derived from existing ecological land classifications or from maps of climate and terrain-derived variables associated with the spatial distribution of vegetation in the landscape (Franklin, 2003; Host et al., 1996). Each landtype is parameterized with a fuel (biomass) accumulation curve, a mean fire return interval,
and the probability of species establishment for all species that are modeled. The climate and terrain-derived variables define how likely it is that a plant species is able to persist or establish on each landtype, and thus can be interpreted as approximating the species’ fundamental niche. These environmental conditions also determine patterns of fuel accumulation and decomposition, contributing to potential fire severity, over time. Fire severity is represented as an ordinal variable (1-5), and fires of different severity classes are able to kill plant species of different age-dependent fire tolerance classes, also represented as an ordinal variable (1-5). High severity fires are a function of long fuel accumulation times (e.g. time since last fire).

The second spatial input needed to run LANDIS is a ‘species age’ map. Unlike the landtype map, which remains unchanged over time, the species age map sets the initial conditions for the model run by mapping the presence or absence of each species (or functional group) in 10-year age cohorts in each map cell (site). Although initially developed as a forest succession model, LANDIS can simulate any vegetative species, as long as the species’ demographic characteristics can be parameterized.

In LANDIS, species are parameterized based on vital attributes (as in Noble and Slatyer 1980), such as mechanism of persistence, ability to become established, and timing of critical life history events such as age of first reproduction or mortality. Individual trees are not simulated in LANDIS as they are in gap models (Shugart, 1998), nor are physiological processes. However, species-specific life history characteristics are used as model parameters. For example, whereas growth rates and
competition are constrained in gap models by geometrically derived light availability indices, competition in LANDIS is driven by broad ordinal categories of shade tolerance or intolerance. Because LANDIS uses life-history information, succession after fire can take “multiple pathways” (as in Cattelino et al., 1979). Therefore, during a model run, plant species composition is determined by resource limitations, species’ response to fire, and inter-specific competition.

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 also spatially explicit in that spread is contagious, with higher probabilities of spread occurring in neighboring cells with longer time since last fire (greater fuel). Severity also differentially affects age cohorts (with younger cohorts most likely to be killed). Fire size is stochastic, but small fires are more likely to occur than large fires, following a lognormal distribution, and the size is associated with a mean specified in the input parameters. Because LANDIS runs on a 10-year time step, groups of individual fires can occur within one time step.

1.2.2 Landscapes

Because the LANDIS model was developed for northern Midwest forests, the Simplified landscape was initially created to determine if the model could be calibrated to simulate the high-frequency fire regimes characteristic of southern California (Franklin et al., 2001). Because we successfully calibrated the model to
simulate fire cycles within 7% of the specified values, we had confidence in using LANDIS to evaluate altered fire regimes on more realistic landscape patterns in southern California and subsequently developed the Foothills landscape (Franklin et al., subm).

Although both of the simulated landscapes used in this study reflect fire regimes and species’ post-fire response strategies characteristic of southern California’s Mediterranean-type ecosystems, the degree of detail between them varies substantially. Each landscape was considered a separate case study of how aggregation would affect the processes and patterns in model simulations. But because the disturbance regime parameters and plant functional types were similar, we wanted to determine whether data aggregation would produce similar effects in model results given these differences, thus potentially helping to generate hypotheses as to how LANDIS is sensitive to aggregation.

The Simplified landscape comprised a square map populated with an initial random distribution of functional groups representative of six dominant plant species in the region. All of the species were even-aged (10 years old), and fell within four equally sized rectilinear landtypes that reflected the topographically mediated environmental gradient from a low elevation xeric environment to a high elevation mesic environment characteristic of the Peninsular Ranges in California. The species were randomly distributed to see the effects of dispersal and establishment on landtypes for which species had high probabilities of establishment. The Simplified landscape represented the generalized landscape pattern and dominant species
composition of the region, but because of the details left out (of both landscape pattern and species diversity), model behavior was easier to interpret during simulations.

The 3,878-km² Foothills landscape dataset describes the foothills and mountains of the Peninsular Ranges, primarily within San Diego County, California (Figure 1). The climate is Mediterranean with cool wet winters and warm to hot dry summers. On the ocean-facing (cismontane) slopes, coastal sage scrub vegetation dominates lower elevations; chaparral, oak woodland, and big cone Douglas fir (*Pseudotsuga macrocarpa*) forest dominate middle elevations; and mixed conifer forest is found at the highest elevations. The majority of the land is undeveloped and managed either by the USDA Forest Service, state park authority, or Native Americans as tribal land. The spatial inputs for the Foothills landscape included 23 plant species in multiple 10-year age cohorts as well as 11 landtypes. These were derived from environmental data layers including a generalized vegetation map (Franklin et al., 2000; Stephenson and Calcerone, 1999), predicted species distribution maps (Franklin 2002), an ecological type map (Franklin, 2003), and fire history available from the California Department of Forestry, Fire and Resource Assessment Program. Because most of the landscape comprises chaparral, and fires are stand replacing in chaparral ecosystems, species age classes were determined by calculating the time since last fire using the fire history database.
1.2.3 Species analyzed

For both landscapes, the same four species, three shrubs and one conifer species, were selected for the analysis because they represented the range of dominant life history strategies and disturbance responses typical of the southern California landscape. Therefore, we could investigate the role of life history strategy in response to aggregation effects (Table 1). *Quercus berberidifolia* (scrub oak), a large evergreen shrub, responds to fire strictly through vegetative propagation (basal sprouting) and was parameterized as a longer-lived, late-maturing, shade-tolerant species with low probability of establishing from seed even in the absence of fire (Zedler, 1995). *Arctostaphylos glauca* (bigberry manzanita) is an “obligate seeder” that regenerates after fire through fire-cued germination from a persistent seed bank (Zedler et al., 1983). *A. glauca* is less shade tolerant than *Q. berberidifolia*. The most widespread chaparral species in southern California, *Adenostoma fasciculatum* (chamise) can regenerate both from seed and through vegetative propagation after fire (Barro and Conard, 1991), and was parameterized as a shorter-lived species with moderate shade tolerance and susceptibility to fire. The conifer species, *Pinus jeffreyi*, is found above 1500 m in the Peninsular Ranges (Stephenson and Calcerone, 1999), and survives fire through self-pruning and thick bark (Keeley and Zedler, 1998). However, fire kills seeds and cones as well as most saplings (Minnich, 1991). *P. jeffreyi* was parameterized as a long-lived shade-tolerant species with a high probability of establishment on high-elevation landtypes. The species does not resprout after fire, nor does it have the capacity for fire-cued germination.
The life history parameters for each of these four species were the same in both landscapes, and dispersal distances for all species were set to 500 m. Although this distance is unrealistically large for most of the shrub species, it allowed us to isolate aggregation effects from the effects of variation in dispersal distance, and to ensure that species could disperse out of the cells at every level of aggregation.

1.2.4 Spatial aggregation

For each landscape, data aggregation began at the original resolution. The spatial input for the Simplified landscape was created with 250 x 250 cells, each representing a 50 x 50 m area. Using a simple majority filter, the resolutions for the species-age map and the landtype map were systematically degraded in 50 m increments (linear dimension) from 50 m to 100 m, 150 m, and so forth up to 500 m x 500 m cell size. The spatial data for the Foothills landscape were aggregated at eight levels of 30 m increments ranging from 90 m to 300 m; the data were also aggregated to 600 m and to 900 m to generalize over the same two orders of magnitude as the Simplified landscape.

1.2.5 Analysis of process: fire

One of the primary determinants of fire disturbance in LANDIS is the specification of, and model calibration for, fire return interval on each landtype. A fire return interval (FRI) is defined as the time required to burn an area equivalent to the size of the area of analysis. To calibrate the model, fire calibration coefficients were systematically adjusted for each landscape until the simulated FRIs
approximated the specified FRIs (for full description of calibration methods, see He and Mladenoff, 1999a; Franklin et al., 2001). LANDIS was calibrated at the finest level of resolution used in each landscape, with the mean FRI specified at 70 years for the Simplified landscape and mean FRI specified at 81 years for the Foothills landscape. FRIs are specified for each landtype in LANDIS; therefore, the mean FRIs differed slightly between the two landscapes due to the difference in number and diversity of landtypes. Because the objective of this research was to understand the relationship between aggregation and model behavior, the model was only calibrated at the finest level of resolution for each landscape. Otherwise, several model parameters would have to be changed with each level of aggregation, potentially confounding the results of the study.

The fire history records for the 20th century indicate that, because of increased ignitions in low-elevation landtypes, fire return intervals in these areas are short (~30-40 years) (Keeley et al., 1999). On the other hand, effective fire suppression in high-elevation landtypes has lengthened fire return intervals by a factor of two or three (Minnich et al., 1995). For this experiment, the distribution of fire return intervals across both landscapes was designed to approximate this fire regime (Table 2). Because no drastic changes in the distributions of these four species have been noted in this period (e.g., Bradbury, 1974), disturbance parameters and probabilities of species establishment were systematically adjusted in the model calibration to prevent unrealistic changes in species distributions at these specified FRIs (Table 3).
To test the effect of aggregation on the simulation of fire disturbance, the average number of fires, mean fire size, and FRIs averaged across the landscape were calculated from each model run. Average number of fires per model run was also calculated. Mean fire return intervals were determined by calculating the size of the landscape and dividing by the mean area of the total landscape burned per time interval (converted from decade to year). Mean fire size is mean area burned per decade. Because LANDIS is a stochastic model, 10 replicated simulations were conducted, and FRIs were averaged, for three of the resolutions (finest, intermediate, and coarsest) in each landscape.

1.2.6 Analysis of landscape pattern

Because of the complex interactions of species competition and disturbance in LANDIS, it is difficult to directly observe patterns of seed dispersal after model runs (He and Mladenoff, 1999b). Therefore, the effects of aggregation on landscape pattern were measured by the areal extent of each species in each time step in the model (the total area of all cells in which it was present). Distribution patterns of the species were also compared visually.

In addition to extent, spatial pattern of each study area was quantified through a lacunarity index. Lacunarity analysis is a multi-scaled approach to quantifying landscape texture, measuring the distribution and variation of gap sizes between geometric patterns on a landscape for each cover type. In other words, lacunarity measures the similarity (or dissimilarity) of the shape (e.g., fractal structure) and
degree of contagion (clumped or uniform) of mapped attributes on a landscape (Plotnick et al., 1993; Wu and Sui, 2001). Higher values of lacunarity reflect heterogeneous landscapes with clustered distributions whereas lower values of lacunarity reflect homogenous landscapes with regular distributions. Sparsely populated maps tend have higher lacunarities than densely populated maps.

Lacunarity is calculated by sampling a landscape with a moving window to determine the frequency distribution of occupied pixels (presence/absence of the mapped attribute) for a given number of window sizes. For each window size, lacunarity is calculated as 

\[ 1 + \frac{\text{var}}{\langle \text{\# occupied pixels per window} \rangle^2} \]

where \( \langle \text{\# occupied pixels per window} \rangle \) is the mean number of occupied pixels per window per iteration and var is its variance. Using a multi-scaled approach for capturing landscape pattern can reveal more information about scale-dependent heterogeneity in a landscape than a single-valued index (Plotnick et al., 1993, Wu and Sui, 2001). Other benefits of lacunarity analysis are that differences in pattern can be detected in sparse maps and results are not sensitive to map boundaries. Because different box sizes can be used to calculate lacunarity, it is important to use consistent box sizes when comparing maps of different resolution. Therefore, lacunarity was calculated using five box sizes (1, 2, 4, 8, 16 cells in length) for each map produced during each time step in all model runs. The statistical package Apack (Mladenoff and DeZonia, 1999) was used for the calculations.
1.3 Results

1.3.1 Fire

In the Simplified landscape, the FRI systematically and substantially lengthened (by an order of magnitude) while the fire size decreased with increasing levels of aggregation (Figure 2). Fire frequency also declined. When averaged across 10 replicate model runs, the FRI at 50 m (fine grain), 250 m (intermediate grain), and 500 m (coarse grain) was 56, 326, and 625 years respectively (Table 4). The FRIs also varied substantially, as reflected in the standard deviations, between model runs at the coarsest levels of aggregation (Table 4). Maps reflecting the sum of all fire disturbances during model runs revealed that aggregation affected fire severity across the landscape (on an ordinal scale of 1 – 5) (Figure 3). At increasing levels of aggregation, lower severity fires diminished, and only class 4 and 5 (high severity) fires were present on maps at the coarsest level of resolution. In the Foothills landscape, aggregation from 90 to 900 m also increased mean FRI, decreased mean fire size (but only about two-fold), and reduced fire frequency (Figure 2), doubling the FRI (Table 4). Again, fewer, yet more severe fires occurred at coarser levels of aggregation (Figure 3).

1.3.2 Extent of species

Aggregating the input data resulted in changes in the initial species extent in the Simplified landscape (Figure 4). Relative to the original resolution, the intermediate grain had less *P. jeffreyi* and *A. glauca* and more *Q. berberidifolia* and *A.
fasciculatum. At the coarsest grain, however, *P. jeffreyi* and *A. glauca* occupied a greater extent of the landscape than *Q. berberidifolia* and *A. fasciculatum*. The Foothills dataset reflected no substantial change in plant species extent in the input data with increasing levels of spatial aggregation. The coarsest level of resolution, however, indicated a slight decrease in the extent of *P. jeffreyi*, and a slight increase in the extent of the other three species.

In the Simplified landscape, the trajectories of species extent over time in the fine-grained model runs formed a cluster with a different pattern than the trajectories of the coarse-grained model runs (details not shown). As the resolution became coarser, the species’ cover dynamics became increasingly variable (Figure 5). Also, the magnitude of change over time was more dramatic in the coarser grains. The two species that resprout after fire, *A. fasciculatum* and *Q. berberidifolia*, occupied a greater proportion of the landscape at the finest resolutions. *P. jeffreyi*, however, occupied a lower proportion of the landscape at finer than at coarser grains. The seeder, *Arctostaphylos glauca*, declined rapidly (and disappeared from the landscape for all aggregation levels) after reaching its longevity, and the species cover declined more rapidly in the coarse-grain simulations. For all four species, the difference in extent between the fine grain and the coarser grains became more pronounced after 50-100 years.

Similar to the Simplified landscape, the Foothills landscape species maintained a more even and constant proportion of the landscape over time at the fine-grained level of aggregation than at the intermediate and coarse grains (Figure 6). The two
sprouting species maintained a larger proportion of the landscape over time in the finest grain; however, the effect of scale was minimal compared to the Simplified landscape. In the third and fourth centuries, the species’ trajectories revealed substantial variability at the intermediate and coarsest levels of aggregation. Although the seeder, A. glauca, declined in the Foothills landscape, as it did in the Simplified landscape, the cover stopped decreasing after approximately 100 years, then maintained a stable pattern of variability in response to fire. P. jeffreyi increased slightly in abundance over time at all resolutions (while it did so only at the coarser levels of resolution in the Simplified landscape). As with the Simplified landscape, the increased variability of species cover became more apparent over time.

1.3.3 Landscape pattern and spatial distribution of species

The effects of aggregation were visually apparent in the Simplified landscape, as illustrated by maps of A. fasciculatum (Figure 7). Moving from finest to coarsest resolution, the spatial patterns became blockier and the species distribution was more restricted to the two middle landtypes where the probability of establishment was highest. At 50 m resolution, concentric rings of dispersal were apparent in the spatial patterns reflecting post-fire recovery over time. At increasingly coarser resolutions, however, these patterns of establishment were less obvious. Fewer age classes dominated the landscape at coarser resolutions.
In the Foothills landscape, the spatial patterns also became blockier and more irregular at larger resolutions in the maps of *A. fasciculatum*. At 90 m, the maps revealed clustered areas of young age cohorts on the left region of the maps (at the more fire-prone lower elevations) at years 250 and 500. However, at 300 m and 900 m, these young, clustered age cohorts were increasingly substituted with older, more sparsely distributed age cohorts. As in the Simplified landscape, fewer age classes dominated the landscape at coarser resolutions.

In both landscapes, the patterns of lacunarity over time had an inverse relationship with species extent, particularly after large fire disturbances. In the Simplified landscape, lacunarity values for the two sprouters increased with increased levels of aggregation, indicating a more heterogeneous pattern (with more variable gap sizes) on the landscape (Figure 9). Lacunarity values for *Q. berberidifolia* increased over time as well as over levels of aggregation, and were consistently higher than lacunarity values for *A. fasciculatum*. On the other hand, lacunarity values for *A. glauca* decreased with increased levels of aggregation as the species disappeared from the landscape, but overall values were substantially higher than those for the other species. Lacunarity values for *P. jeffreyi* remained low over all levels of aggregation.

In the Foothills landscape, large fluctuations in the lacunarity plots corresponded with substantial fire events (Figure 10). For example, large fire events in the middle of the 5th century at 300 m resolution and the middle of the 4th century at 900 m resolution resulted in large increases in lacunarity values for *A. fasciculatum, Q.*
*berberidifolia, and A. glauca.* Lacunarity values for *P. jeffreyi*, however, remained more stable over time and over each level of aggregation, reflecting minor changes in extent in response to the fire events described above. Similar to the Simplified landscape, the overall lacunarity values for *A. glauca* were higher than those for the two sprouters, and the lacunarity values for *P. jeffreyi* were lower than those for the two sprouters.

### 1.4 Discussion

Previous studies have documented that spatial aggregation can lead to information loss or distortion of landscape data on static maps. This study systematically coarsened the resolution of the spatial input to a landscape simulation model to determine if aggregation would not only affect simulated spatial pattern, but also alter dynamic processes over 500-year model runs.

The effect of aggregation on the input spatial data was apparent for the Simplified landscape that was populated with equal but random distribution of cover for each species at the finest level of resolution. Although the relative proportion of species cover changed at different levels of resolution, no systematic trend was apparent (e.g., no species increased or decreased consistently with aggregation), likely due to the initial random distribution and equal initial species abundance. The effect of aggregation on the input data was less dramatic in the Foothills landscape; however, these minor effects are consistent with previous research in which dominant map classes increased and rare classes decreased or disappeared when a
simple majority filter was applied (e.g. Moody and Woodcock, 1995). The only species that declined in initial cover with aggregation, *P. jeffreyi*, occupied 3 percent of the initial landscape, whereas the other species that increased in cover occupied 12 to 24 percent of the landscape. The other 19 species on the Foothills landscape changed only slightly in cover with aggregation, and thus, the overall change in this landscape was more evenly dispersed across many species than in the Simplified landscape, where more substantial changes were apparent for each of the six species. Despite these minor changes in initial spatial pattern, aggregation did affect fire disturbance, species cover, and spatial configuration over the course of model simulations, as expected.

In terms of the first research question, aggregation reduced the amount (and increased the variability) of fire on the landscape, as evidenced by increase in fire return intervals, decrease in fire size, and lower fire frequency on both landscapes. Previous research demonstrated that coarsening the grain of spatial data increases landscape homogeneity (Levin, 1992; Costanza and Maxwell, 1994). Although the lacunarity indices in this study reflected increased heterogeneity in landscape texture (variability in gap sizes), the overall landscape became simpler with fewer age classes and number of patches. In real landscapes, equilibrium is expected when patch sizes are small relative to the homogenous landscape unit (Pickett and White, 1985). However, with aggregation, the cell sizes became proportionally too large compared to the overall extent of the landscapes to capture the more fine-scale
dynamics that would more realistically characterize fire-prone southern California landscapes, leading to less predictable, more infrequent disturbances.

The reduction in fire disturbance with aggregation is likely a product of interplay between fewer cells on the landscape with interactions between both of the spatially explicit processes in the model, fire spread and seed dispersal. In LANDIS (as well as real landscapes), seed dispersal directly affects species abundance, composition, and migration rates (He and Mladenoff, 1999b). The species in this experiment were all parameterized with the same minimum dispersal distances, which were large enough for species to migrate out of their cells, regardless of level of aggregation. Nevertheless, aggregation reduced the number of cells available for establishment because, with progressively larger cell sizes, fewer cells fell within the distances that defined the species’ dispersal radii. In the fine-resolution simulations, concentric rings of seed dispersal were more apparent on parts of the landscape, reflecting successful establishment of species within their dispersal radii. However, in the absence of fire, species distribution patterns became more regular at coarser resolutions. Therefore, with fewer available cells for establishment, competition became an important driver of landscape composition, reducing the abundance of less shade-tolerant species. In our simulations, the more shade tolerant species were also more fire tolerant, thereby increasing the potential for higher abundance of fire tolerant species across the landscape.

Aggregation also reduced the number of cells available for ignition. In LANDIS, the probability of fire ignition is spatially stochastic. Ignition coefficients determine
the proportion of cells to be checked within each landtype, and these cells are then selected randomly. With fewer cells on the landscape, the absolute number of cells to check were also fewer. After a cell is selected, successful ignition is dependent upon time since the last fire as well as the landtype-specific FRI. Once an ignition is successful, the number of additional cells to be checked decreases exponentially so that the number of fires that occur in each time step is not directly determined by the ignition coefficient. If an ignition is successful, the fire spread process is required to actually place a fire on the landscape, and is a function of many factors, including spatial pattern as well as age and fire tolerance of the species in the cell. Older, more fire tolerant species are less likely to burn and carry a fire throughout the landscape. Therefore, it appears that competition gradually increased the abundance of shade and fire tolerant species on the landscape, preventing fires from spreading on the landscape. Even if a successful ignition did not result in an actual spreading fire, the number of additional cells to be checked would have exponentially decreased, thereby also contributing to reduced fire frequency.

With reduced fire frequency, fuel had a longer time to accumulate on the landscape. Therefore, when a fire did occur, it was a high-severity fire that killed older species as well as species with higher fire tolerance. This effect of increased fire severity reflected the intent and design of the (LANDIS) model, based on empirical evidence of fire behavior, that links fire intensity to pre-fire vegetation conditions and the amount of fuel on a site (Turner et al., 1994; He and Mladenoff, 1999a).
In both landscapes, the finest-grained data resulted in more constant proportions of plant species cover over time compared to the larger population fluctuations at coarser levels of aggregation. For example, in the Foothills landscape, species’ cover fluctuated slightly over time in the fine resolution model run, but at the coarsest resolution, two high-severity fires killed a substantial portion of the shrub species, resulting in dramatic population plunges. The trajectory of *P. jeffreyi* only fluctuated slightly in response to these disturbances because this fire-tolerant species grows in high elevation, less fire-prone landtypes that did not burn as completely as the lower-elevation landtypes.

The lacunarity of species cover in both landscapes also changed with data aggregation. Overall, lacunarity values tended to increase as species cover declined, generally in response to large fire events. Because lacunarity reflects the variability in the size of gaps in species cover, it is understandable that fire events increased lacunarity values by creating large gaps. In the absence of fire, landscape patterns became less clumped, particularly due to competition and reduced dispersal, and lacunarity decreased until the next fire event.

Although the two landscapes differed substantially in terms of grain, extent, and number of landscape elements, the general response to spatial aggregation was similar in that fire disturbance declined and species dynamics became more variable. Although it is not possible to isolate all of the factors accounting for similarities or differences in response of these two landscapes, the results nonetheless reflect that
aggregation affected model dynamics through a simplification of the landscape and by increasing the cell size in proportion to the extent of the landscape.

Addressing the second question regarding the differential effect of aggregation on species, plant species responded differently to effects of aggregation, reflecting the importance of life history characteristics in model dynamics. Because the four species were parameterized identically for both landscapes, their responses to aggregation were similar between the two landscapes. The three shrub species, all components of fire-prone vegetation (Zedler and Zammit, 1989), declined with reduction of fire on the landscape. *A. fasciculatum*, a species that can also germinate from seed after fire, maintained a higher proportion of the landscape than the other resprouting shrub, *Q. berberidifolia*, but both species fluctuated in response to fire events. *A. glauca* declined over time more substantially than the resprouters in both landscapes, although the decline was more gradual in the Foothills. With less frequent disturbance, the more competitive *P. jeffreyi* successfully replaced many of the shrubs, resulting in larger, more homogenous patches. In the Simplified landscape, the extreme infrequency of fire resulted in *P. jeffreyi* spreading across almost the entire landscape at the coarsest levels of resolution.

Regarding the third question addressing temporal pattern, a lag time of approximately 100 years or more existed before species extent became more dynamic with aggregation. One explanation for this delay is that the Simplified landscape was initially populated with randomly distributed even-aged cohorts, and the Foothills landscape was populated with a simplified age structure. Therefore,
species dynamics became more pronounced after the initial cohorts either reached age of sexual maturity or reached longevity and died. Also, because of the reduced fire with aggregation, feedback occurred in that fuel accumulated for long periods of time, then severe fires killed the species throughout most of their extent, resetting the clock for the next severe fire and population plunge. The lag time may also result from interactions between data generalization and model stochasticity. Previous research with LANDIS demonstrated that the effect of the initial landscape pattern lasted approximately 100 – 150 years (for northern boreal forests), after which species composition became a product of stochastic feedbacks between disturbance regimes and dominant species (He and Mladenoff, 1999a).

1.5 Conclusion

The results of this study revealed effects of aggregation on pattern, process, and species response for two different landscapes using an ecological simulation model. By simplifying and reducing the total number of cells on the landscapes, aggregation of one to two levels of magnitude substantially stunted simulation of ecological processes, leading to a highly variable fire regime that differed from the targeted one. Aggregation also resulted in larger patches in general (larger cell sizes), and increased lacunarity after fires due to the creation of unrealistically large fire scars. Chaparral landscapes in southern California form more fine-scale heterogeneous species mosaics with smaller, more diverse patches (Keeley and Keeley, 1986). Thus, using overly aggregated results for biodiversity conservation planning could
lead to management decisions that erroneously prescribe a certain fire regime to maintain that habitat homogeneity. In complex landscape simulation models like LANDIS, aggregation effects may not appear immediately. Therefore, modelers should not base the choice of resolution on initial spatial patterns alone, but also over time. Furthermore, because aggregation substantially altered the fire regime, it would be important to recalibrate the model after choosing an appropriate cell size.

Although these results specifically apply to only one simulation model, the similarity in response of two distinctly different landscapes in this study suggests that aggregation effects were systematic and directional for change in fire regime, patch size, and species response. Also, the magnitude of the effect of increasing levels of aggregation declined after intermediate levels of aggregation, suggesting there are ranges of resolutions at both fine and coarse levels for which aggregation produces negligible change in model response. Specifically, effects of aggregation on species extent became more pronounced after the pixel area increased four- to ten-fold, and then lessened after reaching coarser levels of aggregation (e.g., pixel area increased between 11-and 100-fold). Therefore, by using a similar approach to this study, other modelers can make informed decisions when choosing an appropriate level of data resolution. While incrementally increasing cell size, the modeler can detect thresholds of change for which the parameters hold and the model results are comparable and appropriate for their research objectives. Running the model at the coarsest possible resolution while maintaining realistic simulations of ecological processes has practical advantages for researchers and managers of large landscapes.
1.6 References


Franklin, J., Syphard, A. D., He, H., and Mladenoff, D., subm. The effects of altered fire regimes on patterns of plant succession in the foothills and mountains of southern California, Ecology.


Table 1-1. Species life history parameters used in LANDIS for the Simplified and the Foothills landscape

<table>
<thead>
<tr>
<th>Parameter (units)</th>
<th>Q. berberidifolia</th>
<th>A. glauca</th>
<th>A. fasciculatum</th>
<th>P. jeffreyi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Longevity (yr)</td>
<td>120</td>
<td>90</td>
<td>80</td>
<td>400</td>
</tr>
<tr>
<td>Age of maturity (yr)</td>
<td>40</td>
<td>20</td>
<td>10</td>
<td>20</td>
</tr>
<tr>
<td>Shade tolerance (ordinal class 1 – 5)</td>
<td>4</td>
<td>3</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Fire tolerance (ordinal class 1 – 5)</td>
<td>4</td>
<td>2</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Probability veg. propagation (0 – 1)</td>
<td>0.9</td>
<td>0.0</td>
<td>0.5</td>
<td>0.0</td>
</tr>
<tr>
<td>Minimum age of resprouting (year)</td>
<td>0</td>
<td>0</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Landscape</td>
<td>Landtype</td>
<td>Specified FRI</td>
<td>Mean simulated FRI</td>
<td></td>
</tr>
<tr>
<td>-----------------</td>
<td>-------------------</td>
<td>---------------</td>
<td>-------------------</td>
<td></td>
</tr>
<tr>
<td>Simplified</td>
<td>Low elevation</td>
<td>40</td>
<td>34</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mid xeric</td>
<td>60</td>
<td>47</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mid mesic</td>
<td>80</td>
<td>71</td>
<td></td>
</tr>
<tr>
<td></td>
<td>High elevation</td>
<td>100</td>
<td>168</td>
<td></td>
</tr>
<tr>
<td>Foothills</td>
<td>Low north</td>
<td>30</td>
<td>33</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Low south</td>
<td>30</td>
<td>31</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mid north</td>
<td>40</td>
<td>43</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mid south</td>
<td>40</td>
<td>42</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Low interior north</td>
<td>50</td>
<td>62</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Low interior south</td>
<td>50</td>
<td>62</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Low riparian</td>
<td>150</td>
<td>122</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mid riparian</td>
<td>150</td>
<td>109</td>
<td></td>
</tr>
<tr>
<td></td>
<td>High north</td>
<td>150</td>
<td>95</td>
<td></td>
</tr>
<tr>
<td></td>
<td>High south</td>
<td>150</td>
<td>108</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Low interior riparian</td>
<td>150</td>
<td>117</td>
<td></td>
</tr>
</tbody>
</table>

*aMean is based on five replicate model runs for finest-grain landscapes*
<table>
<thead>
<tr>
<th>Landtype</th>
<th>Probability of species establishment</th>
<th>Ignition probability</th>
<th>Fire probability coefficient</th>
<th>Fire size coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(P.) jeffreyi (Q.) berberidifolia</td>
<td>A. glauca</td>
<td>A. fasciculatum</td>
<td>Initial</td>
</tr>
<tr>
<td>High elevation north</td>
<td>0.4</td>
<td>0.4</td>
<td>0.01</td>
<td>0.05</td>
</tr>
<tr>
<td>High elevation south</td>
<td>0.3</td>
<td>0.3</td>
<td>0.01</td>
<td>0.05</td>
</tr>
<tr>
<td>Low interior north</td>
<td>0.1</td>
<td>0</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Low interior south</td>
<td>0.05</td>
<td>0</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Low interior riparian</td>
<td>0.05</td>
<td>0</td>
<td>0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>Mid elevation north</td>
<td>0.05</td>
<td>0.001</td>
<td>0.01</td>
<td>0.3</td>
</tr>
<tr>
<td>Mid elevation south</td>
<td>0.01</td>
<td>0.001</td>
<td>0.01</td>
<td>0.1</td>
</tr>
<tr>
<td>Mid elevation riparian</td>
<td>0.01</td>
<td>0.001</td>
<td>0.001</td>
<td>0.2</td>
</tr>
<tr>
<td>Low elevation north</td>
<td>0</td>
<td>0</td>
<td>0.001</td>
<td>0.01</td>
</tr>
<tr>
<td>Low elevation south</td>
<td>0</td>
<td>0</td>
<td>0.001</td>
<td>0.01</td>
</tr>
<tr>
<td>Low elevation riparian</td>
<td>0</td>
<td>0</td>
<td>0.001</td>
<td>0.01</td>
</tr>
</tbody>
</table>
Table 1- 4: Average simulated fire return intervals (FRIs, year) and number of fires for the Simplified and Foothills landscapes at fine, intermediate, and coarse cell sizes

<table>
<thead>
<tr>
<th>Landscape</th>
<th>Aggregation Level</th>
<th>FRI (year)</th>
<th>S.D Number of Fires</th>
<th>S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Simplified</td>
<td>Fine (50 m)</td>
<td>56</td>
<td>4</td>
<td>109</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>Intermediate (250 m)</td>
<td>326</td>
<td>111</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Coarse (500 m)</td>
<td>625</td>
<td>263</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>Foothills</td>
<td>Fine (90 m)</td>
<td>55</td>
<td>3</td>
<td>678</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>74</td>
</tr>
<tr>
<td></td>
<td>Intermediate (300 m)</td>
<td>67</td>
<td>16</td>
<td>539</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Coarse (900 m)</td>
<td>101</td>
<td>53</td>
<td>412</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>121</td>
</tr>
</tbody>
</table>

*a Based on 10 replicate model runs*
Figure 1-1: The foothills and mountains of the Peninsular Ranges, southern California
Figure 1-2: Simulated mean fire return interval and mean fire size for unreplicated 500-year model runs in the Simplified and Foothills landscapes
Figure 1-3: Fire severity class for all fires during 500-year model runs at the finest, intermediate, and coarsest cell sizes, Simplified and Foothills landscapes.
Figure 1-4: Initial extent of plant species cover at the finest, intermediate, and coarsest cell sizes, Simplified and Foothills landscapes. JP, AG, QB, and AF correspond to *Pinus jeffreyi*, *Arctostaphylos glauca*, *Quercus berberidifolia*, and *Adenostoma fasciculatum*, respectively.
Figure 1-5: Proportion of initial landscape cover for each species at the finest, intermediate, and coarsest cell sizes, Simplified landscape
Figure 1-6: Proportion of initial landscape cover for each species at the finest, intermediate, and coarsest cell sizes, Foothills landscape.
Figure 1-7: Map of *Adenostoma fasciculatum* at model years 1, 250, and 500 for the finest, intermediate, and coarsest cell sizes, Simplified landscape.
Figure 1-8: Map of *Adenostoma fasciculatum* at model years 1, 250, and 500 for the finest, intermediate, and coarsest cell sizes, Foothills landscape
Figure 1-9: Lacunarity values for five box sizes (1,2,4,8,16) at the finest, intermediate, and coarsest cell sizes over 500-year model runs, Simplified landscape. Particularly high lacunarity values for *Arctostaphylos glauca* reflect the rapid decline of this species on the landscape. *A. glauca* can only regenerate from a fire-cued seedbank, is relatively short-lived and shade intolerant, and thus fared poorly with long intervals between fires. The lacunarity trajectories end when this species disappeared from the landscape.
Figure 1-10: Lacunarity values for five box sizes (1,2,4,8,16) at the finest, intermediate, and coarsest cell sizes over 500-year model runs, Foothills landscape.
Chapter 2. Using a cellular automaton model to forecast the effects of urban growth on habitat pattern in southern California

2.0 Abstract

Land use change is one of the most important anthropogenic factors affecting terrestrial ecosystems, causing habitat loss, fragmentation, and interactions with other components of global change, such as biological invasions of non-native species. In southern California, population growth and economic expansion are the primary drivers of land use change, and the population is expected to double in 40 years. Although directly adjacent to the region’s largest metropolitan area, the Santa Monica Mountains National Recreation Area (SMMNRA) remains mostly undeveloped, with 50 percent of the area protected as parkland. In this study, a cellular automaton (CA) model was calibrated using historical growth patterns in the region, and used to forecast three scenarios of urban growth in the SMMNRA from 2000 – 2050, with development prohibited on slopes greater than 25%, 30%, and 60% slope. Habitat pattern and extent under these scenarios was assessed using several landscape metrics, then compared to results from a GIS overlay model developed for the same region. The CA model predicted urbanization to increase from 11% of the landscape in 2000 to 26%, 35%, and 47% in 2050, respectively, for the three slope scenarios. In 2000, the majority of vegetation constituted one large, interconnected patch. With development prohibited beyond 25% and 30% slope, this patch will become, by 2050, increasingly perforated, but should stay relatively intact.
However, if growth is permitted up to 60% slope, the patch breaks apart, resulting in a shift in spatial pattern dynamics on the landscape (as reflected by other landscape metrics). General growth patterns predicted by the GIS overlay model resembled those generated by the CA, but the CA model produced more patches and edge in the landscape. Because it is temporally explicit, the CA model was able to capture nonlinear, emergent behavior and a phase transition in the type of growth occurring in the landscape that was not apparent in the GIS overlay predictions.

2.1 Introduction

Land use change is one of the most important anthropogenic factors affecting terrestrial ecosystems, not only because of direct habitat loss and fragmentation, but also because it interacts with many other components of global change, such as altered fire regimes and biological invasions of non-native species (Wilcox and Murphy, 1985; Noss, 1991; Soule et al., 1992; Vitousek, 1994; McGarigal and Cushman, 2002). Increased fire frequency has been attributed to increased ignitions at the urban-wildland interface (Keeley and Fotheringham, 2003), and biological invasions of non-native grasses, which can disperse out of urban areas, potentially displacing native grasslands and interacting with natural fire regimes, creating feedbacks that further increase fire frequency (D’Antonio and Vitousek, 1992).

In southern California, particularly in the Los Angeles metropolitan region, population growth and economic expansion are the primary drivers of land use change. Growth patterns have been fragmented, with a decentralized network of 177
interconnected communities spreading into the region’s native, fire-prone shrublands (Scott, 1995). The human population in the region (16.7 million) is expected to double in the next 40 years. The great variety of physical environments in southern California supports high levels of biological diversity, as well as a large number of endemic and endangered plant and animal species, and the region is recognized as a global biodiversity ‘hotspot’ (Dobson et al., 1997). However, large expanses of native shrub vegetation are being lost and fragmented, and remnant stands of the coastal sage scrub plant community now provide some of the last remaining habitat for a number of endangered species (Davis et al. 1994).

A number of strategies are being developed to preserve habitat for threatened and endangered species in southern California and other regions experiencing rapid urban growth. One strategy is to convince planners to adopt the paradigm of “smart growth,” which seeks to channel new development into existing urban areas. In addition, California’s Natural Community Conservation Planning (NCCP) program was developed in 1991 to identify land for conservation in southern California that functions as critical habitat for multiple species. The secure way to preserve this habitat is for agencies such as the National Park Service to acquire the land for protection. However, high land values and competition for funding makes land acquisition challenging (Stumpf, 2000). Therefore, it is necessary to prioritize the most critical areas for protection by determining which of the regions with the highest biological value are also most at risk. Models that forecast where urban
growth is likely to occur can be used to determine which of these areas are most likely to be developed.

Urban modeling became widespread in the 1960s (Wilson, 1974; Batty, 1981), and recent technological innovations (such as remote sensing and GIS) have helped the development of more sophisticated approaches that can simulate future development scenarios. However, some lack of success in urban growth modeling has been attributed to incomplete understanding of the urban system (Rakodi, 2001). Because cities are open and nonlinear systems, many newer modeling alternatives are founded upon complex systems theory (e.g., Gar-On Yeh and Li, 2003).

One distinction that should be considered when choosing an urban growth model is the difference between complexity and complicatedness. Clarke (2004) notes that, while models with multiple components and parameter requirements may be complicated, complex systems behavior can be produced with simple models, and multiple variables do not necessarily create complexity. Instead, complexity is created by nonlinear behavior (Malanson, 1999). Although the science of complexity has sometimes been dismissed as lacking unification (Horgan, 1995), general properties inherent to complex systems, such as self-organization, adaptation, emergent behavior, behavioral phase changes, and surprising behavior, are widely agreed upon, and have been used to characterize the process of urban growth (Cheng et al., 1993, Batty, 1998, Couclelis, 2002).

One class of complex systems models, cellular automata (CA), has gained attention for simulating urban development (Gar-On Yeh and Li, 2003, Torrens,
Although urbanization is also a top-down phenomenon (governed by policy decisions, environmental constraints, and societal trends), land development tends to spread as a bottom-up process in which broad-scale patterns, such as growth booms, emerge out of local interactions – a behavior that is well captured in CA. CA models operate on an array of identically programmed automata, or cells, that exist in one of a finite number of states. Through repeated application of behavior rules, macroscale behavior emerges because of interactions between individual cells and their neighbors (Park and Wagner, 1997, Clarke and Gaydos, 1998). CA models are also useful for simulating urban systems because they are inherently spatial, directly compatible with raster GIS (Couclelis, 2002), and temporally dynamic, with state transitions intuitively mimicking the temporal dynamics of urban change.

Detailed models that account for more of the complexity (and complicatedness) of the human-environment system require sufficient and accurate data. Including more variables reduces the number of assumptions needed to apply the model, but also contributes to the model’s uncertainty. Probably the most critical component for choosing a model is its ability to address the specific analytical needs of the project in question. The objective for choosing an urban growth model for this research was to determine how future urbanization would affect the extent and spatial pattern of habitat in the Santa Monica Mountains in southern California. Because urban development is causing increased fire ignition frequency at the wildland urban interface in this region, we also required a model whose output would be compatible with a landscape-scale simulation model of fire disturbance and
succession, (LANDIS, He and Mladenoff, 1999), which will be the focus of future research.

A range of approaches was considered based on criteria including: data needed, data available, data compatibility, spatial/temporal scale, model complexity, model assumptions, and model realism. After ruling out other approaches, (e.g., Gunter et al., 2000, Wickham et al., 2000, Jenerette and Wu, 2001), the choice was narrowed to the Clarke Urban Growth Model (UGM) (Clarke and Gaydos, 1998) and a site suitability-based GIS overlay model (the “GIS overlay model”) that had already been developed for the Santa Monica Mountains (Swenson and Franklin (2000). Both models are driven by spatial influences on urbanization, such as slope and proximity to roads and existing infrastructure. Although the GIS overlay model had already been developed, the UGM was selected because it is a spatially and temporally explicit model capable of simulating alternate growth scenarios using a rigorous calibration process as a performance metric.

Because of the steep terrain in the Santa Monica Mountains, most existing urbanization has occurred along canyon bottoms (Stralberg, 2000). However, increased demand for housing is putting pressure on developers to build on steeper slopes. Management agencies have recognized the potential for using slope restrictions to confine development to more desirable locations. Therefore, the UGM was used to forecast three scenarios of urban growth from 2000 – 2050, with development prohibited beyond 25%, 30%, and 60% slope. The effect of urbanization on the extent and spatial pattern of habitat was quantified over time for
these scenarios using several landscape pattern metrics. The UGM projections were also generally compared to those of the GIS overlay model to explore similarities in results between these fundamentally different approaches. Because the delineation of developed land was binary in this research, the term “urban” will be used to refer developed land cover, regardless of the land use. Likewise, all non-urbanized areas in the landscape are considered wildland consisting of native vegetated habitat.

2.2 Methods

2.2.1 The study area

The Santa Monica Mountain National Recreation Area (SMMNRA) is an administrative unit that encompasses approximately 60,000 hectares of land bordered to the south by the Pacific Ocean, to the north by suburban communities, to the west by agriculture and rural communities, and to the east by the Los Angeles metropolitan area (Figure 1). The Santa Monica Mountains are a rugged east-west trending range with a Mediterranean climate, characterized by cool, wet winters and warm, dry summers. The SMMNRA protects the largest expanse of coastal Mediterranean ecosystem in the United States, and supports tremendous biodiversity with approximately 1,000 different plant species falling into at least nine distinct plant communities (Dale, 2000). The major vegetation types in the mountains include chaparral (approximately 60% of the study area); coastal sage scrub (approximately 25% of the study area) on low-elevation coastal slopes; oak woodland on northern slopes with deep soils; riparian woodland; and (primarily
exotic) grasslands (Radtke et al., 1982). The mountains are also home to 50 mammal, 384 bird, and 36 herpetofauna species. The SMMNRA has an active fire regime characteristic of Mediterranean-type ecosystems. More than 28,000 hectares have burned since 1990, and some areas have burned up to 10 times over the last century; and during that time period, most fire ignitions have been human-caused. Therefore, despite fire suppression efforts, fire-related losses and expenditures are steadily increasing due to urban expansion into the hazardous wildland environment (Keeley, 2002).

Approximately half of the land within the administrative boundary is publicly owned and protected, and jurisdiction is shared between diverse governmental entities including California State Parks, the National Park Service, the city of Malibu, Ventura and Los Angeles Counties, as well as local public parklands. Of the approximately 50% of the land that is privately owned, about 25% is developed. Based on 2000 Census data, residents of the SMMNRA are generally wealthy with median annual incomes more than $100,000, and many of the residences are retirement or second homes. However, commercial and residential development is increasing. Approximately 6% of the nation’s total population lives within an hours drive of the park.

The California Coastal Commission (CCC), which has permit authority for the majority of the study area, conducted a comprehensive analysis of land development patterns and permitting in the Santa Monica Mountains from 1975 – 1996. Development approved in the land use plans for the region would allow current
urban land to double. The report identified constraints and negative cumulative impacts that could result from this future urban development. Among the areas considered sensitive, from which development should be “constrained,” were those with slopes greater than 30% for Ventura County and greater than 25% for LA County.

2.2.2 The Urban Growth Model (UGM)

The UGM is a CA model that predicts the spatial extent of urban expansion based on repeated application of growth rules and weighted probabilities that promote or inhibit growth. As with other CA models, the UGM predictions begin with a set of initial conditions describing the current state of the system, including slope, urban extent, transportation, and portions of the landscape that are excluded from development. The model operates through a series of nested loops in which the outer loop retains cumulative statistics for the growth history, and the inner loop executes growth rules for a single year. Four types of growth occur in the model, and the probabilities of these growth types occurring are a function of five growth control coefficients that affect the behavior of the system (Table 1). The growth types are applied sequentially, one cell at a time, and the entire grid is updated after annual iterations to form the basis for growth in the succeeding year. First, “spontaneous growth” occurs, which is the random selection and urbanization of isolated cells; next, “diffusive growth” determines whether those cells just urbanized from spontaneous growth will become new urban centers; “organic growth” is the most
common type of growth, and simulates expansion from existing settlements; and “road-influenced growth” is based on the tendency for growth to occur near transportation corridors.

The growth control coefficients have values that can range from 0 – 100, and each of their initial values are derived through model calibration. These values evolve during the course of model runs as a function of a second hierarchy of growth rules that cause the model to “self-modify.” The self-modification rules, established \textit{a priori}, control the rate of growth to more realistically simulate how urban development occurs over time (e.g, to prevent linear growth and to simulate the S-curve-type growth rate typical of urban expansion). Specifically, critical threshold values are set so that unusually high or low growth rates lead to either a slowing down or a speeding up of urban expansion through slight alteration of the dispersion, spread, and breed growth-control parameters.

In addition, although growth is generally more likely to occur on flatter terrain than on steep slopes, as the percentage of land available for development decreases, the model will decrease the slope resistance coefficient based on a slope sensitivity parameter established \textit{a priori}, allowing growth to occur on steeper terrain. Furthermore, the “critical slope threshold” specifies a degree of slope beyond which growth cannot occur.
2.2.3 UGM data preparation

The calibration of the UGM statistically and spatially associates future urban growth with historic growth patterns in the study area; therefore, four data layers of historical urban extent and two data layers of road networks were created as model inputs. To create the historical data set, aerial photographs of the entire study area for 1947 and 1976/1977 were acquired from the University of California Santa Barbara (UCSB) Map and Image Library (MIL), and digital orthorectified quarter quadrangles (DOQQs) for 1989 and 2000 were acquired from the U.S. Geological Survey (via the National Park Service) (Table 2). After scanning all the airphotos, the 1976/1977 photos were registered to the 1989 DOQQ, and the 1947 photos were registered to the 1976/1977 photos. Due to the mountainous terrain in the Santa Monica Mountains, ERDAS Imagine/Orthobase™ (ERDAS, 1997) was chosen to register the images because the software corrects for terrain displacement using a digital elevation model (DEM).

The airphotos were mosaicked, and urban extent was delineated for all four dates using onscreen digitizing. To begin the digitizing process, all areas classified as urban (Anderson level I, Anderson et al., 1976) in the 1993 land use coverage (Table 2) were extracted and overlaid on the 2000 DOQQ. To create the urban extent layer for 2000, the land use coverage was then edited based on airphoto interpretation (e.g., additional urban areas were added, and erroneously classified urban areas were deleted). All land use types with built structures, as well as golf courses, were delineated as urban, and roads within urban areas were subsumed into the urban
extent. Otherwise, the roads were part of the separate transportation layers. After creating the 2000 layer, urban areas were then successively deleted to create urban extent layers for each of the earlier dates (1947 and 2000 shown in Figure 2).

The original transportation data were created by Thomas Brothers, including roads from 1990 (Los Angeles County) and 1995 (Ventura County). The National Park Service updated this coverage to include roads as current as 2001. To create 1947 coverage, roads were deleted from the 2001 coverage using heads-up digitizing and airphoto interpretation of the 1947 image mosaic (Figure 2).

Other data created for model input included a layer of slope in percentage, derived from a DEM, and a binary “excluded land” layer to specify areas prohibited from development. A property-ownership-coverage (Table 2) was used to select all protected parklands (regardless of ownership), and then convert those areas into a layer of (100%) excluded land (Figure 2). Although land is protected under diverse ownership, it exists within the administrative boundaries of the National Recreation Area owned by the NPS. Together with the Santa Monica Mountains Conservancy, the NPS is working to protect more land. Therefore, no development was anticipated in these excluded areas over the next 50 years.

Because the UGM requires *.gif images as input, and because the calibration of the model occurred in four phases at different resolutions, all coverages were converted to grids at 240m, 120m, 60m, and 30m; then they were transformed into *.gif images by first converting them to *.tifs in ARC/INFO™.
2.2.4 UGM calibration and predictions

The “brute force” calibration process for the UGM is based on a combination of Monte Carlo techniques and hindcasting, and is described extensively elsewhere (e.g., Clarke and Gaydos, 1998, Silva and Clarke, 2002). Hindcasting is a method used to explain patterns observed up to the time and place where the original data were gathered (Morrisson et al., 1992). In the case of the UGM, hindcasting fits simulated data to historical data with the assumption that calibrating the model to the growth patterns in the past can be used to reasonably forecast into that regions’ future (Clarke et al., 1997). The key to this process involves systematic manipulation of the five growth control coefficients (described previously, Table 1) to find the unique combination of values that best fits the simulated to the observed historical data.

Although improving the calibration process has been the subject of recent work (e.g., Yang and Lo, 2003, Goldstein, 2004), the methods used for this research followed the standard procedures as described in Clarke and Gaydos (1998). The calibration occurred in four separate phases that iteratively searched for the best coefficient combination by stepping through the calibration space (all of the 1005 possible combinations of the coefficients) using progressively smaller ranges of values at progressively finer resolutions. As the model iterated through these combinations of coefficient values, the simulated growth was compared to the growth in the years for which the historic data sets were available using a number of Pearson $r^2$ statistics. These statistics helped to determine the goodness of fit between
the actual and predicted data by comparing, for example, the number of urban pixels;
number of edges (urban adjacent to non-urban); number of separate clusters
(calculated with an image processing routine that erodes urban cluster edges until all
separate blobs collapse into one pixel, and then counting those pixels (Clarke and
Gaydos, 1998); spatial correspondence was determined through a modified Lee-
Sallee shape index (the ratio of intersection over the union).

The coarsest phase of calibration was initiated with the full range of possible
values (0 – 100) for each coefficient, stepping through the calibration space at
increments of 25, at a resolution of 240m. An automated calibration routine (see
Clarke and Gaydos, 1998, Silva and Clarke, 2002) was used to run multiple
simulations from 1947 – 2000 (the earliest through the latest dates of historic data)
using each possible \(5^5\) combination of coefficients (e.g., each of the five
coefficients had five possible values when stepping from 0 – 100 at increments of
25). Simulations for each coefficient combination were repeated for four Monte
Carlo iterations so that the statistical tests could be averaged, allowing confidence
limits to be placed on predicted spatial patterns. The method for selecting the best
range of coefficients to use for each successive phase of the calibration was to sort
the statistics output log file based on three measures: the product (all of the fit scores
multiplied together), the Lee-Sallee shape index, and the modeled urbanization for
the final year / actual urbanization for the final year. The top 10 scores for these
measures were compared, and the coefficient combinations that most frequently
produced the maximum scores were used to initialize each subsequent phase of
calibration. Because of the self-modifying properties of the UGM, the coefficient parameters used to initialize simulations may be slightly altered by the end of the model runs. Therefore, the best coefficient combination selected from the final phase of calibration, known as the “derive coefficients”, was used to run the model through the historical data for 100 Monte Carlo iterations. The average terminating coefficient values from these runs (the “prediction coefficients”) were then used to seed the model for prediction.

Given the steep terrain in the Santa Monica Mountains (approximately 30 percent of the land has slopes greater than 40%), three different growth scenarios were developed based on critical slope values. Because the CCC report identified areas with slopes greater than 30% or 25% for Ventura and LA Counties as sensitive to development, and because development nevertheless tends to occur on slopes steeper than that, predictions were run from 2000 to 2050 using critical slope threshold values of 25%, 30%, and 60%. Each scenario was replicated with 100 Monte Carlo iterations, allowing the generation of variance estimates and the development of probability images. Annual probabilistic images of urban growth were thresholded at 95% or greater likelihood of development to develop binary model output.

2.2.5 Landscape pattern analysis

Predicting ecological response to changing landscape heterogeneity is complex due to differences in species habitat preferences, difficulties in distinguishing the effects of habitat loss from fragmentation, and the variability of landscape patterns
and processes over time. However, several direct and general landscape metrics can be calculated that not only serve as the basis for deriving other indices, but are also related to myriad ecological processes (Gustafson, 1998). These metrics are useful for monitoring change in landscape structure over time as well as for comparing different landscapes (Turner, 1989). Because the objective of this research was to forecast the impact of different urban development scenarios on habitat extent and patterns, and to generally compare those scenarios to the GIS overlay model, these general landscape-level metrics (Table 3) were chosen to quantify model output using FRAGSTATS version 3 (McGarigal et al., 2002).

One of most important components in a landscape is the area of its patches because most species have minimum area requirements (Beier, 1993). The positive relationship between habitat area and species richness is well documented (e.g., Gleason, 1922), and one principle of reserve design is that preserving habitat patches large enough to support species with large area requirements will protect other species under this “umbrella” (Noss, 1990).

Core area/interior habitat represents the portion of habitat patches that is farther than a specified distance from the patch boundary. Because species composition and abundance is typically different at or near the perimeter of habitat patches than away from the perimeter (Formon and Godron, 1986), core area may better represent habitat availability than absolute area in fragmented landscapes. Using a 100 m buffer width (as in Swenson and Franklin, 2000), the total core area, number of patches containing core area, and mean of core areas for all patches were calculated.
Increased urbanization was expected to reduce total core area and fragment the landscape into small, dispersed patches, thus resulting in a higher number of patches with smaller mean core areas.

Another indicator of habitat quality is the amount of edge between landscape elements. Edge affects the movement of organisms across boundaries, alters the structure and composition of vegetation, and influences different species based on habitat preferences (Turner, 1989, McGarigal et al., 2002). Smaller habitat patches tend to have a higher edge-to-interior ratio; therefore, fragmentation can increase the amount of edge in a landscape (Pearson, 2002). Total edge (urban adjacent to non-urban) and the number of habitat patches were calculated with the expectation that both would increase (edge as a function of the number of habitat patches) with urbanization.

When habitat is distributed over few large patches, the landscape is more highly connected. Connectivity is important for processes such as migration, seed dispersal, and competition (Green, 1994). Currently, a single, large patch of uninterrupted vegetation dominates the Santa Monica Mountains landscape. Therefore, the Largest Patch Index (LPI), a measure of the percentage of the landscape occupied by the largest patch, was calculated to evaluate how that patch would fragment under the different urbanization scenarios. The LPI was expected to decrease with increased urban growth.

To prepare the annual UGM output for landscape pattern analysis, all *.gif images were converted to *.tif images, a format accepted by ARC/INFO. An Arc
Macro Language (AML) script was created to automatically convert the images to ArcGrids so they could be reclassified for use in FRAGSTATS. All natural vegetation was considered one class, and all urban or water areas were designated background, but were included in overall landscape area calculation. Grid cells outside of the study area boundary were also designated background, but these areas were excluded from area calculations. Landscape metrics were calculated on grids for each year of the UGM output for all three scenarios.

2.2.6 Comparison with the GIS overlay model

The GIS overlay model (Swenson and Franklin, 2000) used a static, site suitability approach with four variations to project different development patterns in the Santa Monica Mountains from 5 to 25 years forward. The projected dates for the predicted growth were estimated from previous development rates for the region. Development likelihood was assumed based on an overlay of five equally weighted Boolean (or binary) GIS data layers, leading to a rank of five ordinal categories. Values of 3, 4, or 5 were assumed to have a “medium to high” likelihood of development. Growth was more likely in areas that were: on more level slopes, in areas of proposed development, in areas zoned for high density development, located near roads, or located near existing development. The two major model variations were the Standard Development scenario and the Maximum Development scenario. In the Standard Development scenario, points were randomly selected from medium or high likelihood classes, and ownership tracts in which the points fell became
developed. In the Maximum Development scenario, all ownership tracts that partially or completely coincided with areas of medium or high likelihood classes became developed.

The predicted results from the Standard and Maximum Development scenarios were clipped to the same boundary and classified identically to the UGM output, then analyzed with the same landscape metrics. Because of the static nature of the GIS overlay model, grids from the two dates of each UGM slope scenario that had the closest total area of natural vegetation as the Standard and Maximum Development scenarios of the GIS overlay model were selected for comparison.

2.3 Results

2.3.1 UGM calibration and simulations

The UGM was successfully calibrated to the historical data set, resulting in a selection of final coefficients to use for prediction (Table 4). During the predictions, the self-modifying properties of the UGM resulted in similar changes in the values of the growth coefficients for all three of the slope scenarios (Figure 3). For the first 30 years, the breed and spread coefficients were at the maximum values possible, the slope coefficient was at the lowest value possible, and the diffusion and road gravity coefficients gradually increased at mid-range. In the middle of the 2030s, however, the breed, spread, and diffusion coefficients bottomed out to 0, slope increased to 100, and the road gravity coefficient declined, but remained at a mid-range. These
transitions occurred most rapidly at 25% slope, and were the slowest at 30% slope, with 60% slope falling in between.

Throughout most of the 50-year simulations, urban growth was predicted to occur faster at higher critical slope thresholds (Figure 4). However, the growth rate dropped to nearly 0% in the 60% slope scenario faster than it did in the 30% slope scenario. In all three scenarios, less than 1 ha per year was predicted to be developed by approximately 2040.

At the beginning of the simulations (year 2000), 11% (6,380 ha) of the landscape was urban. However, only 50% (28,967 ha) of the landscape was available to be urbanized due to the protected parks that were excluded from development (Table 5). When accounting for the portion of the landscape with slopes above the three critical slope thresholds, the area of developable land in the initial conditions predictably decreased with tighter slope restrictions, though only slightly at 60%. At the end of the simulations, the remaining amount of developable land was highest at 30%, but the differences between scenarios were not substantial. However, greater proportions of the initial developable area were urbanized with higher critical slope thresholds. Substantially more area of land became urban (thus decreasing the total core area of natural vegetation) when development was allowed at higher-degree slopes (Table 5, Figure 5, Figure 6a).

The number of distinct core area patches in the landscape increased slowly over time, particularly in the first two decades, for the 25% and 30% slope scenarios (Figure 6b). In the middle of the 2020s, the number increased a bit faster and then
leveled off in the last two decades with more core area patches at 25% slope. The mean area of those distinct core area patches decreased nonlinearly during the first decade, with a more gradual decline continuing for the remainder of the simulations for the 25% and 30% slope scenarios (Figure 6c). The core area was slightly larger in the 25% slope scenario than the 30% slope scenario.

At 60% slope, the number of patches of core area declined slightly for the first two decades, but the mean size of the core-area patches increased substantially in the first decade, then declined gradually until approximately 2025 (Figure 6b). At that time, the number of core areas increased substantially, but their mean size plummeted (Figure 6c). Within five years, the number of core areas decreased again, became larger on average, and stabilized for the remainder of the simulations. Throughout the entire simulation, the 60% slope runs had larger, but fewer patches of core area than the 25% and 30% scenarios.

While the number of distinct core areas declined over time in the 25% and 30% slope scenarios, the total number of patches in the landscape increased substantially (Figure 6d). In the first decade, the number of patches increased almost linearly in both scenarios, with slightly more patches at 25%. The rate of increase then slowed at the 25% slope scenario, but the number of patches in the 30% slope scenarios increased at approximately the same rate until the middle of the 2030s, resulting in almost twice as many patches in the landscape than the 25% slope scenario. Except for a temporary spike in the late 2020s for the 60% slope scenario, the number of patches declined slowly throughout the entire simulation.
The total edge in the landscape also increased progressively over time in both the 25% slope and 30% slope scenarios, but was higher in the 25% slope scenario until the middle of the 2030s (Figure 6e). The rate of increase then slowed, and the 30% slope scenario ended up having more edge than the 25% slope scenario for the remainder of the simulations. Again, except for a temporary spike in the late 2020s, the total edge slowly declined over time for the 60% slope scenario.

The majority of vegetation existed in one large patch at the beginning of the simulations. At 25% and 30% slope, this patch became increasingly perforated, and became smaller with increased urbanization; however, the patch remained connected throughout the simulations. At 60% slope, however, the large patch eventually broke up into several disconnected patches in the middle of the 2020s (Figure 6f).

2.3.2 Comparison to GIS overlay model

Landscape metrics calculated for the Standard and Maximum Development scenarios of the GIS overlay model were compared to those of the UGM predictions in the projected years with the most similar area of natural vegetation for each of the three slope scenarios (Figure 7). For all of the landscape metrics, the direction of change created by increased urbanization (and decreased vegetation) was the same for the GIS overlay predictions and the 25% and 30% slope scenarios of the UGM predictions for those comparable years. The direction of change for comparable area in the 60% slope scenario was the same as the GIS overlay model for all of the metrics except total edge, which declined with higher urbanization. The magnitude
of difference between lower and higher levels of urbanization was greater for the number of patches and total edge in the 25% and 30% slope scenarios of the UGM predictions. There were more patches and edge to begin with in the UGM model, and that number increased more dramatically with increased urban growth.

Spatially, the GIS overlay model and the UGM predicted future urban growth to occur in similar regions of the study area (Figure 8), primarily along the coast and adjacent to major thoroughfares through the mountains. The primary difference is that the GIS overlay model predicted more growth along the coast than the UGM, whereas the UGM predicted more growth in the interior of the mountains.

2.4 Discussion

The pace and scale of urban growth is occurring at an unprecedented rate across the globe, and the number of people living in urban areas is expected to double to more than 5 billion in the next 25 years (WRI, 1998). Consequently, urban growth models are becoming critical tools for projecting where urban expansion is likely to occur. Our research objective was to predict urban growth impacts on habitat extent and pattern based on land management strategies that prohibit development beyond varying percentages of slope.

Not surprisingly, greater habitat loss was predicted when development was allowed to occur on steeper slopes. As evidenced by the phase transition apparent in plots of the growth control coefficients, slope-dominated growth became most critical after approximately 30 years. At that time, the amount of flatter land initially
available for development had become mostly developed in all three scenarios, and slope began to drive the entire system. This phase transition occurred at similar points in time for each scenario because, although more land became urbanized with growth allowed on steeper slopes, there was also more land available for development in those scenarios. The self-modification properties of the model decrease the slope resistance coefficient based on proportion of available land as a way to realistically capture the real-life tendency to build on flatter terrain before attempting development on steep slopes. Although habitat area declined inversely with the degree of slope restrictions, allowing growth to occur almost regardless of slope in the 60% scenario resulted in fundamentally different patterns in the landscape metrics than in the 25% and 30% slope scenarios, which differed only in a matter of degree.

In the 25% and 30% slope scenarios, the mean size of the patches containing core habitat declined at a faster rate than total habitat area. Although the total number of patches and total edge in the landscape increased dramatically, the number of distinct core patches increased only slightly over time. Therefore, future landscape patterns under these scenarios are likely to be characterized by many patches too small to contain high-quality interior habitat; and the patches that do contain core habitat are expected to become smaller. This reduction in interior habitat could favor increases in species that are adept at using more disturbed, edge habitats; and species with minimum area requirements might need to depend more heavily on corridors and patch connectivity for migration.
Urbanization affected habitat patterns differently when growth was allowed up to 60% slope. Although total core habitat declined substantially, the mean size of core area patches increased in the first decade, as small patches of habitat were lost first to urban growth. Then mean size slowly decreased until approximately 2025, when the initially large, connected patch of vegetation broke into several medium patches, and mean core patch area plummeted. This abrupt change in landscape dynamics explains the temporary spikes in the number of habitat patches and total edge in the landscape, as well as the temporary drop in mean core patch area, revealing correlations that tend to be inherent in landscape metrics (Gustafson, 1998).

However, using landscape metrics together can be helpful when interpreting landscape dynamics. For example, the increase in mean core patch area in the 60% slope simulation could be misleading without other metrics to explain what was happening in the landscape. Because the total number of patches and distinct core areas declined, the mean size of remaining core patches increased because the landscape was still dominated by one large patch. The total edge also declined because the landscape was comprised of fewer patches with simpler shapes, resulting from urban infill and development saturating the available land. Unlike natural disturbances, which increase landscape complexity, human-influenced landscapes tend to exhibit simpler patterns (Turner et al., 1989).

Due to the growing number and variety of urban models, choosing an approach that is appropriate for the study in question is challenging. Although the GIS overlay model had already been completed for the study area, the more complicated UGM
approach was chosen for this analysis because the model is dynamic, rigorously calibrated, and more compatible for coupling with the ecological model of disturbance and succession that we will use in future research. Goldstein and others (2003) used the UGM in a historic reconstruction of urban growth in Santa Barbara, CA, where the UGM performed well at simulating the general growth pattern in the city, but failed to capture the exact locations of several small new settlements. Jantz et al. (2003) reached a similar conclusion in the Baltimore-Washington metropolitan region. In another study evaluating the differential impact of future growth scenarios on wildlife habitat, output from three models, including the UGM, was intersected with predicted distribution of vertebrate species (Cogan et al., 2001). One of the models, developed by Landis and Zhang (1998) used extensive socioeconomic and physical data to predict areas of future growth. The other model was a simple 500 m buffer around existing urban areas. The UGM predicted more growth than the Landis and Zhang model, and the pattern of growth tended to occur along roads and contiguous to existing development, whereas the Landis and Zhang model predicted more isolated clusters of new development. Regardless, the two models produced similar magnitudes and rank order of impacts on vertebrate species.

In the above examples, the UGM tended to underestimate the number of separate clusters of new development, with growth more heavily attracted to roads and existing settlements. Compared to the GIS overlay model, however, the UGM predicted a patchier landscape with more total edge. Given the differences in initial conditions as well as the difference in fundamental approach, comparison between
the UGM and the GIS overlay model should be interpreted with caution. In addition, because UGM calibration uniquely fits each study area to its local environment, comparison across UGM simulations may also be misleading (Silva and Clarke, 2002). However, if the UGM generally tends to underestimate patchiness in a landscape, but projected a higher number of patches and total edge than the GIS overlay model, the UGM predictions might be more realistic portrayals of future growth in the Santa Monica Mountains than the GIS overlay scenarios. One explanation for higher patchiness in the UGM model is that the GIS overlay approach used ownership tracts as minimum development units instead of grid cells. As Swenson and Franklin (2000) noted, actual development may only occur on portions of the ownership tracts.

Because of assumptions shared by the UGM and the GIS overlay model, there were also similarities in predictions for comparable years. The direction of change in landscape metrics was the same, but of different magnitudes, and the spatial pattern of the predictions overlapped in a substantial portion of the study area, primarily along major thoroughfares. Despite these similarities, the GIS overlay model nevertheless had some disadvantages. As a static model, it could not capture some of the intricacies in landscape change that was possible with a dynamic, temporally explicit model. Some complex system properties, such as self-organization of urban clusters that emerged from local interactions between cells and their neighbors, as well as the nonlinear behavior in growth patterns, were captured in the UGM predictions, particularly when slope-dominated growth began to drive the system. In
addition, no performance metric could be used to calibrate the formulations in the static model, and the different growth scenarios of the GIS overlay model were developed using independent methods. On the other hand, the use of Monte Carlo averaging to generate variance estimates on the predictions, combined with the rigor of the calibration process and repeatability of model experiments added more justification to the UGM model results. However, because the objective of both models was to identify possible consequences of alternate scenarios of future development, only the real future can validate these predictions.

2.5 Conclusion

Southern California, particularly the Los Angeles metropolitan area, has been long recognized as one of the most rapidly urbanizing, yet one of the most biologically diverse, areas in the United States (Rundel and King, 2001). Consequently, private land development has been identified as one of the key factors affecting ecological integrity in the region. A range of studies has been conducted in southern California documenting the impacts of habitat fragmentation on species richness (Tigas et al., 2003), and species including amphibians (Fisher and Case, 2000), birds (Stralberg, 2000), rodents (Bolger et al., 2000), arthropods (Suarez et al., 1998), and large carnivores (Tigas et al., 2003).

The SMMNRA, one of the few remaining places in coastal southern California with a substantial area of connected core habitat, is home to several large carnivore species. Carnivores are critical components to biological communities, and are
often used as indicator species of ecosystem health (Noss et al., 1996). At least two carnivores residing in the mountains, the bobcat and the gray fox, have demonstrated sensitivity to edge habitat at the urban/wildland interface (Sauvajot et al., 2000). One species of special concern is the mountain lion, an apex predator with a large area requirement (as much as 220,000 ha for a population), and a long-distance traveler (Beier, 1993). Because the mountain lion’s survival in the SMMNRA will likely depend on its ability to disperse into and out of the mountain range, the narrow section extending to the north of the SMMNRA, Cheeseboro Canyon, is an important corridor for migration to the Los Padres National Forest. All three of the growth scenarios (as well as the GIS overlay scenarios) predicted a growing cluster of urbanization separating the main mountain range from Cheeseboro Canyon. Development completely filled in with the 60% scenario, suggesting that slope restrictions may be important for keeping parts of that corridor open.

The landscape metrics used in this analysis are broadly suggestive of the types of impacts that future urban development will have on the habitat in the Santa Monica Mountains. Although the metrics were chosen primarily for comparing multiple simulations over time, land managers could calculate additional metrics specific to different conservation strategies or to particular species’ habitat preferences. Differential impacts to vegetation types could also be assessed.

Owing to the convoluted boundary of the study area, however, edge effects should be taken into account when making specific ecological inferences about the effects of fragmentation.
2.6 References


Table 2-1. Sequential Growth Types and Controlling Coefficients in the UGM, after Jantz et al. (2003)

<table>
<thead>
<tr>
<th>Growth cycle order</th>
<th>Growth type</th>
<th>Controlling Coefficient</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Spontaneous</td>
<td>Dispersion, slope resistance</td>
<td>Randomly selects cells for new growth</td>
</tr>
<tr>
<td>2</td>
<td>Diffusive</td>
<td>Breed, slope resistance</td>
<td>Expansion from cells urbanized in spontaneous growth</td>
</tr>
<tr>
<td>3</td>
<td>Organic</td>
<td>Spread, slope resistance</td>
<td>Expansion from existing settlements</td>
</tr>
<tr>
<td>4</td>
<td>Road-influenced</td>
<td>Road gravity, dispersion, breed, slope resistance</td>
<td>Growth along transportation network</td>
</tr>
</tbody>
</table>
Table 2-2: Spatial data used to calibrate the UGM

<table>
<thead>
<tr>
<th>Data</th>
<th>Source</th>
<th>Resolution /Scale</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>Airphotos</td>
<td>UCSB/MIL&lt;sup&gt;1&lt;/sup&gt;</td>
<td>1:24,000</td>
<td>1947</td>
</tr>
<tr>
<td>Airphotos</td>
<td>UCSB/MIL</td>
<td>1:24,000</td>
<td>1976/1977</td>
</tr>
<tr>
<td>DOQQs&lt;sup&gt;2&lt;/sup&gt;</td>
<td>USGS/NPS&lt;sup&gt;3&lt;/sup&gt;</td>
<td>1:12,000/1 meter</td>
<td>1989</td>
</tr>
<tr>
<td>DOQQs</td>
<td>USGS/NPS</td>
<td>1:12,000/1 meter</td>
<td>2000</td>
</tr>
<tr>
<td>Roads</td>
<td>NPS/Thomas Bros.</td>
<td>1:24,000</td>
<td>Current to 2001</td>
</tr>
<tr>
<td>DEM</td>
<td>USGS/NPS</td>
<td>10m</td>
<td>N/A</td>
</tr>
<tr>
<td>Land Use</td>
<td>SCAG&lt;sup&gt;4&lt;/sup&gt;</td>
<td>1:24,000</td>
<td>1990/1993</td>
</tr>
<tr>
<td>Property tracts</td>
<td>NPS</td>
<td>1:24,000</td>
<td>2002</td>
</tr>
</tbody>
</table>

<sup>1</sup> University of California, Santa Barbara Map and Imagery Library

<sup>2</sup> Digital Orthophoto Quarter Quads

<sup>3</sup> United States Geological Survey / National Park Service

<sup>4</sup> Southern California Association of Governments
Table 2-3. Landscape Metrics used in the analysis

<table>
<thead>
<tr>
<th>Metric</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total core area (TCA)</td>
<td>TCA equals the sum of the area of all (interior) natural vegetation located within a 100 m buffer of patch edge.</td>
<td>Hectares</td>
</tr>
<tr>
<td>Number of distinct core patches (NDCA)</td>
<td>NDCA is the number of patches in the landscape that contain habitat within 100 m of the patch edge.</td>
<td>NDCA ≥ 1, no limit</td>
</tr>
<tr>
<td>Mean core patch area (CORE_MN)</td>
<td>CORE_MN equals TCA divided by NDCA</td>
<td>Hectares</td>
</tr>
<tr>
<td>Total Edge (TE)</td>
<td>TE is the sum of all edge lengths in the landscape</td>
<td>Kilometers</td>
</tr>
<tr>
<td>Number of patches (NP)</td>
<td>NP equals the total number of patches of natural vegetation in the landscape</td>
<td>NP ≥ 1, no limit</td>
</tr>
<tr>
<td>Largest Patch Index (LPI)</td>
<td>LPI equals the percent of the landscape occupied by the largest patch</td>
<td>Percent (0 – 100)</td>
</tr>
</tbody>
</table>
**Table 2.4: Coefficients used for UGM calibration and prediction in the Santa Monica Mountains**

<table>
<thead>
<tr>
<th>Resolution</th>
<th>240 m</th>
<th>120 m</th>
<th>60 m</th>
<th>30 m</th>
<th>Derive Coefficient</th>
<th>Prediction Coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Diffusion</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Start</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>15</td>
<td>19</td>
<td>31</td>
</tr>
<tr>
<td>Step</td>
<td>25</td>
<td>5</td>
<td>5</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stop</td>
<td>100</td>
<td>25</td>
<td>25</td>
<td>25</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Eroded</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Start</td>
<td>0</td>
<td>0</td>
<td>45</td>
<td>63</td>
<td>69</td>
<td>100</td>
</tr>
<tr>
<td>Step</td>
<td>25</td>
<td>15</td>
<td>6</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stop</td>
<td>100</td>
<td>75</td>
<td>75</td>
<td>75</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Spread</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Start</td>
<td>0</td>
<td>50</td>
<td>60</td>
<td>66</td>
<td>82</td>
<td>100</td>
</tr>
<tr>
<td>Step</td>
<td>25</td>
<td>10</td>
<td>6</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stop</td>
<td>100</td>
<td>100</td>
<td>90</td>
<td>86</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Slope</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Start</td>
<td>0</td>
<td>25</td>
<td>55</td>
<td>55</td>
<td>55</td>
<td>1</td>
</tr>
<tr>
<td>Step</td>
<td>25</td>
<td>15</td>
<td>9</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stop</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>65</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Road Gravity</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Start</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>25</td>
<td>33</td>
</tr>
<tr>
<td>Step</td>
<td>25</td>
<td>25</td>
<td>25</td>
<td>25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stop</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*The Start and Stop values are the minimum and maximum coefficient values used for each phase of the calibration, and the Step values are the change intervals within those ranges. The Derive coefficient is the final coefficient derived from the calibration process, and the Prediction coefficient is the final parameter used after running the model 100 Monte Carlo iterations using the Derive coefficient.
Table 2-5. Land available for development (hectares, percent of landscape) and land urbanized in 2000 and 2050 for three slope restrictions

<table>
<thead>
<tr>
<th>Slope Restriction</th>
<th>Available 2000</th>
<th>Urban 2000</th>
<th>Available 2050</th>
<th>Urban 2050</th>
</tr>
</thead>
<tbody>
<tr>
<td>25% slope restriction</td>
<td>15,187 (26%)</td>
<td>6,380 (11%)</td>
<td>6,343 (11%)</td>
<td>15,223 (26%)</td>
</tr>
<tr>
<td>30% slope restriction</td>
<td>23,414 (40%)</td>
<td>6,380 (11%)</td>
<td>9,396 (16%)</td>
<td>20,398 (35%)</td>
</tr>
<tr>
<td>60% slope restriction</td>
<td>28,965 (49%)</td>
<td>6,380 (11%)</td>
<td>8,125 (14%)</td>
<td>27,220 (47%)</td>
</tr>
</tbody>
</table>
Figure 2-1: The Santa Monica Mountains in southern California
Figure 2-2: Input data layers for the Urban Growth Model: urban development and road networks in 1947 and 2000, and land excluded from development (in black)
Figure 2-3: UGM self-modification of growth coefficients (range 0 – 100) from 2000 – 2050 with development prohibited beyond 25%, 30%, and 60% slope
Figure 2-4: Predicted growth rate of urbanization in the Santa Monica Mountains from 2000 – 2050 with development prohibited beyond 25%, 30%, and 60% slope.
Figure 2-5: Predicted urban development in the Santa Monica Mountains in 2025 and 2050 with development prohibited beyond 25%, 30%, and 60% slope.
Figure 2-6: Landscape metrics (see Table 3) calculated for urban growth predictions with development prohibited beyond 25%, 30%, and 60% slope: (A) total core area, (B) number of distinct core patches, (C) mean core patch area, (D) total edge, (E) number of patches, and (F) largest patch index.
Figure 2-7: Landscape metric values (Table 3) calculated for the Standard Development and Maximum Development scenarios of the GIS overlay model and the for dates with the closest corresponding total class area from the Urban Growth Model predictions when growth was prohibited beyond 25%, 30%, and 60% slope. Number of patches and total edge have been divided by 10.
Figure 2-8: Overlay of the Standard Development and Maximum Development scenarios of the GIS overlay model with the Urban Growth Model predictions that had the closest total area of remaining vegetation.
Chapter 3. Calibrating a forest landscape model to simulate high fire frequency in Mediterranean-type shrublands.

3.0 Abstract

The expected influence of rapid global change on disturbance dynamics and plant species distributions has prompted the development of numerous computer simulation models that can forecast long-term change in terrestrial plant communities. 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. Because altered fire regimes may be even more influential than climate factors in shaping future MTE vegetation dynamics, models that can simulate the high-frequency fire and unique 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 of MTEs over long time frames and broad spatial scales. We refined an existing landscape disturbance and succession model (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 for the region, we calibrated the model to simulate very high fire frequencies, and evaluated the simulations under a series of 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 calibrating the model, the two dominant plant functional types in the region responded realistically to different fire regime scenarios. Therefore, this model offers a new alternative for simulating the potential long-term effects of altered fire regimes on the distribution and composition of vegetation in MTE landscapes.

3.1 Introduction

Natural disturbance regimes play an important role in shaping ecosystem structure and function (Pickett and White 1985). 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 to land cover condition and community dynamics may be extreme and/or irreversible if the disturbance regime exceeds its natural range of variability (Crutzen and Goldammer 1993, 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 (Naveh 1975, Espelta et al. 2002, Pausas 2003). The magnitude and direction of these changes vary across the landscape and from region to region; however, the impact of altered fire regimes may be more influential than climate factors in shaping in Mediterranean-type ecosystem dynamics (Noble and Gitay 1996, Pausas 1999).
In southern California, a typical MTE, fire suppression has effectively lowered fire frequency in higher-elevation conifer forests. However, population growth and urban development in low-elevation chaparral shrublands have increased ignitions to the point that they have increased fire frequency, offsetting the effects of fire suppression along the wildland urban interface (Keeley et al. 1999, Stephenson and Calcarone 1999). Also, biological invasion of non-native grasses in the region are interacting with the natural fire regime, creating feedbacks that further increase fire frequency (e.g., Haidinger and Keeley 1993). Although California chaparral is generally resilient to a range of fire frequencies (Zedler 1995), successively short intervals between fires are threatening the persistence of some species and habitat types (Zedler et al. 1983, Keeley 2001). 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, especially in the face of increasing urbanization, invasion of nonnative 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 (Crutzen and Goldammer 1993, Tilman and Lehman 2001), computer simulation models have become effective tools for testing and generating hypotheses about vegetation dynamics under various landscape change scenarios. Also, as a result of 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 (Baker 1999, Keane et al. 2004). However, very few of these landscape forest succession models have been developed that 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, Pausas 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 under modeled scenarios. On the other hand, 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 also a process-based simulator, similar to forest gap models, that requires detailed physiological parameters to simulate phenomena such as photosynthesis, soil evaporation, and root water uptake. Pausas and Ramos (in press) recently developed a model, LASS, to be used specifically for fire regimes and plant species characteristic of MTEs at landscape scales. LASS is a command-driven framework of three integrated models of vegetation dynamics designed to simulate a wide range of landscape and disturbance scenarios with varying degrees of complexity.

Pausas and Ramos (in press) developed LASS because of problems involved with using existing landscape models to simulate MTE characteristics, including difficulties in implementing some of these models as well as their lack of
applicability to MTEs. They argued that one of the most well-documented and widely used 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.” The LANDIS model was originally developed to simulate the longer fire rotation intervals and forest dynamics of northern Wisconsin.

Despite concerns with using the model in MTEs, we calibrated LANDIS for fire regimes and vegetation dynamics in the foothills and mountains of southern California (referred to hereafter as the “foothills landscape”) in previous research (Franklin et al. 2001, Syphard and Franklin 2004, Franklin et al. in press). We selected the LANDIS model for these simulations 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 landscape because the fire rotation intervals in that region (ranging from 30 to 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 five 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 specified fire regime parameters, 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.

3.2 Methods

3.2.1 Study area

The Santa Monica Mountain National Recreation Area (SMMNRA) is an administrative unit that protects the largest expanse of mainland Mediterranean ecosystem in the USA’s national park system (NPS 2004) and encompasses approximately 60,000 hectares of land adjacent to the Pacific Ocean and the Los Angeles, CA metropolitan area (Figure 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 (approximately 25% of the landscape) (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, Rundel et al. 1980, Conard and Regelbrugge 1994, Keeley and Fotheringham 2003).

The SMMNRA has an active fire regime characteristic of Mediterranean-type ecosystems, and fire frequency and total area burned has steadily increased over the last 75 years (NPS 2004). 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 2004). The bulk of the landscape burns in the autumn after six or more months of drought and during extreme fire weather fanned by 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).

3.2.2 The LANDIS Model

The LANDIS model has been described extensively in the literature and was recently the focus of a special issue of the journal Ecological Modelling. In that
issue, Mladenoff (2004a) provides a thorough review of the model, its history, and future directions. 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 and Mladenoff 1999, He et al. 1999). Species-level successional dynamics can be simulated for large, heterogeneous landscapes over long time periods (Mladenoff et al. 1996).

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 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 severity also differentially affects species (younger age cohorts and species with lower fire tolerances are more likely to be consumed). 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. Groups of individual fires are 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 to LANDIS 3.6 in addition to an annual time step. LANDIS 4.0 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. in press). The realism of fire disturbance simulation in LANDIS 4.0 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 in addition to 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.
3.2.3 LANDIS Input and parameters

LANDIS simulations require the development of two types of spatial data layers, the landtype map and the species-age map, as well as several types of corresponding non-spatial inputs:

3.2.3.1 Landtype Map

Ecological land classifications stratify landscapes into unique combinations of physical and biological variables that reflect differences in fundamental ecological processes. Based on the “Landtype Association” level of the National Hierarchical Framework of Ecological Units (Miles and Goudey 1997), the LANDIS landtype map is used to stratify the landscape into areas with uniform species establishment probabilities, rates of fuel accumulation, and fire regime characteristics (Mladenoff and He 1999). Landtype maps have been developed for LANDIS input in a variety of environmental settings (e.g., Host et al. 1996, Shifley et al. 2000, He et al, 2002, Franklin 2003).

The landtype map for the SMMNRA was created based on methods used to classify the foothills landscape (see Franklin 2003). After comparing supervised and unsupervised classification methods, an unsupervised clustering approach using the ISODATA method (Ball and Hall 1965) was employed for the classification of five gridded environmental variables that were prepared using ARC/INFO GIS software (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).

To create the landtype map, the five gridded environmental variables were normalized between 0 – 255 to ensure they would be equally weighted in the clustering. Using K-means clustering, 20 classes were generated using the Euclidean Distance measure. Based on statistics generated from the classification, 10 class pairs with the best minimum separability (most homogenous based on cluster means) were selected as initial landtype groups. These pairs were characterized according to their ranges of values for the environmental variables, and then were iteratively compared to all other classes based on these dominant characteristics. The landtype classes resulted from combining and/or splitting the groups according to similarities in environmental characteristics and from mapping and evaluating their spatial correspondence. Three versions of the landtype map were generated based on level of aggregation (four, five, and seven classes). After consultation with National Park Service vegetation scientists at the SMMNRA, the map with seven landtypes was selected as the final version because it maintained a distinction between northeast and southwest aspects (low vs. high potential solar insolation) throughout most of the landscape, which is an important variable for species establishment probabilities and biomass accumulation in the region. The final landtype map was therefore composed of the classes that formed the most uniform groupings of environmental variables based on correspondence of variable means as well as spatial congruence.
This map was then merged with maps of urban extent and other non-vegetated land (Figure 2).

3.2.3.2 Species Age Map

In addition to the landtype map, LANDIS requires a map of species presence by age class to establish initial distributions for the species included in the simulations. The map can include a maximum of 255 classes. Species age maps have been derived from classified satellite images and/or forest plot data (e.g. Wolter et al. 1995, He et al. 1998). Alternatively, Franklin (2002) developed predictive models to map dominant plant species due to the lack of other species-level maps or extensive forest plot data.

For the SMMNRA, 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 or drastic changes have occurred in southern CA chaparral in the time since the VTM maps were developed (Bradbury 1974, Franklin et al. 2004), these maps were assumed to represent plausible distributions of the species included in the simulations. For a small portion of the study area (8% of the landscape) not covered by the VTM maps, these areas were filled in with 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 each of the 19 species used in the simulations (see section on life history database), a binary GIS map was generated, delineating that species’ distribution in the study area. These binary maps were then overlaid, producing 220 map classes with different combinations of species. A hierarchical, agglomerative cluster analysis using PC-ORD software (McCune and Mefford 1999) was then employed to group classes together based on similarity of species membership. This agglomerative clustering helped to merge the 220 combinations of species presence into 24 vegetation classes. The species assemblages occurring in the resulting vegetation classes were compared to a classification of California vegetation (Sawyer and Keeler Wolf 1995) to ensure that the co-occurrence of these species also realistically occurred in the field.

Because fires are stand replacing in California chaparral, a fire history GIS map (produced by Jim Woods at CSU Long Beach) was overlaid on the map of vegetation classes to determine the age of the vegetation by subtracting the time of last fire from the current year. The final 72 map classes that comprised the species-age map were produced by first separating any species-age combination (produced by the overlay) that occupied at least 0.005% of the map into its own class. Map classes smaller than 0.005% of the map were then sorted by vegetation type, merged together, and then attributed with their weighted average age for that vegetation class. The final species distributions in the species-age map were spatially compared to the original species distributions selected out of the VTM maps to ensure that the merging process maintained most of the original extent for all species.
The comparison between the original extents of species’ presence with those species’ extents after their reclassification into species-age assemblages revealed no substantial gain or loss in abundance of any of the 19 species. To illustrate, the initial distribution of *Ceanothus megacarpus*, the most widespread obligate seeder (see next section) in the region, is slightly patchier after reclassification, but the overall extent and distribution is approximately the same as the original map (Figure 3).

3.2.3.3 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. Classification of plant species into functional types has been an effective way to simulate and analyze vegetation dynamics in disturbance-prone ecosystems (Pausas 1999, Franklin et al. 2001, Pausas 2003, Rusch et al. 2003). Because species belonging to the same functional types share similar adaptations and responses to disturbance, analysis of these species as groups provides a better framework for understanding the fundamental mechanisms driving vegetation responses (Pausas 1999). Therefore, the calibration of LANDIS in the SMMNRA focused on the behavior of functional types instead of individual species. Although all of the functional types in the study area were examined, the primary focus of this model evaluation was on the two functional types that best represent the differences between post-fire response strategies characteristic of the vegetation in the region: obligate seeders and obligate resprouters (described below). These two
functional types have also been the focus of modeling efforts in other MTE landscapes (e.g. Pausas 2003). The other functional types in the study area are:
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); oaks; early successional subshrubs; and annual grass.

3.2.3.4 Obligate seeders (e.g. Ceanothus megacarpus)
Also referred to as “disturbance –dependent” species (Keeley 1998), obligate seeders recruit after fire from long-lived dormant seed banks that are cued by intense heat, charred wood, or chemical stimuli. Obligate seeders are incapable of regenerating vegetatively and rarely recruit new individuals in fire-free intervals. Because obligate seeders produce new individuals with recurrent fires, their root systems are young and shallow, and these species are also more tolerant of water stress than obligate resprouters (Keeley 1986). Further, because of the high frequency of reproduction in the obligate-seeding mode, these species have likely adapted their physiological and anatomical tolerance to drought and higher insolation (Keeley 1998). Consequently, they are often located on drier, equator-facing slopes (Keeley 1986, Meentemeyer and Moody 2002). Although their life 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).
3.2.3.5 Obligate resprouters (e.g. Quercus berberidifolia)

In contrast to obligate seeders, obligate resprouters do not recruit seedlings but persist on burned sites because they resprout. Resprouting can occur from stems, root crowns and/or underground burls/lignotubers. These species are long-lived and rejuvenate their canopy through new sprouts during fire-free periods. Although resprouters recover rapidly after fire and begin producing seed crops at an early age, successful seedling recruitment is extremely rare in young stands. In fact, even in older, more mesic stands, the rate of successful recruitment is low and spatially quite variable (Keeley 1986). The seeds of resprouters are short-lived, and can be widely dispersed by animals (Zedler 1995). Unlike seeders, the root systems of resprouters are old and deep; therefore, these species are drought avoidant instead of drought resistant (Keeley 1986) and tend to occur on more mesic, north facing slopes.

3.2.3.6 Species life history database

In LANDIS, species are parameterized based on vital attributes that are relevant for predicting species composition after disturbance (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 and yield relationships) (Mladenoff and He 1999). For example, whereas growth rates and competition are constrained in gap models by geometrically derived light availability indices, competition in LANDIS is driven by broad ordinal categories of shade
tolerance or intolerance. 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 a preliminary vegetation classification of species for a current mapping project in the SMMNRA, a literature review, and consultation with National Park Service scientists, 19 species, falling into seven different functional types, were selected to include in the simulations (Table 2). Although exact values for some of the life history traits are unknown, generalized estimates have been widely published in the literature. Therefore, when specific life history values were published, they were used as the model parameters. However, to avoid false precision, many of the LANDIS life history parameters reflect qualified estimates and highlight the relative differences between functional types (and species within those functional types). For example, Zedler (1981) published longevity values for dominant species within four functional types on a scale of Low, Low-Medium, Medium-High, and High (where High = greater than 100 years). Likewise, the longevity values for the species in the simulations were kept constant by functional group to reflect these relative differences. For the age of maturity parameter, we had to use values that would mimic the most realistic species’ response based on the way LANDIS behaves. Specifically, the age of maturity in LANDIS indicates the year in which species are able to begin recruiting new individuals. Because obligate resprouters regenerate from mature rootstocks, they become sexually mature at a much earlier age;
however, 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 in the simulations 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 – 25 years (Keeley 1986).

3.2.4 LANDIS calibration

Over the last decade, the LANDIS model design has been verified and calibrated in various forested landscapes in North America as well as other countries such as China (He et al. 2002) and Finland (Pennanen and Kuuluvainen 2002). Our previous work in the foothills of southern California (Franklin et al. 2001, Franklin et al. in press) remains the only calibration of LANDIS in a MTE. Detailed descriptions of the model verification and calibration process have been published (e.g. He et al. 1999, He and Mladenoff 1999, Mladenoff and He 1999), and, as noted, recent modifications of the model are described in the special issue of Ecological Modelling referenced previously (Volume 180, 2004).

The standard method for calibrating the LANDIS model is based on manual optimization techniques 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. In LANDIS, 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 for those parameters. In previous versions of LANDIS (versions 1.0 – 3.6), including the one used for the foothills landscape, two fire calibration coefficients had to be explicitly specified to relate the simulated burn area and frequency to these targeted values. These coefficients were then systematically adjusted until the simulated FRIs approximated the specified FRIs. In LANDIS 4.0A, these scalars relating specified to simulated fire frequency and size are no longer in use. 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 (Yang et al. 2004). Therefore, calibration for fire was carried out primarily through the fire ignition coefficient, which specifies the average number of ignitions attempted per hectare (ha) for each landtype.

3.2.5 Calibrating LANDIS for the SMMNRA 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).

The fire regime treatments were developed based on average FRIs calculated for the whole study area and for each landtype using fire history data from the last century, in addition to average FRIs cited in the literature for the two counties in which the study area is located. Keeley et al. (1999) calculated FRIs of 44 and 121 yr for Los Angeles and Ventura Counties respectively before 1951 and FRIs of 30 and 34 yr respectively after 1951. The average FRI for the “long” treatment (average FRI 60 years) was designed to approximate the historic fire frequency that maintained species’ abundance and persistence on the landscape over the last century. The “medium” and “short” treatments (average FRI 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 at the growing wildland urban interface.

In LANDIS, fire size occurs stochastically, but follows a lognormal distribution so that small fires are more likely to occur than large fires and are a function of a mean and variance specified in the parameters. Because the fire size distribution is strongly skewed in the SMMNRA (NPS 2004), the average fire size was specified to be 40 ha, with a variance of 20,000 ha.
3.2.6 Objectives for scenario analysis

Scenario analysis is a modeling technique that can be used for a range of purposes such as comparing the effects of different management strategies (e.g. Syphard et al. in press) or evaluating model robustness (e.g. Voinov et al. 2004). Also, when simulation models are highly complex, involving multiple nonlinearities and spatial relationships as in LANDIS, scenario analysis is usually the only feasible method that can be used for model optimization (Seppelt and Voinov 2004). Model optimization is the process of exploring multiple parameter combinations to find the ones that bring the system as close as possible to a certain desired state. Instead of systematically searching over the entire control space automatically (as can be done with less complex models), using scenario analysis for optimization involves the formulation and comparison of multiple parameter combination scenarios to determine which ones produce the most desirable outcome (Seppelt and Voinov 2004).

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. The premise for determining expectations was based on evidence that, although much of the vegetation in the region has remained stable over the last century (e.g., Bradbury,
115, Franklin et al. 2004), extremely high fire frequencies in some locations are beginning to threaten the persistence of certain vegetation types, differentially affecting species based on their functional type (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 average fire regime of the 20th century (the long treatment) would result in vegetation composition similar to the current landscape, with little change in species abundance over time. On the other hand, the medium and short treatments were expected to differentially alter the extent of cover on the landscape for obligate seeders versus obligate resprouters. Because obligate seeders require 5-25 years to generate a sufficient seed bank to recruit following fire, these species were expected to remain stable at the long treatment, but to progressively decline with the increased fire frequencies of the medium and short treatments (because fire could recur before a seed bank was established). On the other hand, obligate resprouters were expected to be favored by the highest fire frequencies due to their ability to resprout successfully after only two to three years following a previous fire and to also favor the lowest fire frequencies because they are longer-lived and more shade-tolerant than obligate seeders. Although resprouters are less sensitive to high fire frequency, there have been circumstances in which they also experienced mortality after repeated fires (e.g. Haidinger and Keeley 1993).
The process of evaluating model simulations according to these parameter scenarios was adaptive such that, if one of the parameter scenarios resulted in unrealistic species’ response, that scenario was eliminated from the evaluation process. The parameter scenarios were tested under all three of the model treatments to ensure that the functional groups were responding appropriately in response to increasing fire frequencies. The simulations were evaluated according to the direction of functional type response under the three treatments and how stable the species cover remained in the long scenario over the 50-year simulations. This eventually resulted in a naming of parameter space that produced realistic functional type response to fire frequency while maintaining stable cover under the long scenario. Simulations using the final set of parameters were replicated 10 times each over 50-year model runs. Four sets of parameters were varied, including species probabilities of establishment; species fire tolerance; fuel accumulation rates over time; and species dispersal distances.

3.2.6.1 Probability of establishment scenarios

The landtype map approximates the species’ fundamental niche through specification of probabilities of establishment and growth under varying site conditions. Because a realized niche is influenced by additional factors such as disturbance history or inter-specific competition (Shugart 1998), the species’ probabilities for establishment were initially assigned based on the proportion of their extent within each landtype, but were then adjusted based on a literature review
of their general site preferences (e.g. obligate resprouters tend to prefer mesic, north-aspect landtypes and obligate seeders prefer more xeric, south-facing landtypes).

Two alternate scenarios were evaluated based on establishment probabilities (Table 4). One scenario evenly weighted the establishment probabilities of the species based on environmental factors. In the other scenario, the probabilities of establishment for the obligate resprouters were lowered and those for the obligate seeders and coastal sage scrub species were increased. The reason for creating a bigger gap in site advantages between the obligate resprouters and the other species was to better 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). Therefore, the probabilities of establishment reflected general landtype preferences for the species, but also regulated the overall capability for different functional groups to successfully establish.

3.2.6.2 Fire tolerance scenarios

In LANDIS, fire is a bottom-up disturbance, and fires of increasing severity differentially affect species based on their age and their fire tolerance. Fire tolerance is specified through five classes, from low tolerance at 1 and high tolerance at 5. Fire susceptibility by age is also simulated through five classes representing the current age in proportion to its longevity. In previous simulations in southern CA, the obligate seeders have been parameterized as having a lower fire tolerance (class
3) than obligate resprouters (class 4) because obligate seeders suffer 100 percent mortality during the stand-replacing fires they experience (Keeley and Zedler 1978, Zedler 1995). Although obligate resprouters are also usually top-killed by fire, they tend to prefer more mesic, highly productive landtypes that, under the severest conditions, should be expected to generate the highest intensities (Keeley and Fotheringham 2003).

Two scenarios of simulations were compared based on the fire tolerances of obligate seeders and obligate resprouters. In the first scenario, the functional types were given different fire tolerances as in the previous simulations. However, because obligate seeders and obligate resprouters may also co-exist in mixed stands that would then experience the same intensity of fire, another scenario was evaluated using the same fire tolerance for both functional types.

3.2.6.3 Fuel accumulation scenarios

Fuel quantity is an important factor affecting fire severity, but the rate of biomass accumulation over time generally varies according to site factors. For example, xeric landtypes tend to have slower decomposition rates and, due to low fuel moisture, can usually carry a fire more quickly than mesic sites, despite the higher primary productivity and more rapid fuel accumulation on mesic sites (Radtke et al. 1982, He and Mladenoff 1999). 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. This relationship is
generalized categorically and can be expressed differently by landtype (fire severity classes range from 1 – 5, with class 5 fire being the most severe).

In southern CA, studies have demonstrated differential fuel accumulation in chaparral due to factors such as elevation, topography, slope aspect, and weather (Green 1981, Payson and Cohen 1990, Regelbrugge 2000). North-facing slopes and higher elevation sites are more mesic, and post-fire plant cover has been positively related to elevation (Keeley and Keeley 1981). Regardless of site conditions, shrub biomass increases rapidly after fire and continues for several decades, and then primary production slows after approximately 20 years (Keeley 2000). Due to this rapid fuel accumulation, these shrublands can burn at young ages (e.g. Zedler et al. 1983, Keeley et al. 1999). However, the largest-scale fires (at the highest intensities) are carried within 10 years for coastal sage scrub species (drought-deciduous, short-lived shrubs that cover many of the coastal slopes), 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 in fuel dynamics, the landtypes were first classified according to whether they are dominated by coastal sage scrub, south-slope chaparral, or north-slope chaparral. Each of these three classes was then assigned a different fuel accumulation curve according to the approximate time it takes to carry a large-scale fire (from Radtke et al. 1982).
Two simulation scenarios were compared using different fuel accumulation curves (Figure 4). In one scenario, it was 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 class, assuming that the dominant vegetation types on the different landtypes ultimately burned at different intensities, even when full canopy had been developed.

3.2.6.4 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). Although exact seed dispersal distances are unknown for many species in the SMMNRA, there is substantial evidence that distance varies according to mode of dispersal, which varies by functional type. For example, the obligate seeder species usually only disperse within 5-10 meters from the parent plant, but the animal-dispersed obligate resprouter seeds are more likely to travel 100 meters from the parent plant (Zedler 1995, Keeley 2000).
In the foothills landscape (Franklin et al. in press), 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 with effective distances set at 5 meters, their landscape extent substantially declined under all of the parameter scenarios, even in the long scenario. Therefore, because the new function is probability based, additional simulations were evaluated with increased effective dispersal distances (50, 75, and 100 m) for the obligate seeders.

3.2.7 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, additional simulations were run with FRIs ranging from 5 to 150 years to test the range of the functional types’ simulated 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, the hypothetical
resilience of obligate seeders and obligate resprouters across a range of FRIs was
expected to resemble the pattern shown in Figure 5, which was modified from
Keeley (1986) so that obligate resprouters had 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.

3.3 Results

3.3.1 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). The overall error was −13% in the short treatment, −6% in the
medium treatment, and −2% in the long treatment. The error was slightly higher for
the distribution of FRIs across separate 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.

3.3.2 Probability of establishment scenarios

The first parameter scenarios compared were those with different probabilities of
establishment, 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 (A vs B; Figure 6). However, the overall effect of altering this parameter was minimal. The model simulations under both scenarios resulted in a substantial net increase in obligate resprouter cover and net decrease in obligate seeder cover (A and B; Figure 7), 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, however, was more realistic because the obligate seeders lost substantially more cover at higher frequencies while the obligate resprouters favored the highest and lowest fire frequencies. Because the PHIGH scenario (A) closed the gap between the net gain in cover for the obligate resprouters and the net loss of cover for the obligate seeders, this was the parameter scenario chosen to use in the next step of the evaluation.

3.3.3 Fire tolerance scenarios

The next simulations evaluated were those in which the obligate seeders were given the same fire tolerance value as the obligate resprouters. Although the fire tolerance value for the obligate resprouters didn’t change, the overall extent of cover was lower when the obligate seeders had a lower fire tolerance value (A vs C; Figure 6). Correspondingly, the overall extent of cover was also higher for the obligate seeders, substantially closing the gap in extent between the two functional types (A vs. C; Figure 7). 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, Figure 7). These results were unrealistic because the obligate seeders' cover is expected to continue declining with shorter FRIs (as in Figure 3); therefore, evaluations continued with the PHIGH scenario and the FTDIFF scenario (A).

3.3.4 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 FHIGH (D vs. A; Figure 7). However, increasing the fire severity across the landscape substantially lowered the cover of obligate resprouters, especially in the short scenario that experienced the highest fire frequency (D; Figure 7). Although the obligate seeders’ response to this scenario was acceptable, the obligate resprouters should not succumb to this extent to high frequency fire.

3.3.5 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; Figure 8), but this gain in extent did not affect the cover of the obligate resprouters (B; Figure 8). Because the dispersal distance of 75m resulted in the final extent most even with 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; Figures 6 and 7). Although the real biological dispersal distances of obligate seeders are closer to 5 meters, inflating the dispersal parameter did not result in unrealistic species patterns.
under the three scenarios. In other words, even with the long scenario, in which the obligate seeders persisted the most, the spatial pattern of cover does not reflect any extensive expansion of the species on the landscape (Figure 9).

3.3.6 Test of final parameter set across varying fire frequency

The final parameter set was used to run 10 simulations across a range of FRIs from 5 to 150 years. Although the obligate resprouters would be 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 (Figure 10) closely matched the hypothetical ones (as in Figure 3). Using the final parameter set, all functional groups maintained very stable cover over the 50-year simulations in the long scenario, although the obligate resprouters did increase slightly in cover under all three scenarios (Figure 11).

3.4 Discussion

Although LANDIS was initially developed for forests in northern Wisconsin, this research demonstrated how LANDIS 4.0A could be calibrated to simulate the high fire frequency and unique post-fire response strategies characteristic of MTE shrublands. Previous simulations were conducted in southern California using LANDIS 3.6 (Franklin et al. 2001, Syphard and Franklin 2004, Franklin et al. in press); however, they used a 10-year time step that prevented simulation of some of the finer-scaled temporal dynamics that occur in the region e.g. annual grass dynamics, early sexual maturity of some species, and extremely short intervals
between fires. By calibrating LANDIS 4.0A, these dynamics were successfully simulated, and the model results reasonably reflected how dominant plant species functional groups are expected to respond under a range of fire return intervals.

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 average simulated FRIs were two years shorter than the targeted FRIs in all of the treatments. Therefore, the objective of creating three “different” treatments was met. As in other LANDIS applications (He and Mladenoff 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), they fared better in the medium treatment than in the long treatment and had approximately the same amount of cover in the short and long 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; and the FRIs in the
short treatment should result in substantially reduced cover (compared to the long treatment) because the shorter the FRIs, the more susceptible the obligate seeders are to becoming locally extinct (NPS 2004). Therefore, even though the two functional types may be equally susceptible to fires in mixed stands, as hypothesized, this phenomenon should not translate into even resilience in all locations. Although obligate seeders and obligate resprouters do co-occur on certain parts of the landscape, they are more likely to be distributed according to site preferences. For example, although obligate resprouters are generally more shade tolerant than obligate seeders, obligate seeders will often replace obligate resprouters on xeric, equator-facing slopes (Keeley 1986).

Although 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 (especially compared to the forests LANDIS was designed to simulate with FRIs ranging from 200 – 1000 years), 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, and the length of the simulations was only 50 years. Therefore, although inflating the dispersal distance of the obligate seeders was unrealistic, there were relatively few opportunities for recruitment via dispersal to occur, which is why the species’ pattern on the landscape was not unrealistically different from the initial distribution. Another reason inflating the dispersal distance did not substantially affect species pattern is that, regardless of whether the distance was 5m or 75m, 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, which really don’t 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 Figure 3. Although most chaparral species are resilient to a range of fire frequencies (Zedler 1995), obligate resprouters will replace obligate seeders at FRIs shorter than 10 years and longer than 100 years, while the obligate seeders favor more intermediate FRIs between 10 and 100 years (Keeley 1986). Another goal in the calibration was to ensure that all functional types would remain fairly stable over time at the long scenario because those specified FRIs have maintained the current composition of the vegetation over the last century. However, the obligate resprouters increased their cover under all three scenarios, resulting in a net gain in extent. Yet, this net increase was on only about 5 percent of the landscape and did not affect the response of the other functional types, which remained stable in the long scenario and responded appropriately to the different scenarios.

Despite the integrity of the core LANDIS design, as emphasized previously, 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 intended to simulate. The results of the calibration 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 still be improved to further 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 meters because this distance was translated into a probability, which was very small. One reason for this behavior is that, if the species is not able to disperse to another cell, no new recruitment is possible. Therefore, a useful improvement to the LANDIS model 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 switch could be added to allow that functionality for certain species and not for others.

Although species can’t recruit via dispersal in the same cell, LANDIS 4.0A does allow for obligate seeders to establish a long-lived persistent seed bank in the same cell; however, the reverse problem occurs because a dormant seed bank can’t be established in adjacent cells. Therefore, another improvement to the model would be to enable a species to disperse to a new location, but to establish a seed bank in that location instead of automatically recruiting a new individual. This would allow the seed bank to remain dormant until the next fire instead of automatically recruiting.
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 or dispersal; 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). Although this phenomenon is not always relevant in other ecosystems, it nevertheless cannot be simulated because the maturity parameter only allows one age to be specified, regardless of the origin of the new cohort. 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.

3.5 Conclusion

Model evaluation procedures usually vary according to the stage of the modeling process, but specific techniques depend on the objective of the research and the nature of the modeling approach (Loehle 1997, Giudici 2002). For predictive ecological simulation models, verification tends to be performed more frequently than calibration, which is usually performed more frequently than validation (Shugart 1998, Barrett 2001, Gardner and Urban in press). In most circumstances, the more detailed the parameter requirements and the more complex the model formulations, the more difficult evaluation becomes (Morrison et al. 1992). Therefore, validation
is often not performed due to difficulties in acquiring independent data sets, particularly for a future that hasn’t occurred yet (Oreskes et al. 1994, Rastetter, 1996, Parker et al. 2003).

Although no model can be perfectly validated, many landscape change models, including LANDIS, were not intended to predict exactly when and where future change could occur. Rather, they were designed to provide estimates of potential future conditions, to generate and test hypotheses, and to allow an experimental approach without the need for direct manipulation (Mladenoff 2004b). As such, an unvalidated model can still be a useful research and policy-making tool if it elucidates meaningful relative differences between landscape scenarios that are relevant and sufficient for management objectives (Keane et al. 2004). However, if validation is not performed, verification and calibration become important components of the modeling process to establish the credibility of model results.

The standard LANDIS calibration approach was used for this research because the algorithms in the model have been tested and verified in a variety of settings, and many of the core parameters and coefficients (that haven’t changed with new versions of the model) have also been evaluated in other sensitivity analyses (e.g. He and Mladenoff 1999, Mladenoff and He 1999, He et al. 1999). Therefore, we believed that devising a more sophisticated, automatic calibration approach was unnecessary, particularly for the ultimate objectives of the research: evaluating potential consequences of altered fire regimes on the general distribution and composition of dominant functional types in the study area. Furthermore, we were
able to build upon the techniques and parameter sets that were developed for our previous research in the foothills landscape (Syphard and Franklin 2004, Franklin et al. in press).

Although all of the calibration parameter scenarios were designed according to realistic assumptions about the dynamics in the study area, some of the parameter combinations produced more realistic results than others. In complex models such as LANDIS, characterized by factors including stochastic functions, nonlinear relationships, feedbacks, and emergent behavior, difficulties in evaluation may arise because different parameter combinations might produce the same ultimate response (equifinality) or because model output cannot be directly related to the effects of input parameters (parameter indeterminancy) (Baird 1999). Many parameter combinations will also remain undiscovered, with a probability proportional to the complexity of the model (Villa et al. 2004). Therefore, this iterative process of comparing single model runs with adjusted parameter sets and evaluating results based on ecological assumptions (e.g. parameter scenario analysis) was an effective way to optimize the fit between the parameters and model behavior (He and Mladenoff 1999). This strategy provided a better understanding of how the model responded to change in the parameters that were most important and relevant to the modeling objectives. These efforts were also necessary to ensure that we can use the model and calibrated parameters for other studies, such as the interactions of urban growth with fire disturbance.
Southern California and other MTEs are biologically rich regions with high species endemism; yet, they have also been labeled as biodiversity hotspots due to extensive and intensive impacts from human activities (Myers et al. 2000). Scientists have predicted that MTEs and grassland ecosystems will experience the greatest change in biodiversity by 2100 than any of the other terrestrial biomes (Sala et al. 2000), and they also have a worse ratio of habitat converted to habitat protected than the other biomes in the world (Hoekstra et al. 2004). Clearly, more ecological research and conservation planning is needed for these imperiled regions. This new version of LANDIS, along with other simulation models that are being developed for MTEs, can be very effective tools for testing and generating hypotheses about vegetation dynamics under altered fire regimes. The methods used in this research may be modified and applied to other regions. Model results can help target areas for protection, can be used to evaluate the consequences of various fire management scenarios, and can help to focus field-based observations and experiments.
4.6 References


Franklin, J., Syphard, A. D., He, H. S., and Mladenoff, D. J. in press. The effects of altered fire regimes on patterns of plant succession in the foothills and mountains of southern California. Ecosystems.


Green, L. R. 1981. Burning by prescription in chaparral. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, General Technical Report PSW-51, Berkeley, CA


Syphard, A.D., Clarke, K.C. and Franklin, J. in press. Using a cellular automaton model to forecast the effects of urban growth on habitat pattern in southern California. Ecological Complexity.


Table 3-1. Variables used to create landtype classes in the SMMNRA

<table>
<thead>
<tr>
<th>Variable</th>
<th>Resolution</th>
<th>Source, description</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual precipitation</td>
<td>1 km²</td>
<td>J. Michaelson, interpolated by kriging (see Franklin 1998)</td>
<td>330.1 to 623.4 mm</td>
</tr>
<tr>
<td>January minimum temperature</td>
<td>1 km²</td>
<td>J. Michaelson, interpolated by kriging (see Franklin 1998)</td>
<td>3.76 to 8.6 °C</td>
</tr>
<tr>
<td>July maximum temperature</td>
<td>1 km²</td>
<td>J. Michaelson, interpolated by kriging (see Franklin 1998)</td>
<td>22.6 to 28.0 °C</td>
</tr>
<tr>
<td>Elevation**</td>
<td>10m</td>
<td>USGS Digital Elevation Model</td>
<td>106 to 948 m</td>
</tr>
<tr>
<td>Slope gradient</td>
<td>10m</td>
<td>Derived from DEMs by first order finite difference</td>
<td>0 to 73°</td>
</tr>
<tr>
<td>Southwestness</td>
<td>10m</td>
<td>Derived from DEMs,</td>
<td>0 (southwest) to</td>
</tr>
<tr>
<td></td>
<td></td>
<td>swness = (con(aspect(&lt;dem&gt;) == -1, 201, ~</td>
<td>201 (northeast)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>((cos((aspect(&lt;dem&gt;) - 225) div deg) + 1) * 100))))</td>
<td></td>
</tr>
</tbody>
</table>

**Elevation was not used in the clustering due to its strong correlation with slope gradient and southwestness**
Table 3-2. Final species life history attributes and parameters used in LANDIS for seven functional groups

<table>
<thead>
<tr>
<th></th>
<th>Obligate Resprouters</th>
<th>Obligate Seeders</th>
<th>Coastal Sage Scrub</th>
<th>Facultative Seeders</th>
<th>Annual Grass</th>
<th>Oak Woodland</th>
<th>Early Successional</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of species in group</td>
<td>6</td>
<td>2</td>
<td>6</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Longevity (year)</td>
<td>150</td>
<td>75</td>
<td>50</td>
<td>100</td>
<td>1</td>
<td>250</td>
<td>10</td>
</tr>
<tr>
<td>Age of maturity (year)</td>
<td>20</td>
<td>10</td>
<td>2-3*</td>
<td>15</td>
<td>1</td>
<td>40</td>
<td>1</td>
</tr>
<tr>
<td>Shade tolerance (ordinal class 1 – 5)</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>3-4*</td>
<td>1</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Fire tolerance (ordinal class 1 – 5)</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>3-4</td>
<td>1</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Effective seed dispersal distance (m)</td>
<td>100</td>
<td>75</td>
<td>75</td>
<td>75</td>
<td>10,000</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Maximum seed dispersal distance (m)</td>
<td>500</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>-1**</td>
<td>500</td>
<td>500</td>
</tr>
<tr>
<td>Probability resprout (0-1)</td>
<td>80 - 1.0*</td>
<td>0</td>
<td>.25 – .75*</td>
<td>.70 - .80*</td>
<td>0</td>
<td>.50</td>
<td>0</td>
</tr>
<tr>
<td>Minimum age of resprouting (year)</td>
<td>3</td>
<td>0</td>
<td>4</td>
<td>3</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
</tbody>
</table>

* Indicates a range of values for the species within that functional group

** A dispersal distance of –1 means the species can disperse to anywhere on the landscape
Table 3-3. Targeted and mean simulated fire rotation 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)

<table>
<thead>
<tr>
<th>Landtype</th>
<th>Proportion of Study Area</th>
<th>Targeted and simulated FRIs</th>
<th>Targeted and simulated FRIs</th>
<th>Targeted and simulated FRIs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Short Treatment</td>
<td>Medium Treatment</td>
<td>Long Treatment</td>
</tr>
<tr>
<td>Entire Landscape</td>
<td>1.0</td>
<td>15</td>
<td>13 (0)</td>
<td>30</td>
</tr>
<tr>
<td>Interior North</td>
<td>0.18</td>
<td>25</td>
<td>20 (1)</td>
<td>40</td>
</tr>
<tr>
<td>Interior South</td>
<td>0.20</td>
<td>20</td>
<td>19 (1)</td>
<td>35</td>
</tr>
<tr>
<td>High North</td>
<td>0.15</td>
<td>15</td>
<td>13 (0)</td>
<td>30</td>
</tr>
<tr>
<td>High South</td>
<td>0.11</td>
<td>15</td>
<td>12 (0)</td>
<td>30</td>
</tr>
<tr>
<td>Transition</td>
<td>0.16</td>
<td>10</td>
<td>8 (0)</td>
<td>25</td>
</tr>
<tr>
<td>High Slope Coast</td>
<td>0.06</td>
<td>5</td>
<td>5 (0)</td>
<td>20</td>
</tr>
<tr>
<td>Low Slope Coast</td>
<td>0.14</td>
<td>5</td>
<td>5 (1)</td>
<td>20</td>
</tr>
<tr>
<td>Scenario</td>
<td>One</td>
<td>Two</td>
<td>One</td>
<td>Two</td>
</tr>
<tr>
<td>------------------</td>
<td>-----</td>
<td>-----</td>
<td>-----</td>
<td>-----</td>
</tr>
<tr>
<td><strong>Species Name</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ceanothus megacarpus ***</td>
<td>0.4</td>
<td>0.8</td>
<td>0.7</td>
<td>0.9</td>
</tr>
<tr>
<td>Ceanothus crocifolius ***</td>
<td>0.4</td>
<td>0.8</td>
<td>0.5</td>
<td>0.8</td>
</tr>
<tr>
<td>Ceanothus spinosus ++</td>
<td>0.4</td>
<td>0.6</td>
<td>0.2</td>
<td>0.4</td>
</tr>
<tr>
<td>Adenostoma fasciculatum+++</td>
<td>0.4</td>
<td>0.6</td>
<td>0.6</td>
<td>0.8</td>
</tr>
<tr>
<td>Adenostoma sparsifolium *</td>
<td>0.1</td>
<td>0.1</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Quercus lobata ++</td>
<td>0.5</td>
<td>0.3</td>
<td>0.3</td>
<td>0.1</td>
</tr>
<tr>
<td>Fraxinus excelsior *</td>
<td>0.3</td>
<td>0.2</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Malus pumila *</td>
<td>0.3</td>
<td>0.4</td>
<td>0.3</td>
<td>0.1</td>
</tr>
<tr>
<td>Cercocarpus betuloides *</td>
<td>0.5</td>
<td>0.3</td>
<td>0.3</td>
<td>0.1</td>
</tr>
<tr>
<td>Fagus grandifolia *</td>
<td>0.1</td>
<td>0.1</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Quercus agrifolia+</td>
<td>0.3</td>
<td>0.2</td>
<td>0.2</td>
<td>0.1</td>
</tr>
<tr>
<td>Salvia miltiorrhiza**</td>
<td>0.3</td>
<td>0.9</td>
<td>0.4</td>
<td>0.3</td>
</tr>
<tr>
<td>Salvia leucophylla**</td>
<td>0.5</td>
<td>0.8</td>
<td>0.4</td>
<td>0.7</td>
</tr>
<tr>
<td>Eucalyptus californica***</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Eriogonum fasciculatum**</td>
<td>0.5</td>
<td>0.8</td>
<td>0.5</td>
<td>0.8</td>
</tr>
<tr>
<td>Eriogonum cinnemon***</td>
<td>0.05</td>
<td>0.2</td>
<td>0.1</td>
<td>0.4</td>
</tr>
<tr>
<td>Artemisia californica**</td>
<td>0.3</td>
<td>0.6</td>
<td>0.5</td>
<td>0.8</td>
</tr>
<tr>
<td>Lotus scoparius++</td>
<td>0.2</td>
<td>0.5</td>
<td>0.2</td>
<td>0.5</td>
</tr>
<tr>
<td>Annual grass</td>
<td>0.3</td>
<td>0.7</td>
<td>0.3</td>
<td>0.8</td>
</tr>
</tbody>
</table>

*** Obligate Seeder  ** Coastal Sage Scrub  * Obligate Resprouter  +++ Facultative Seeder
++ Early Successional  + Oak Woodland
Table 3-5. Parameter scenarios listed in the order that they were evaluated

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Abbreviation</th>
<th>Scenario Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Probabilities of Establishment</td>
<td>PLOW *</td>
<td>Species’ probabilities of establishment based solely on site preference</td>
</tr>
<tr>
<td>Probabilities of Establishment</td>
<td>PHIGH *</td>
<td>Species’ probabilities of establishment increased for obligate seeders and decreased for obligate resprouters</td>
</tr>
<tr>
<td>Fire Tolerance</td>
<td>FTSAME</td>
<td>Fire tolerance of obligate seeders and obligate resprouters is the same</td>
</tr>
<tr>
<td>Fire Tolerance</td>
<td>FTDIFF**</td>
<td>Fire tolerance of obligate resprouters is higher than fire tolerance of obligate seeders</td>
</tr>
<tr>
<td>Fuel Accumulation Rate</td>
<td>FUELS**</td>
<td>Fuel accumulation curves scaled so the maximum severity fire differs by landtype</td>
</tr>
<tr>
<td>Fuel Accumulation Rate</td>
<td>FUELNS</td>
<td>Fuel accumulation curves allow all landtypes to reach fire severity class 5</td>
</tr>
<tr>
<td>Effective Dispersal Distance</td>
<td>DISP5**</td>
<td>Biologically realistic dispersal distance (5 m) used initially for obligate seeders</td>
</tr>
<tr>
<td>Effective Dispersal Distance</td>
<td>DISP75</td>
<td>Dispersal distance (75 m) used for obligate seeders in the final parameter set</td>
</tr>
</tbody>
</table>

* Represents the first two scenarios that were evaluated
** Represents the ‘baseline” scenarios.
Figure 3-1. The Santa Monica Mountains in southern California.
Figure 3-2. Map of seven landtypes overlaid with roads, urban areas, and wildland urban interface in the Santa Monica Mountains, CA
Figure 3-3. Distribution of *Ceanothus megacarpus* before (A) and after (B) classification into species-age classes for the LANDIS model.
Figure 3-4. 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.
Figure 3-5. Hypothetical resilience of obligate resprouters and obligate seeders across a range of fire return intervals in California chaparral (modified from Keeley 1986)
Figure 3-6: 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 FT SAME; D = PHIGH and FTDIFF and FUELNS; E = final parameter set (PHIGH, FTDIFF, FUELS, and DISP75). See Table 5 for definition of scenarios.
Figure 3-7: 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.
Figure 3-8: Proportions of study area occupied by obligate seeders (A) and obligate resprouters (B) with dispersal distances of obligate seeders at 5m, 50m, 75m, and 100m 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 5m; OR OS 50 in the legend corresponds to obligate resprouter extent with obligate seeder dispersal distance set to 50 m, etc.
Figure 3-9: Maps illustrating presence of obligate resprouters and obligate seeders at year 0 and at year 50 for the short, medium, and long model treatments
Figure 3-10: Simulated resilience of obligate resprouters and obligate seeders across a range of fire return intervals in the Santa Monica Mountains, CA
Figure 3-11: 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
Chapter 4. Simulating the effects of frequent fire on southern California coastal shrublands

4.0 Abstract

Fire disturbance is a primary agent of change in the Mediterranean-climate chaparral shrublands of southern California. 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 proportionately more cover to other functional types, including 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.
4.1 Introduction

The coastal ranges and interior foothills of southern California 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, woody shrub species that are approximately 1-4 meters tall and almost entirely evergreen with small, thick, stiff sclerophyllous leaves. Chaparral reaches its maximum extent at middle elevations (300 – 1500 meters), but the distribution of different species is strongly influenced by slope aspect, coastal-desert exposure, elevation, substrate, and fire regime (Hanes 1971). Because of the complex topographic, edaphic, and climatic conditions in southern California, chaparral often forms a mosaic pattern interspersed with other vegetation types, including coastal sage scrub, oak woodland, and grassland (Keeley 2000). Coastal sage scrub is the next most extensive vegetation type and consists of drought-deciduous subshrubs that cover many coastal slopes in drier locations and at lower elevations than chaparral (Westman 1981).

Chaparral shrublands are quite flammable relative to other ecosystems due to low decomposition rates, high dead-to-live fuel ratios, dense community structure, and low fuel moisture (Countryman and Philpot 1970, Christensen 1985, 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 that
consume large portions of the landscape (Keeley and Fotheringham 2003).

Although these periodic crown fires kill all aboveground vegetation, chaparral is
generally resilient to fire and returns rapidly to its pre-fire composition (Bond and
van Wilgen 1996). The post-fire environment is usually dominated by opportunistic
and “fire-following” herbs, but after several years, these shorter-lived species are
ovetopped by the shrubs that were originally present (Keeley 1981, Keeley 1986).
The life history strategies of chaparral species are related to fire, and shrubs are
usually classified based on three post-fire regeneration modes: obligate resprouters
respond to fire through vegetative propagation from underground burls or
lignotubers; obligate seeders are unable to regenerate vegetatively, but recruit from
long-lived dormant seed banks that are cued by fire to germinate; and facultative
seeders 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 in the region using common dendroecological methods (Keeley
and Fotheringham 2001). Determining the natural fire regime is also complicated by
the fact that humans have set fires in the region for hundreds to thousands of years
(Keeley and Fotheringham 2003). Fire frequency has likely fluctuated somewhat
throughout the Holocene in response to changes in climate, human population, and
land use (Zedler 1995). However, evidence from charcoal deposited in marine
sediments in the Santa Barbara Channel suggests that large fire events in the region
have historically been associated with extreme fire weather, and these large fires have been responsible for most of the land area burned (Mensing et al. 1999). Despite some of this uncertainty regarding the region’s fire history, chaparral is thought to be resilient to fire at rotation intervals ranging from 20 to 150 years, with an average fire rotation interval of approximately 50 to 80 years (Keeley 1981, Minnich 1983, Conard and Weise 1998, Zedler 1995). A fire rotation interval 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 some controversy over how the fire regime has changed (Keeley and Fotheringham 2001, Minnich 2001). On the one hand, 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, 1995, 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 (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 tremendously, beyond the historic range of variability, and this increase was correlated with population density (Keeley et al. 1999, Keeley 2002). Fire patterns remained similar over time, with a small percentage of fires leading to the greatest area burned. Furthermore, an analysis of fire perimeter maps from 1967 to 1996 in the Santa Monica Mountains revealed that the majority of vegetation that burned was younger than 20 years old, suggesting that young age classes are limited in preventing fire spread (Keeley et al. 1999). This increase in fire frequency has been attributed to human-caused ignitions at the wildland-urban interface (Conard and Weise 1998, Rundel and King 2001, Keeley and Fotheringham 2003). Therefore, unlike the higher-elevation montane conifer forests where fire suppression has effectively excluded fire from the landscape in some regions, suppression in the lower-elevation shrublands has likely offset the potential impacts of increased ignitions and fire frequency (Keeley et al. 1999).

Local fire regimes influence the distribution of plant communities in southern California due to species’ differences in post-fire regeneration strategies (Keeley 1986, Franklin et al. 2001, Meentenmeyer and Moody 2002). Although chaparral is resilient to a range of fire frequencies, extremely short time intervals between fire events can threaten the persistence of some shrub species (Zedler 1995). In fact, these shrublands may irreversibly convert to other vegetation types (“vegetation type conversion”) such as coastal sage scrub or to 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 reseeded with annual ryegrass (*Lolium multiflorum*) to prevent erosion, or from areas that have been planted with grass and cleared for fuelbreaks (Zedler et al. 1983, Keeley 1986, Byers 2004). Consequently, certain fire management activities can ironically contribute to positive feedbacks that further increase fire frequency (Keeley in press).

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). In fact, southern California contains the highest number of endangered plant species in the conterminous U.S. (Dobson et al. 1997).

The complex interactions and 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, the purpose of this research was to use a
landscape-scale simulation model of fire disturbance and succession (LANDIS) to examine the effects of high frequency fire on the distribution and extent of dominant plant species in southern California shrublands, represented by five different plant functional types, or disturbance response strategies (Pausas 1999). Because of the limited understanding of how much and where vegetation change may occur in the future, three fire regime treatments of increasing fire frequency were applied to the landscape 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?

Based on prior field observations (e.g. Zedler et al. 1983, Haidinger and Keeley 1993, Jacobsen et al. 2004), we hypothesized three changes to be predicted by this model: 1) obligate seeders will be most susceptible to type conversion, but facultative seeders will also decline with frequent fire, 2) obligate resprouters will be favored by the shortest FRIs, and 3) parts of the landscape will shift from chaparral shrubland to coastal sage scrub and alien grasslands at higher fire frequencies.

4.2 Methods

4.2.1 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 (Figure 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 of land is publicly owned and protected, and approximately 25% of the privately owned land is undeveloped. The major vegetation types in the mountains include chaparral (approximately 60% of the area); coastal sage scrub (approximately 25% of the area); oak woodland on northern slopes with deep soils (approximately 3% of the area); and (primarily alien) grasslands (approximately 3% of the study area) (Radtke et al. 1982). The biologically rich region is home to nearly 1,000 plant species, 50 mammal species, 400 bird species, and 35 species of reptiles and amphibians (NPS 2004).

This region has a largely anthropogenic fire regime. Lightning-ignited fires are rare (2 recorded during 80 years of record) and humans account for a substantial number of fires. Over the last 75 years, fire frequency and total area burned have increased, and some areas have burned up to 10 times (NPS 2004). The steep terrain and general alignment of the Santa Monica Mountains promotes intense, rapidly spreading fires that can move rapidly from north to south with extensive lateral spread (Radtke et al. 1982). Essentially all of the large fires are driven by hot, dry Santa Ana winds (with velocity up to 145 k.p.h.) that occur every autumn (NPS 2000).

4.2.2 The LANDIS model

LANDIS is a widely recognized landscape fire succession model that has been subjected to intensive peer review and is the focus of a special issue of the journal
Ecological Modelling (Volume 180, 2004). In that issue, Mladenoff (2004) provides a thorough review of the model’s history and future directions. Additional descriptions of the model and how we calibrated it for another southern California landscape can be found elsewhere (Franklin et al. 2001, Syphard and Franklin 2004, Franklin et al. in press); and details of how LANDIS was parameterized and calibrated for the SMMNRA are provided in Chapter 3 and Syphard et al. (in prep), but will be summarized.

LANDIS is a raster-based, stochastic, spatially explicit model that simulates forest landscape dynamics, including multiple disturbances (although only fire disturbance was applied in this study) and resulting multiple pathways of succession (Mladenoff et al. 1996, He and Mladenoff 1999). Successional dynamics result from interactions between fire regimes, plant life history behaviors, and site conditions, and are 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. LANDIS is a multi-scale, multi-process model. 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 FRIs and disturbance history (fire is more
likely at longer times since last fire). Fire size is also stochastic, but small fires are more likely to occur than large fires, following 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 to adapt it for fire regimes and plant functional types that are characteristic of Mediterranean-type ecosystems (see Chapter 3 and Syphard et al. in prep). These modifications include fire-cued germination from a dormant seed bank (characteristic of obligate and facultative seeders) and an annual time step to simulate the fine-scale temporal dynamics characteristic of these regions. LANDIS version 4.0A was used in this study.

4.2.3 Input Data

LANDIS requires spatial and non-spatial inputs, including a map of species distribution by age class, a landtype map representing site classes of species’ affinities and rates of fuel accumulation, and species life history parameters (longevity, maturity, dispersal distance, ability to resprout, relative shade and fire tolerance) for the simulation of dispersal, establishment, competition, persistence, and mortality.

Based on a preliminary vegetation classification of species for a future mapping project, a literature review, and consultation with NPS vegetation scientists, 19
species were selected to include in the simulations. The values for the species’ life
history attributes were derived from the literature, and the species were classified
into functional groups.

The primary data source used to map the initial distribution of species-age classes
was a digital map 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 were filled
in with a contemporary map of vegetation types (Franklin et al. 1997). For each of
the 19 species selected to use in the simulations, a separate, binary GIS map was
generated, delineating 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 then used to group classes together
based on similarity of species membership, which eventually resulted in 24
vegetation classes. Because the majority of fires are stand replacing in California
shrublands, a current fire history GIS map was used to determine the age of the
vegetation by subtracting the time of last fire by the current year.

The landtype map for the study area was derived from the primary environmental
variables that are known to affect plant distributions and productivity in the region -
local climate and topographically mediated soil moisture availability (Franklin 1995,
Franklin et al. 2000). Based on methods described in Franklin (2003), five gridded
layers (January minimum temperature, July maximum temperature, annual mean
precipitation, slope, and transformed slope aspect) were subjected to unsupervised classification using the ISODATA method (Ball and Hall 1965). The clusters generated through the classification were characterized according to their ranges of values from the input grids, then were combined and/or split according to similarities in environmental characteristics and from mapping their spatial correspondence. The final landtype map, consisting of seven classes, was merged with maps of urban extent and other non-vegetated land. Landtype-related parameters, including probabilities of species establishment and fuel characteristics were derived from the literature as well as through empirical calculation from spatial data (see Chapter 3 and Syphard et al. in prep for more detail). The probabilities of establishment reflected general landtype preferences for the species, but also reflected differences in the overall capability for different functional groups to successfully establish. For example, the obligate resprouters generally had low probabilities of establishment because their overall rate of successful seedling establishment is very low (Keeley 1986, Meentenmeyer and Moody 2002).

4.2.4 Fire regime modeling experiment

The fire regime treatments were developed based on average fire rotation intervals calculated for the whole study area and for each landtype using fire history data from the last century, in addition to average FRIs cited in the literature for the two counties in which the study area is located. The fire rotation interval that was calculated from the fire history in the SMMNRA was 29 years; however, that
number reflects variation in fire frequency over time and across locations. The average inter-fire interval, expressing the average time between fires for any set of randomly determined locations, was 32 years (NPS 2004). Keeley et al. (1999) calculated fire rotation intervals of 44 and 121 yr for the shrublands in Los Angeles and Ventura Counties (the two counties where the SMMNRA is located) respectively before 1951 and fire rotation intervals of 30 and 34 yr respectively after 1951.

Three fire regime treatments were developed and calibrated using fire rotation intervals that varied according to landtype to capture the relative differences in fire frequency across the landscape (Figure 2). The landscape averaged fire rotation interval for the “long” treatment (average fire rotation interval 60 years) was designed to approximate the historic fire frequency that maintained species’ abundance and persistence on the landscape over the last century. The “medium” and “short” treatments (average fire rotation interval 30 and 15 years respectively) were designed to mimic the increasingly shorter fire rotation intervals that have been observed during the last half of the century resulting from human ignitions at the growing wildland urban interface. The model simulations for each treatment were run for 50 years, and then were replicated 10 times each to quantify variability in results due to the stochasticity of the model.

4.2.5 Classification of model output into functional types

Although LANDIS simulates the dynamics of individual species during model runs, the output can be reclassified into assemblages of species. Therefore, the
analysis focused on model output that was reclassified into five functional types, comprising three vegetation types (Wells et al. 2004). Two additional functional types were present in the simulations: oak woodlands (*Quercus agrifolia*) and the early successional species, *Lotus scoparius*. Details of results for these species are not discussed, however, because each occupied approximately 3% of the landscape, and were not the primary focus of our research questions. Using functional types to simulate vegetation dynamics has been an effective way to analyze vegetation change, particularly in disturbance-prone Mediterranean-type ecosystems (Pausas 1999, 2003, Franklin et al. 2001, Rusch et al. 2003). Because species within functional types share similar life history traits and responses to disturbance, analysis of these species as groups provides a framework for understanding the mechanisms driving vegetation response (Pausas 1999).

Chaparral is the most extensive vegetation type in the study area and comprises mixtures of three distinct functional types, as mentioned previously: obligate seeders, facultative seeders, and obligate resprouters. Estimates for species life history values in California shrublands have been widely published in the literature (see Keeley 1995). To avoid false precision, most of the parameter values reflected qualified estimates and highlighted the relative differences between functional types (Table 1). The greatest distinction between the chaparral functional types was between the obligate resprouters and obligate seeders, and the facultative seeders usually had intermediate parameter values.
Generally, the obligate resprouters found in the study area are longer-lived, have higher shade tolerance, and longer dispersal distances than the facultative seeders and the obligate seeders (Keeley 1998). However, the parameterized dispersal distances for the obligate seeders and facultative 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 (see Chapter 3 and Syphard et al. in prep).

The age of maturity parameter in LANDIS specifies the age that species can begin recruiting new individuals. For this parameter, species were assigned values that would elicit the most realistic response according to the way LANDIS behaves. For example, 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 recruit following fire, which ranges from 5 – 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, the duration of the model runs. Facultative seeders were less likely to resprout following fire than the obligate resprouters, and the obligate seeders were not able to regenerate vegetatively.
The coastal sage scrub and grass vegetation types also served as separate functional types in the simulations (Wells et al. 2004). Unlike chaparral, coastal sage scrub occupies lower-elevations on coastal mountains and inland valleys (Malanson and O’Leary 1995). Although coastal sage scrub is less shade tolerant and more sensitive to fire than chaparral species, these species also mature early and have high probabilities of establishment, particularly on drier landtypes, because they recruit continuously between fires (Westman 1982, Zedler 1995, DeSimone and Zedler 1999, 2001). Like facultative seeders, the coastal sage species included in the simulations respond to fire both from resprouting and from seeding, but the primary regeneration strategy in the SMMNRA is by resprouting (Malanson and O’Leary 1982). The potential vigor of resprouting species varies within genera, and this variation is reflected in the parameter values.

The grass functional type was parameterized to reflect an invasive annual habit because these species are of particular concern, especially in terms of vegetation type conversion (Keeley 2002). Although native grasses are highly threatened in the region, they are spatially restricted to small isolated populations (Seabloom et al. 2003) and simulating this behavior would have been difficult at the scale of our simulations. The initial distribution of grass was clumpy, with the species present in a few isolated patches along the perimeter of the study area, reflecting the initial conditions specified by the vegetation map. Grasslands in the region, however, tends to be highly fragmented and widely dispersed (Wells et al. 2004). Grasses also invade from diffuse sources such as residential areas and fuel breaks (where they are
frequently planted). To mimic this likelihood to spread from these sources throughout the landscape, grass was parameterized with a high dispersal distance.

4.2.6 Analysis

4.2.6.1 Extent

LANDIS generated binary GIS maps of functional type presence for every time step in the simulations. These results were analyzed first by calculating the proportion of area occupied by each functional type (extent) over time and comparing the total final area of cover for each fire regime treatment. Because multiple species can exist within any one cell at a given time, the five separate maps of functional type presence for years 0 and 50 were overlaid for each treatment. The resulting maps were reclassified to show the locations of gain and loss of functional type cover over the course of the simulations.

4.2.6.2 Aggregation Index

Spatial pattern metrics are often used to quantify landscape heterogeneity and to relate spatial pattern to ecological processes (Gustafson 1998). Fire is a major mechanism that affects vegetation pattern, which can consequently affect the disturbance regime (Li and Wu 2004). Therefore, the objective for using a spatial pattern index to evaluate the model simulations was to determine whether the different fire regimes of the treatments would generate differences in spatial pattern beyond which could be detected from area calculations.
Recently, the behavior and utility of many of these metrics has been questioned due to their tendency to be highly correlated and/or to show inconsistency in relating landscape pattern to ecological processes (Calabrese and Fagan 2004). As a result, several new indices have been developed to overcome some of these deficiencies. The aggregation index (developed by He et al. 2000) was designed to improve upon the contagion index, which quantifies the degree of clumpiness in landscape patterns. Unlike the contagion index, the aggregation index is class-specific and independent of landscape composition. The index is calculated by comparing the number of shared edges of a particular class with the total possible number of shared edges. The level of aggregation can vary from 0 (completely disaggregated with no shared edges) to 1 (totally aggregated with a maximum number of shared edges). One drawback, as in the contagion index, is that different spatial patterns can produce the same value. However, because the aggregation index has been effective at quantifying LANDIS-generated output and comparing different landscapes (He et al. 2000), it was used to evaluate the relative differences in spatial pattern of species’ functional groups between the fire regime treatments.

4.2.6.3 Fire frequency

LANDIS generated maps of fire events for each time step of the simulations. These maps were overlaid and summed to generate new maps of fire frequency (number of times burned over the course of the simulations). These maps also allowed the calculation of fire return intervals. Unlike the fire rotation interval, the fire return interval indicates the average number of years between two successive fire
events at specific locations. Therefore, they revealed whether certain portions of the landscape were being burned frequently. The fire frequency maps were then overlaid with the maps of functional type gain and loss to compare the effects of fire frequency on functional type extent. The total net area gained or lost for each functional type was then evaluated relative to the fire return intervals.

4.2.6.4 Vegetation change and type conversion

To quantify predicted vegetation type conversion, the areas of gain and loss over time for each functional type were selected and converted to separate GIS maps, which were then overlaid with the combined maps of functional type presence from years 0 or 50. Overlaying maps of areas lost with the combined maps of functional type presence at year 50 determined which functional types those areas had converted to. On the other hand, overlaying the maps of area gained with the maps of functional type presence at year 0 determined which functional types were originally present in those locations. In addition to quantifying change between the three primary vegetation types, change was also quantified between the transition 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 transitional successional processes. Because very little overlap between grass and chaparral occurred, this combination of vegetation types was not considered.
4.3 Results

4.3.1 Extent and aggregation index

The two functional types with the largest relative differences in extent between model treatments were the obligate seeders and the facultative seeders (Figures 3 and 4). Both functional groups declined in extent as the fire rotation interval got shorter, but lost proportionately more cover between the medium and short treatments than between the long and medium treatments. Although the extent of the three other functional groups also differed between treatments, the change in cover was less extensive. 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 annual grass cover steadily expanded as the fire frequency increased (Figures 3 and 4). When looking at the change in cover over time, the decrease in cover for the coastal sage scrub species occurred close to the end of the simulations in the long treatment, at approximately 40 years (Figure 3). Until then, the extent was closer to that in the medium and short treatments.

The clumpiness of landscape pattern over time for the three treatments, as calculated by the aggregation index, closely followed the total extent of the functional groups (Figure 3). Generally, the treatments and functional types with the largest extents on the landscape were also the most highly aggregated. One difference between aggregation index and extent was for the facultative seeders, which remained highly aggregated over time in all three treatments despite the
decline in extent in the short and medium treatments. On the other hand, the obligate seeders became slightly more disaggregated as their extent declined under higher fire frequency.

4.3.2 Fire frequency

The maximum number of times any location on the landscape burned was five in the long treatment (fire return interval of 10), seven in the medium treatment (fire return interval of 7), and 11 in the short treatment (fire return interval of 4), although less than 1 percent of the landscape burned more than 8 times (Figure 5). The locations that experienced the highest simulated fire frequencies generally matched those in the actual fire history of the region (Figure 6). The lower-elevation coastal landtypes burned at higher fire frequencies than the inland, higher-elevation landtypes, and the western side 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 fire frequency patterns in the simulations versus those in the fire history 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 had a substantial net gain at fire return intervals of 50 and 25 (1 and 2 fires) and a substantial net loss when no fires occurred during the simulations (Figure 7). In the medium treatment, in which more of the landscape burned at higher fire frequencies, the obligate seeders also had
a substantial net loss at fire return intervals of 17 years and shorter (3 or more fires).

In the short treatment, where the average simulated fire return interval on the
landscape was 12 years, the obligate seeders experienced a net loss across the whole
landscape, regardless of the fire return interval. However, the net loss was
substantially greater at fire return of 17 or more years than at fire return intervals of
25 or 50 years. Overall, the obligate seeders did best at fire return intervals between
25 and 50 years.

In the long treatment, the facultative seeders substantially gained in extent at an
fire return interval of 50 years and gained slightly less with no fires and at a 25-yr
fire return interval (Figure 7). There was a slight net loss at fire return intervals at 17
years or shorter. In the medium treatment, the only fire return interval under which
the facultative seeders gained in extent was 50 years. Otherwise, the most
substantial loss was at an fire return interval of 17 years, and unlike the long
treatment, there was a slight net loss in areas with no fires. Like the obligate seeders,
the facultative seeders experienced a net loss across the landscape in the short
treatment, and largest extent lost was at fire return intervals of 17 and 13 years. Also
like the obligate seeders, the facultative seeders were favored at fire return intervals
of 50 years; however, they didn’t do quite as well, relatively, at fire return intervals
of 25 years.

The obligate resprouters experienced no net loss of extent in the long treatment,
and the fire return intervals under which there was a net gain ranged from 50 years to
13 years, with the highest gain at 50 years (Figure 7). In the medium and short
treatments, the obligate resprouters experienced gains in extent in areas that experienced no fires or fire return intervals of 50 years in addition to areas with short fire return intervals ranging from 17 to 6 years. The only fire return interval that didn’t favor the obligate resprouters was 25 years.

Unlike the obligate resprouters, the coastal sage scrub species experienced net loss of extent in areas with no fires under all three treatments (Figure 7). In the long and medium treatments, the coastal sage scrub species gained substantial area under fire frequencies ranging from 50 years to 17 years, but also gained extent at higher fire frequencies. Although most of the net gain in the short treatment also ranged from 50 to 17 years, the coastal sage scrub species declined in extent at fire return intervals of 13 years and shorter.

In all three treatments grass experienced a net loss in areas that didn’t burn and in areas with fire return intervals of 50 years (Figure 7). Grass gained the most extent under fire return intervals of 25 in the long and medium treatment and under a fire return interval of 17 years in the short treatment. Although grass gained area at the highest fire frequencies in the long and medium treatments, there was a slight net loss at fire return intervals of 8 and 6 years in the short treatment.

4.3.3 Vegetation change

The spatial pattern of vegetation change for the obligate seeders differed substantially between the three treatments, reflecting changes in fire frequency (Figure 8). In the long and medium treatments, the obligate seeders expanded in the
northwest corner of the landscape where fire frequencies were intermediate. Much of the decline in extent occurred in the northeast and middle regions in the long treatment, where no fires occurred; but in the medium and short treatments, the decline occurred primarily in the southern part of the functional types’ range, reflecting the high fire frequencies that occurred in those locations.

The facultative seeders expanded and declined in the same general regions of the landscape as the obligate seeders in the long and medium treatments, with most of the gain occurring in the western side of the region and most of the decline occurring on the eastern end for the long treatment and in the south for the medium treatment (Figure 9). In the short treatment, the facultative seeders also declined in the southern portion of the middle of the landscape; however, unlike the obligate seeders, they expanded in the lower east end of the landscape. Most of this expansion occurred farther south than the range of the obligate seeders, but fire frequency was intermediate to high in this location.

The patterns of expansion and decline for the obligate resprouters were more evenly distributed and interspersed than those of the obligate and facultative seeders (Figure 10). As fire frequency increased from the long to the short treatments, however, the obligate resprouters increasingly expanded in the southern locations of the landscape where the obligate and facultative seeders declined.

In all three treatments, coastal sage scrub species expanded substantially in the middle and northern regions of the landscape under low to medium fire frequencies (Figure 11). They also expanded in the coastal region in the middle of the landscape,
but to the east and west of this expansion, the coastal sage scrub species declined under the highest fire frequencies.

The patches of blue in all three of the treatments reflect the ephemeral nature of the grass functional type (Figure 12). Because the species has a one-year lifespan and the model runs on an annual time step, the patterns of grass changed constantly, and the initial patches of grass in the species age map disappeared as the species dispersed widely across the landscape. The primary difference between the three treatments is the overall increase in abundance of grass at higher fire frequencies.

4.3.4 Type conversion

In the long treatment, the obligate seeders gained approximately the same amount of cover from coastal sage scrub species as it lost to other chaparral functional types in other locations (Figure 13a). The obligate seeders also gained some area from grass and from a coastal sage scrub/chaparral mix. Although the obligate seeders also gained the most area from coastal sage scrub and lost the most area to other chaparral in the medium treatment, there was also a small net loss to a coastal sage scrub/chaparral mix. In the short treatment, the obligate seeders experienced an overall net loss of cover with a substantially larger proportion of its original extent lost to coastal sage scrub/chaparral mix than in the other treatments. Also, the obligate seeders experienced a net loss of cover to coastal sage scrub species and to coastal sage scrub/grass mix in the short treatment.
The relative proportions of net gain and loss to other functional types for the facultative seeders almost exactly matched those of the obligate seeders (Figure 13b). The only difference was that the facultative seeders experienced a small net gain from coastal sage scrub in the short treatment, whereas the obligate seeders experienced a net loss.

In all three treatments, the obligate resprouters replaced coastal sage scrub in similar proportions, representing the largest area of net gain across the board (Figure 13c). In the medium treatment, the net gain from coastal sage scrub was the only major change in vegetation type, except for a small gain from grass. In both the short and long treatments, the obligate resprouters also gained from coastal sage scrub/chaparral mix in addition to 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 (Figure 13d). 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 annual grass to coastal sage scrub in all three treatments is approximately the same as the net gain from grass to coastal sage
scrub (Figure 13e). 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.

4.4 Discussion

The objective of this research was to use a landscape model of disturbance and succession, calibrated to simulate increasing fire frequency in southern California, to evaluate potential change in the distribution of dominant plant functional types. Evidence suggests that repeated fire in some locations is beginning to threaten the persistence of certain shrub species and that susceptibility to vegetation type conversion may differ according to species’ life history strategies (Zedler et al. 1983, Haidinger and Keeley 1993, Jacobsen et al. 2004). However, because increased fire due to human ignitions has primarily occurred in the last part of the 20th century (Keeley et al. 1999), no broad-scale changes have yet become apparent in the distribution and extent of the chaparral (Franklin et al. 2004). Simulation modeling, therefore, allowed us to project potential cumulative impacts of high fire frequency over broader space and time scales. Using a spatially explicit model also helped to identify locations where repeated fires and sensitive species are most likely to co-occur.

Because the focus of the analysis was on the differential impact of repeated fire on the functional types, it was important that the model effectively simulated the specified fire rotation intervals of the three different treatments and that the general locations of repeated fire were consistent with the patterns expected in the study area.
Although the simulations predicted high frequency fire more extensively along the coast than the historic pattern, the coastal areas are generally expected to experience the highest fire frequency of all areas within the Santa Monica Mountains (Radtke 1981). Also, the minimum mapping unit for the fire history map (figure 6) was 40 ha. Therefore, a large number of smaller fires are not represented on this map.

For the most part, the changes predicted by the model agreed with our hypotheses. The obligate seeders and facultative seeders experienced the most overall change during the simulations, which occurred primarily by declining under high fire frequencies in the short treatment. The maps illustrating the fire frequencies under which the functional types lost or gained area support that much of the loss of these functional types did occur under the highest fire frequencies. While the obligate resprouters didn’t shift in extent as much as the obligate or facultative seeders, they did experience a net gain under all three treatments, including the short treatment as we expected. However, the obligate resprouters were most extensive in the long treatment, likely because they were more shade tolerant than the other functional types. Although the obligate and facultative seeders declined with repeat fires, they both preferred some fire on the landscape (fire return intervals between 25-50), which would be expected since both functional types are disturbance-dependent (Keeley 1998). In fact, the obligate seeders declined in locations where no fires burned during the 50 years of the simulations.

Although facultative species can resprout after fire, repeated disturbances have also reduced populations of these plants due to high mortality of lignotubers as well
as killing seedlings recovering from previous fires (Zedler et al. 1983, Haidinger and Keeley 1993). The ability to resprout three years following fire gave the facultative seeders an advantage over the obligate seeders in the simulations. However, the probability of these species resprouting was lower than the obligate resprouters. The facultative seeders also had lower shade tolerance and shorter dispersal distances than obligate resprouters.

One of the primary reasons for the decline of both the obligate seeders and the facultative seeders in the simulations was that the age of maturity was 10 and 15 years, respectively, in an attempt to simulate the long time required to replenish a seed bank. Therefore, if fire recurred before the species reached maturity in the simulations, there would be no opportunity for fire-cued germination. Because the species within these functional groups rarely recruit seedlings in the absence of fire, the late age of maturity also served the purpose of limiting recruitment through dispersal. Because only one age of maturity can be specified for each species, the maturity parameters in the simulations were somewhat arbitrarily specified, erring on the conservative side. The implication is that, if these species do require longer than 10 or 15 years to establish a seed bank, the consequences under high fire frequency could be even graver than the simulations suggest.

Although the maturity parameters were set to 10 and 15 years for the obligate and facultative seeders, both functional types declined in all three treatments when the fire return interval was 17 years or shorter. In fact, the facultative seeder declined in the medium treatment when the fire return interval was 25 years. Therefore, there
were other factors in addition to the length of time required to establish a seed bank that contributed to these functional types’ susceptibility to frequent fire. Due to the complexity of the LANDIS model and the emergent behavior that occurs during simulations, the model output cannot be directly traced back to the effects of input parameters (parameter indeterminacy) (Baird 1999). However, the susceptibility of these species is likely due to the fact that high fire frequency leads to a younger landscape, and young age cohorts are more likely to be killed by (even low-intensity) fire in the simulations (He and Mladenoff 1999, Franklin et al. 2001). The obligate and facultative seeders also had lower fire tolerance values than the obligate resprouters.

One of the issues involved with applying LANDIS (originally designed for northern hardwood forests) to Mediterranean-type shrublands like chaparral is that, almost regardless of the fire intensity, all fires are stand replacing in chaparral and fire hazard does not change with age (Moritz et al. 2004). Therefore, differences in fire tolerance are somewhat artificial in these landscapes. The intensity of the fire in chaparral has little relative impact on fire mortality (because all species are killed above ground), but has more of a consequence on the success of post-fire recovery.

One of the ways that we accounted for these differences was to parameterize fuel accumulation curves so that fires could occur and reach intensities that were able to kill species in the model very quickly. Due to rapid post-fire fuel accumulation, chaparral and coastal sage shrublands can burn at young ages, and no significant changes in burning occur after approximately 20 years (e.g. Zedler et al. 1983,
Keeley et al. 1999, Schoenberg et al. 2001). Although the species in the model could carry fire almost immediately, we designed the fuel accumulation curves so that the largest-scale fires (at the highest intensities) would 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 coastal sage scrub species (Radtke et al. 1982). Also, by specifying different fire tolerance values for the different functional types, we accounted for the greater overall vulnerability of obligate and facultative seeders to repeat burning.

Our third hypothesis was that parts of the landscape would shift from chaparral to coastal sage scrub and alien grasslands at higher fire frequencies. Vegetation type conversion has already been observed in localized field studies in the SMMNRA (NPS 2000, Jacobsen et al. 2004). In one study, non-native annuals completely replaced an obligate seeder and a large extent of a facultative seeder after an area burned three times in 11 years (Fabritius and Davis in prep). The obligate resprouter persisted throughout these fire events. In another experiment, four sites with fire return intervals of 6 years and 2 sites with fire return intervals of 7-12 years were compared to nearby control sites of similar slope, aspect and elevation, but had fire return interval of 12 years (Jacobsen et al. 2004). The obligate seeders declined in all of 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 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 a type conversion from chaparral.

Coastal sage scrub species can often persist under fire frequencies that eliminate chaparral and may replace chaparral at fire return intervals of 5-10 years (O’Leary 1995, Keeley 2000). 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 these species had in the simulations were that they had higher probabilities of establishment on their preferred landtypes (coastal areas and interior valleys) and they could resprout with varying success after fire.

Despite greater resilience to repeated fire, coastal sage scrub may also decline when the fire frequency becomes extremely high. In some cases, coastal sage scrub has converted to grasslands under high fire frequencies, but the decline has also been attributed to interactions with other disturbance types, such as livestock grazing or air pollution (Freudenberger et al. 1987, Callaway and Davis 1993, Minnich and Dezzani 1998). One of the advantages of using a spatially explicit model is that, although the coastal sage scrub species experienced an overall net gain in the short
treatment, the maps of gain and loss revealed that the coastal sage scrub species actually declined in the areas that experienced the very highest fire frequencies.

Coastal sage scrub generally tends to be susceptible to change due to its extensive coexistence with alien annuals (Minnich and Dezzani 1998), and different studies have shown conversion from coastal sage scrub to grassland and vice versa. For example, Callaway and Davis (1993) found that grassland converted to coastal sage scrub in vegetation that hadn’t burned for more than 40 years. However, the transition rates from grassland to coastal sage scrub were much lower on plots that had burned three times in the same period, and the transition rates from coastal sage scrub to grassland increased. Freudenberger et al. (1987) also found that, although coastal sage scrub replaced grassland in some areas in the Los Angeles Basin, alien grasses have invaded other large expanses of coastal sage scrub.

Despite the tendency for alien grass and coastal sage scrub to intermix, the simulation results that were most questionable, however, were those in which large patches of the original grassland area converted to coastal sage scrub. Part of the reason these results were unrealistic is that this conversion happened even under the medium and short treatments where the high fire frequencies should have favored grass. Generally, 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 more 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).
Based on the way annual grass had to be parameterized for LANDIS (having a one-year lifespan in a model running on an annual time step), the functional type took on ephemeral qualities that prevented it from persisting on the landscape. Part of the reason for this is that the species kept dispersing out of their cells and establishing in new locations, but they were also dying on site every time step because of their longevity. Because grass had a low shade tolerance, it established profusely in recently burned locations, but had trouble establishing in locations where other species already existed. Although the dispersal function in LANDIS follows a negative exponential distribution, grass nevertheless dispersed more diffusely (to open, disturbed areas) instead of establishing closer to the parent. Although wide-ranging dispersal was intended to capture the tendency for grass to invade from widespread sources, this design had the unintentional effect of completely disaggregating the original species clusters.

To evaluate the effect of longevity on the grass distribution, we ran simulations in the long and short treatments with the grass longevity specified at 50 years. Although grass persisted in the original locations in the long treatment, it still disaggregated in the short treatment. However, in both simulations, particularly the long treatment, the grass unrealistically and exponentially exploded across the landscape. Although another solution might be to increase the shade tolerance of grass, this alternative (like increasing longevity) would defeat the purpose of the annual grass habit.
Perhaps the best solution for keeping grassland as aggregated patches, as suggested in Chapter 3 and Syphard et al. (in prep), would be to modify the LANDIS. In the current version of LANDIS, if the species is not able to disperse to another cell, no new recruitment is possible.

In addition to the unrealistic distribution of grass, the area that obligate seeders and facultative seeders gained from coastal sage scrub and lost to other chaparral might be a bit more exaggerated than what would be expected to occur. The reason that a smaller amount of change would be expected is that chaparral species generally have short dispersal distances and the community typically returns to its pre-fire composition with little extinction or invasion of other species (Keeley 1986, Zedler and Zammit 1989). Regardless, there was no substantial movement 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.

The objective of evaluating the model results using the aggregation index was to determine if the treatments produced differences in spatial pattern that weren’t detectable using area measurements alone. Although the aggregation index did reveal differences between model treatments, the results were highly correlated with the area calculations. Several issues concerning landscape pattern metrics have been recently identified, including similar problems with correlation between metrics (Calabrese and Fagan 2004). Although new methods are being developed to
improve these metrics’ utility (Li and Wu 2004), the results from these simulations suggest that calculating species’ extent is a sufficient indicator of the relative impacts of different treatments on the vegetation. Moreover, caution should be used when interpreting landscape pattern metrics calculated for maps generated by stochastic models because the patterns may be an artifact of the model and/or the grain and extent of the spatial data (Shen et al. 2004).

4.5 Conclusion

The dominant fire management paradigm in the western United States is that the unnatural accumulation of fuels after a century of fire suppression has contributed to severe wildfires. Although the current fire management program in southern California subscribes to this paradigm, evidence that old age classes have led to fewer, larger fires in these shrublands has been refuted, and fire frequency is steadily increasing (Keeley et al. 1999, Moritz et al. 2004). Yet, the past fire and vegetation management program in the region has focused on creating a landscape mosaic of varied age classes of chaparral through the use of prescribed fire.

The majority of ignitions in southern California are human-caused and attributed to the growing wildland urban interface. Housing developments and human lives are most vulnerable to fire in these locations, and ignitions are most likely to originate from these areas (Cardille et al. 2001, Rundel and King 2001, Keeley and Fotheringham 2003, Radeloff et al. in press). In fact, fires at the wildland urban interface are producing damages in the $100s of millions (Halsey 2004).
The U.S. National Park Service has recommended that the current fire management program be changed from landscape-scale prescribed burning to fuel reduction and prescribed fire in strategic locations such as the wildland urban interface (NPS 2004). The results of our simulations support the premise that this alternative is desirable over the current fire management program not only because resources would be focused on the locations that are most hazardous to human lives and property, but also because it would reduce the ecological impact of unnecessarily burning vegetation in a landscape that is experiencing unprecedented increases in fire frequency. Although broad-scale changes to the distribution of chaparral have not yet become apparent, our model results support the hypotheses that repeated fires will likely lead to a substantial decline in facultative and obligate seeders; that alien grass will continue to expand across the landscape; and that some parts of the landscape will shift from chaparral to other vegetation types, particularly to coastal sage scrub.

4.6 References


Countryman, C. M. and Philpot, C. W. 1970. Physical characteristics of chamise as wildland fuel. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station.


Fabritus, S. and Davis, S. D. Is increasing fire frequency causing vegetation-type conversion among chaparral plant communities of the Santa Monica Mountains? Manuscript in preparation.


Franklin, J., Coulter, C., and Rey, S. 2004. Change over 70 years in a southern California chaparral community related to fire history. Journal of Vegetation

Franklin, J., Syphard, A. D., He, H. S., and Mladenoff, D. J. in press. The effects of altered fire regimes on patterns of plant succession in the foothills and mountains of southern California. Ecosystems.


He, H.S.; DeZonia, B.E.; Mladenoff, D.J. 2000. An aggregation index (AI) to


Keeley, J.E. in press. Fire management impacts on invasive plant species in the western United States. Conservation Biology


Minnich, R. A. and Dezzani, R. J. 1998. Historical decline of coastal sage scrub in
the Riverside-Perris plain, California. Western Birds 29: 366-391.


National Park Service. 2000. Fire regime, fire management, and the preservation of biological diversity in the Santa Monica Mountains N.R.A. Santa Monica Mountains National Recreation Area.


Radtke, K. W. H. 1983. Living more safely in the chaparral-urban interface. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station.


Syphard, A. D., Yang, J., Franklin, J., He, H. S., and Keeley, J. E. in prep. Calibrating a forest landscape model to simulate high fire frequency in
Mediterranean-type shrublands.


Table 4-1. Final species life history attributes and parameters used in LANDIS for seven functional groups

<table>
<thead>
<tr>
<th></th>
<th>Obligate Resprouters</th>
<th>Obligate Seeders</th>
<th>Coastal Sage Scrub</th>
<th>Facultative Seeders</th>
<th>Annual Grass</th>
<th>Oak Woodland</th>
<th>Early Successional</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of species in group</td>
<td>6</td>
<td>2</td>
<td>6</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Longevity (year)</td>
<td>150</td>
<td>75</td>
<td>50</td>
<td>100</td>
<td>1</td>
<td>250</td>
<td>10</td>
</tr>
<tr>
<td>Age of maturity (year)</td>
<td>20</td>
<td>10</td>
<td>2-3*</td>
<td>15</td>
<td>1</td>
<td>40</td>
<td>1</td>
</tr>
<tr>
<td>Shade tolerance (ordinal class 1 – 5)</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>3-4*</td>
<td>1</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Fire tolerance (ordinal class 1 – 5)</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>3-4</td>
<td>1</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Effective seed dispersal distance (m)</td>
<td>100</td>
<td>75</td>
<td>75</td>
<td>75</td>
<td>10,000</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Maximum seed dispersal distance (m)</td>
<td>500</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>-1**</td>
<td>500</td>
<td>500</td>
</tr>
<tr>
<td>Probability resprout (0-1)</td>
<td>80 - 1.0*</td>
<td>0</td>
<td>.25 – .75*</td>
<td>.70 - .80*</td>
<td>0</td>
<td>.50</td>
<td>0</td>
</tr>
<tr>
<td>Minimum age of resprouting (year)</td>
<td>3</td>
<td>0</td>
<td>4</td>
<td>3</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
</tbody>
</table>

* Indicates a range of values for the species within that functional group

** A dispersal distance of –1 means the species can disperse to anywhere on the landscape
Figure 4-1: The Santa Monica Mountains in southern California.
Figure 4-2: Expected and mean simulated fire rotation intervals (FRI, by year) by landtype for the long (upper), medium (middle), and short (lower) fire regime treatments. Only one label is used when the expected and simulated values are the same.
Figure 4-3: Proportion of study area occupied and aggregation index values for the five functional groups under the long, medium, and short fire regime treatments. OR = obligate resprouter; OS = obligate seeder; FAC = facultative seeder; CSS = coastal sage scrub; GRASS = annual grass
Figure 4-4: Mean extent (area) of functional type cover at the end of 10 replicates of 50-year model simulations (with standard errors shown) for the long, medium, and short fire regime treatments. OR = obligate resprouter; OS = obligate seeder; FAC = facultative seeder; CSS = coastal sage scrub; GRASS = annual grass
Figure 4-5: Maps for the long, medium, and short fire regime treatments illustrating fire frequency in the Santa Monica Mountains over 50 - year model simulations
Figure 4-6: Map produced by the National Park Service illustrating fire frequency in the Santa Monica Mountains from 1925 – 1997
Figure 4-7: Distribution of net gain and/or net loss of functional type extent in the three treatments over fire return intervals. Note that the scale of the long treatment differs from the medium and short treatments.
Figure 4-8: Map showing the distribution of areas lost and areas gained by the obligate seeder functional group over a range of fire frequencies from year 0 to year 50 in the simulations. H = high fire frequency (5 or more fires); M = medium fire frequency (3-4 fires); L = low fire frequency (1-2 fires); NF = no fires occurred; PB = functional type present in year 0 and year 50 (no loss or gain); AB = functional type absent in year 0 and year 50
Figure 4-9: Map showing the distribution of areas lost and areas gained by the facultative seeder functional group over a range of fire frequencies from year 0 to year 50 in the simulations. H = high fire frequency (5 or more fires); M = medium fire frequency (3-4 fires); L = low fire frequency (1–2 fires); NF = no fires occurred; PB = functional type present in year 0 and year 50 (no loss or gain); AB = functional type absent in year 0 and year 50
Figure 4-10: Map showing the distribution of areas lost and areas gained by the obligate resprouter functional group over a range of fire frequencies from year 0 to year 50 in the simulations. H = high fire frequency (5 or more fires); M = medium fire frequency (3-4 fires); L = low fire frequency (1-2 fires); NF = no fires occurred; PB = functional type present in year 0 and year 50 (no loss or gain); AB = functional type absent in year 0 and year 50.
Figure 4-11: Map showing the distribution of areas lost and areas gained by the coastal sage scrub functional group over a range of fire frequencies from year 0 to year 50 in the simulations. H = high fire frequency (5 or more fires); M = medium fire frequency (3-4 fires); L = low fire frequency (1–2 fires); NF = no fires occurred; PB = functional type present in year 0 and year 50 (no loss or gain); AB = functional type absent in year 0 and year 50
Figure 4-12: Map showing the distribution of areas lost and areas gained by the annual grass functional group over a range of fire frequencies from year 0 to year 50 in the simulations. H = high fire frequency (5 or more fires); M = medium fire frequency (3-4 fires); L = low fire frequency (1–2 fires); NF = no fires occurred; PB = functional type present in year 0 and year 50 (no loss or gain); AB = functional type absent in year 0 and year 50
Figure 4-13 (a,b,c): Vegetation type conversion represented by net area gain or loss for the long, medium, and short fire regime treatments. 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 obligate resprouters, obligate seeders, and/or facultative seeders.
Figure 4-13 (d,e): Vegetation type conversion represented by net area gain or loss for the long, medium, and short fire regime treatments. 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 obligate resprouters, obligate seeders, and/or facultative seeders.
Chapter 5. Coupling two landscape models to simulate frequent fire and urban growth on southern California coastal shrublands

5.0 Abstract

Fire disturbance is a primary agent of change in the Mediterranean-climate chaparral shrublands of southern California. Recent records show fire frequency is steadily increasing in coastal regions due to ignitions at the growing wildland urban interface. Although chaparral is resilient to a range of fire frequencies, shorter intervals between fires can threaten the persistence of some species depending on their functional type. In a previous study, a spatially explicit simulation model of landscape disturbance and succession (LANDIS) was used to forecast the effects of frequent fire on the distribution of dominant plant functional types in a study area administered by the National Park Service. Because human settlement is the primary driver of increased ignitions, the objective of this study was to integrate LANDIS with an urban growth model to simulate combined effects of urban growth and high fire frequency on coastal shrublands. The potential spatial distribution of habitat change under different assumptions was modeled and mapped. A secondary objective was to determine whether full model integration (tight coupling) was necessary (e.g. updating the LANDIS simulations every year with urban growth predictions) or if the same results would be produced by incorporating the final urban growth prediction in the initial conditions of the LANDIS simulations without updating the model every time step (loose coupling). Because the type of
development predicted by the urban growth model was predominantly aggregated, the amount of edge between urban and wildland did not increase as much as expected. Therefore, urban growth did not increase the overall fire frequency through increased ignitions at the wildland urban interface. Model results suggested that direct loss to urbanization would likely be the primary threat to coastal sage scrub species that tend to be distributed in locations that favor development. On the other hand, increased fire frequency appeared to be more of a threat to obligate seeder species that germinate from a persistent seed bank. Habitat loss occurred more gradually over time when the models were tightly coupled; however, the overall cover of the functional types at the end of the simulations was similar to that of the loosely coupled runs.

5.1 Introduction

The California Floristic Province supports a large proportion of the biodiversity in the United States and comprises a vascular plant flora that exceeds 4,400 species, 30% of which are endemic (Raven and Axelrod 1978, Stein et al. 2000). This biodiversity, combined with massive habitat loss and fragmentation in the southern part of the state has made the California floristic province a global biodiversity hotspot (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, Stralberg 2000, Seabloom et al. 2002, Tennant et al. 2001), indirect effects of human population expansion, particularly through altered fire
regimes and biological invasions, are also becoming serious risks to the region’s native habitat (Keeley 2001).

Fire is an integral influence on the distribution of plant species in southern California. Chaparral is considered a fire-type vegetation because its component species are resilient to the periodic wildfires in the region (Keeley 2000). Lightning fires are uncommon in the coastal shrublands (Keeley 1982), but Native Americans occupied the region for approximately 10,000 years before present and have been a source of ignitions by using fire as a cultural tool. However, the frequency and geographic extent of their fire use is unknown (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 and Fotheringham 2003). Although chaparral remains resilient to a range of fire frequencies, extremely short time intervals between fires are starting to threaten the persistence of some shrub species; and the impacts vary according to species’ life history strategies, or functional type (Zedler et al. 1983, Haidinger and Keeley 1993).

Combined with increased fire frequency, the introduction and spread of non-native species, particularly exotic annual grasses, have become a threat to native vegetation communities in southern California. Exotic grasses can sustain very high fire frequencies and can even promote fire through positive feedbacks (Mack and D’Antonio 1998). As a result, these grasses have replaced native shrublands in some areas that have experienced repeat fires in short succession, thereby causing a “vegetation type conversion” (Zedler et al. 1983, Haidinger and Keeley 1993,
Callaway and Davis 1993, Minnich and Dezzani 1998) Although nonnative plant species were initially introduced during European colonization, they have proliferated exponentially in the last century, paralleling human population growth and increased fire frequency (Randall et al. 1998, Keeley 2001).

The interactions between human activities and natural dynamics, contributing 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 undeveloped wildland vegetation is termed the Wildland-Urban Interface (WUI) (Radeloff et al. in press). The WUI has received national attention recently because housing developments and human lives are most vulnerable to fire in these locations, and because human-caused ignitions are also most common there (Yool et al. 1985, Cohen 2000, Cardille et al. 2001, Rundel and King 2001, Keeley and Fotheringham 2003). Furthermore, urban settlements contribute to higher rates of exotic species introductions because humans plant grass in residential areas, fire scars, and areas cleared for fuel breaks (Suarez et al. 1998, Byers 2004); and exotic grasses are particularly successful invaders of disturbed areas (Rundel 2000, Rundel and King 2001).

As more development diffuses from urban centers to chaparral shrublands in southern California, 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). Although impacts such as vegetation type conversion have been observed in localized field studies, no extensive or drastic changes have been observed in species’ distributions during the last century (Bradbury 1974, Franklin et al. 2004). Also, the most dramatic increase in fire frequency has only been observed in the latter part of the 20th century (Keeley et al. 1999). Therefore, broad-scale change may only begin to become apparent after cumulative impacts from multiple fires (Zedler 1995). Considering this potential for vegetation change, land managers are struggling to determine how to best manage for preserving ecological integrity and protecting human lives and property under future conditions (Zedler 1995, Conard and Weise 1998, NPS 2004).

Because environmental change is also occurring rapidly on a global scale, computer simulation models are being developed that can forecast long-term effects of natural disturbance on terrestrial plant communities. The potentially enormous environmental impact of recent land-use change has sparked a proliferation of models that project where future urban growth is likely to occur and what the impacts of that growth may be (e.g., Agarwal et al. 2000). The predictions of these landscape simulation models of disturbance dynamics and urban growth models are important for envisioning potential consequences of alternate management options (Mladenoff and Baker 1999). However, no simulation model has yet been developed that predicts the combined effects of urban growth and altered fire regimes on vegetation dynamics.
Simulation models are often limited in scope to a specific subset of physical reality because more comprehensive models are difficult to develop effectively; and models are, by definition, tools that simplify a reality that is too difficult to understand in all its complexity (Frysinger 2002). Nevertheless, because of the interactions and feedbacks in processes that contribute to global change, as well as the combined effects this change has on human and environmental conditions, environmental decision-makers may need to understand a system broader than that of a particular model. Therefore, model coupling is receiving attention as a means of expanding the scope of environmental decision-making (Westervelt and Hopkins 1999, Frysinger 2002).

The concept of model coupling initially focused on the joining of one model with a Geographic Information System (Goodchild et al. 1993, Park and Wagner 1997, Stocks and Wise 2000). However, two or more models can also be integrated together, and the methods of exchanging information between them can vary based on the complexity of the real world interface and the degree of integration needed to adequately emulate the coordinated system. This continuum of model integration ranges from “loose” to “tight” coupling. Generally, when models are loosely coupled, the user interface between the models is separate and the frequency of interaction between the models is low (Nyerges 1992, Park and Wagner 1997). For example, one of the models (or a GIS) can preprocess data and provide/prepare input for the other model; or (in the case of GIS), can manage, visualize, or analyze maps of model results. On the other hand, tight coupling provides a more seamless
environment in which model interaction is frequent and automatic (Nyerges 1992, Park and Wagner 1997).

A debate revolves around how tightly models (and/or GIS) should be coupled. Loose coupling provides the benefits of using results from two different models to understand a broader problem space and requires less work in terms of software development. However, the interface between the simulated systems may not be fully or accurately modeled if the real-world interface involves more frequent interaction and feedback. On the other hand, tight coupling provides a seamless environment that allows model feedbacks, but also requires substantial software development and could potentially reduce flexibility in future modeling endeavors (Park and Wagner 1997, Frysinger 2002). Tightly coupled models allow for more complex interactions between two models, far more than simply linking outputs from model A to inputs to model B, permitting positive and negative feedbacks, both linear and non-linear. Modeling complex systems where non-linear feedbacks are anticipated favors such tight coupling.

In previous research, we used a landscape-scale simulation model of fire disturbance and succession (LANDIS) to examine the effects of high fire frequency on native vegetation composition in southern California shrublands (Chapter 3 and Syphard et al. in prep a, Chapter 4 and Syphard et al. in prep b). We also used the Clarke Urban Growth Model (UGM) to forecast the effect of urban growth on habitat and spatial pattern in the same study area (Chapter 2 and Syphard et al. in press). Anthropogenic ignitions along the WUI are the primary cause of fire in the region, so
the objective of this research was to couple LANDIS with the UGM to explore the combined effect of increased fire frequency and urbanization on the distribution of three dominant plant functional types.

To address the ongoing debate about how tightly models should be integrated, results were compared based on two different methods of incorporating the urban growth predictions into the LANDIS simulations. Loose coupling incorporated the final year of urban growth predictions (2050) into the first time step (2000) of the LANDIS simulations. This approach allows the first model’s future to inform the behavior of the second model. The tight coupling approach was designed to more realistically simulate how urban development expands over time by updating the LANDIS simulations with urban growth predictions at every time step from year 2000 to 2050. Both the loosely and the tightly coupled model runs finished with the same amount of urban development. The coupled model results were then compared to the original results from the LANDIS simulations alone (as in Chapter 4 and Syphard et al in prep b). If the difference in results between the loosely coupled runs and the tightly coupled runs was negligible, we would then be able to conclude, at least for these models, that the extra effort required to more seamlessly integrate the models was not necessary.

The means by which the UGM predictions could affect the LANDIS simulations included: direct loss of habitat cover; change in extent and configuration of the WUI (a 90m buffer adjacent to all urban areas and roads that was parameterized with higher ignition probabilities and probabilities of establishment of exotic grasses), and
resulting change to the fire regime. Therefore, the primary research questions were: how will the patterns of urban growth predicted by the UGM affect the distribution of the WUI, and how will the parameters of the WUI interact with the LANDIS simulations to affect the fire regime? In turn, how will these changes affect the distribution of the vegetation?

As urban development is projected to increase over time, we expected the WUI to also expand in our simulations. The probabilities of ignition were parameterized to be higher in the WUI; consequently, we also expected the fire frequency to increase and therefore affect the distribution of vegetation. Specifically, because shrubs dependent on fire-cued seed germination are most sensitive to frequent fire, we predicted that these species would decline the most. However, we expected all vegetation types to decline in proportion to the increase in urban development over time.

**5.2 Methods**

**5.2.1 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 mountain chain in the Transverse Ranges of southern California (Figure 1). Slightly more than half of the land in the mountains is protected through public ownership (including the National Park Service); however, the majority of the privately owned
land is available for development (Rundel and King 2001, NPS 2004). The SMMNRA exemplifies issues related to the expanding WUI and increased fire frequency in southern California in part because of its proximity to the highly developed, rapidly expanding Los Angeles metropolitan area, and in part because the region has a very active fire regime. Ninety-eight percent of the fire starts are of human origin, and some locations have burned up to 10 times in the last 75 years (NPS 2004). The region is biologically rich, with 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% of the area) and coastal sage scrub vegetation (approximately 25% of the area). Approximately 25% of the flora consists of naturalized alien species with a high frequency of annuals. The occurrence of alien species is strongly correlated with landscape disturbance (Rundel 2000). Vegetation type conversion has been observed in the Santa Monica Mountains in several locations that experienced repeated fires in short succession. (NPS 2000, Jacobsen et al. 2004, Fabritius and Davis, manuscript in preparation).

5.2.2 LANDIS model description and simulations

The LANDIS model was selected to simulate the effects of altered fire regimes on the distribution of dominant plant species in southern California. General information on the model 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.
LANDIS is a spatially explicit raster-based model that simulates forest dynamics on a heterogeneous landscape, including stochastically driven interactions between fire regimes, plant life history strategies, and site conditions (He and Mladenoff 1999, He et al. 1999). Successional dynamics, simulated over broad spatial extents and long time periods, 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) (Mladenoff et al. 1996).

The landscape 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, 19 dominant species were selected to use in the simulations based on a literature review and consultation with National Park Service vegetation scientists. The values for the species life history attributes were also derived from the literature, and the species were classified into functional groups 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 (Pausas 1999). 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 (Franklin et al. 1997). 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-derived variables associated with the spatial distribution of vegetation in the landscape, the landtype map reflects the environmental conditions affecting potential growth and establishment, approximating a fundamental niche. Each landtype is parameterized with uniform species establishment coefficients, fuel accumulation curves representing rates of biomass accumulation and potential fire severity over time, and fire regime characteristics such as mean fire return intervals and probabilities of ignition (Mladenoff and He 1999). The landtype map for the SMMNRA consisted of seven classes that stratified the landscape according to slope-aspect, elevation, and distance to the coast (Figure 2). The LANDIS simulations using this landtype classification (and related fire regime and species establishment parameters) reasonably captured the spatial pattern of vegetation distribution and fire frequency in the study area (Chapter 3 and Syphard et al. in prep b).

In the 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 the fire size is associated with a mean that is specified in the input parameters. Groups of individual fires are allowed to occur within one time step.

Over the last several decades, other models have been developed that can simulate fire spread, or that can simulate successional dynamics in small plots (“gap” models); however, LANDIS is unique in its ability to simulate long-term, species-level, post-disturbance dynamics stochastically over a range of spatial scales (He and Mladenoff 1999). The model was initially developed for northern Midwest forests, so several modifications to the model code were added to more realistically simulate the high fire frequency and unique post-fire response strategies characteristics of Mediterranean-type shrublands. These changes, described more thoroughly in Chapter 4 and Syphard et al. (in prep b), include fire-cued germination from a persistent seed bank, an annual time step, and an option to update spatial inputs at every time step. This annual time step version of the model is LANDIS 4.0A.

Three fire regime treatments were developed to evaluate the effects of increasing fire frequency on the distribution of the plant functional types (see Chapters 3 and 4 and Syphard et al. in prep a and b). Using fire history data from the SMMNRA and data developed by Keeley et al. (1999), average fire rotation intervals were calculated for the landscape before and after 1951. A fire rotation interval is defined as the time required to burn an area equivalent to the area in question. LANDIS simulates
different fire frequencies by parameterizing specific fire rotation intervals for each landtype and calibrating the model to burn at those fire rotation intervals. The “long” treatment (average landscape fire rotation intervals of 60) was designed to approximate the historic fire rotation intervals that maintained species’ distribution patterns over the last century. The “medium” treatment (average landscape fire rotation interval of 30) reflected the shorter fire rotation intervals that have been occurring since 1951; and the “short” treatment (average landscape fire rotation interval of 15) used fire rotation intervals that are beginning to be seen in parts of the landscape that are burning at the highest fire frequencies.

5.2.3 UGM model and simulations

After considering other approaches, (e.g., Gunter et al. 2000, Wickham et al. 2000, Swenson and Franklin 2000, Jenerette and Wu 2001), the Clarke Urban Growth Model (UGM) (Clarke et al. 1996, Clarke and Gaydos 1998) was selected to link with LANDIS because it is a spatially and temporally explicit model (with compatible scales) capable of simulating alternate growth scenarios using a rigorous calibration process based on performance metrics.

UGM is a cellular automaton model (CA) 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 (Park and Wagner 1997, Clarke and Gaydos 1998), and growth is more likely to occur on
gentler slopes, near existing settlements, and along transportation corridors. The model also simulates the development of isolated clusters of urban land.

The predictive strength of the model results from a rigorous calibration process that statistically and spatially associates future urban growth with historic growth patterns in the study area using extensive historical data sets as model inputs. Model calibration is based on 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 case of 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 (Clarke et al., 1997). The key to this process involves manipulating the values of five coefficients that affect the application of growth rules in the model to find the best combination of these parameters that fit the simulated to the observed historical data. Monte Carlo techniques are used to run through thousands of simulations using different combinations of the control parameters. Every time the model simulations reach a date for which there is historic data, a number of statistics are calculated to test the fit between these spatial layers, including the r-squared fit between actual and predicted 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 (computed by combining the actual and predicted distributions as binary urban/non-urban layers, then computing ratio of intersection over the union).
The UGM was calibrated to the SMMNRA using data from four dates of historic urban extent (1947, 1976/1977, 1989, and 2000) and two dates of transportation coverage (1947 and 2000). After calibrating the model, Syphard et al. (Chapter 2 and in press) predicted urban growth from 2000-2050 using three alternate scenarios in which development was prohibited beyond 25%, 30%, and 60% slope (see Chapter 2). The scenarios were developed based on a report by the California Coastal Commission (1999) that identified areas with slopes greater than 30% or 25% for Ventura and Los Angeles Counties respectively as “constrained.” The 60% scenario was included for comparison because development nevertheless occurs on slopes greater than 30% in the study area. However, because only 4% of the current urban land is on slopes steeper than 30%, the predictions from the 30% scenario were used for the integration with the LANDIS simulations. Although the UGM forecasts were simulated using 100 Monte Carlo iterations, the annual probabilistic images generated as model output were thresholded at 95% or greater likelihood of development and converted into binary maps for input into the LANDIS model.

5.2.4 Model integration

The urban growth predictions were assimilated into LANDIS by manipulating the landtype map. Although the basic purpose of the landtype map is to partition the landscape into ecological units, the LANDIS model allows the specification of additional land cover types that are treated differently in the simulations. Specifically, a landtype can be designated as “active” or “non-active.” During the
simulations, LANDIS ignores non-active landtypes so that no species can establish on them and fire cannot spread on or across them. Therefore, all urban land (current urban areas and areas predicted to become urban by the UGM) was overlain on the original landtype map and parameterized as a new, non-active landtype designated as “urban core.” In reality, it is possible that fire can spread into developed areas, and a co-evolution of feedbacks between urbanization and wildfire can occur (Goldstein 2000). However, fires that penetrate urban areas are usually suppressed rapidly and burn little area; therefore, the urban core landtype was assumed to be inflammable, as in CSFS (2002).

In addition to urban land, a map of roads in 2000 (Syphard et al. in press) was overlain on the original landtype map and parameterized as a separate landtype. Instead of designating roads as non-active, however, they were made an active landtype so that fire could potentially spread across them, but at a low probability. Although roads may act as fire breaks in some circumstances (Radtke et al. 1982), fires have also jumped roads in the chaparral under high wind conditions (Halsey 2005). Although the roads were active, they were parameterized with species’ establishment probabilities set to zero to prevent successional processes from occurring on them.

In addition to the urban core and roads landtypes, a WUI landtype was created as a buffer region surrounding urban areas and roads. The purpose of the WUI landtype was to capture the spatial pattern of human influence on the fire regime through increased probability of ignition and increased probability of establishment of non-
native grass. To maintain the distinctive parameters of the original landtypes, however, the WUI was divided into seven separate landtypes.

In the Santa Monica Mountains, 98% of the recorded fire starts were anthropogenic in origin, and the majority of fire starts originated along roadsides. Fire frequency and total area burned have both increased in the last 75 years, and this has been attributed to population growth and urban expansion (NPS 2004). Although fire frequency and population density are positively correlated in the region (Keeley et al. 1999), there are no spatial ignition data for the SMMNRA that provide empirical estimates of the degree and distance of influence that roads and urban areas have on ignition frequency. Therefore, assuming that most human-caused ignitions occur within close proximity to roads and urban areas, a buffer distance of one pixel (90 m) was used. The selection of this distance was also based on a multi-agency effort to map wildfire risk in Colorado that used a 100 m buffer distance around roads to specify higher risk of human-caused ignitions (CSFS 2002). Although the relationship between ignitions and urban areas is likely much more complex, we tried to avoid introducing false precision into our design.

As a consequence of the lack of empirical data, we again tried to avoid false precision by specifying the targeted fire rotation intervals in all of the WUI landtypes to be 25% shorter than their corresponding non-WUI landtypes, resulting in average landscape fire rotation intervals for non-WUI and WUI landtypes, respectively, to be 60 and 45 years for the long treatment, 30 and 22 years for the medium treatment, and 15 and 11 years for the short treatment. Although the fire rotation intervals
became approximately 70 percent shorter in Ventura County and 30 percent shorter in LA County over the last century, this landscape-level change was accounted for through the three model treatments in which the average landscape fire rotation intervals were decreased twice by 50 percent. Therefore, the shorter targeted fire rotation intervals in the WUI landtypes were intended to simulate the higher likelihood of ignitions starting in those areas without attributing all of the change in fire frequency to those areas alone. The probabilities of establishment for annual grasses was set 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.

5.2.5 Simulation experiments

The loose coupling design involved running the LANDIS simulations with the final urban extent prediction (2050) incorporated into the first time step. The 2050 urban extent was overlain on the landtype map from the model runs using LANDIS alone (as in Chapter 4 and Syphard et al. in prep b) so that the new urban core areas and a WUI buffer around them were given precedence over the old landtypes, including the roads (road growth was not predicted by the UGM). As in the model runs using LANDIS alone, the landtype map for the loosely coupled runs remained the same for the duration of the simulations. The simulations were run for 50 years for the three fire regime treatments and were each replicated 10 times.
The tightly coupled approach accounted for incremental urban expansion over time by updating the landtype maps with the urban growth predictions every time step. Therefore, instead of using one landtype map with the final year of UGM predictions in the initial time step, a new landtype map was generated for every year. These landtype maps were generated by writing a GIS script that automatically imported the UGM output maps, buffered the urban areas to update the WUI landtypes, and then overlaid these maps with the original landtype map (Appendix 1). Although 50 landtype maps were used for the tight coupling model runs, only one landtype attribute file was needed because their parameters remained the same. The LANDIS model code was modified to enable the automatic landtype map update, and these changes have been incorporated as options in the standard LANDIS 4.0A (Chapter 3 and Syphard et al. in prep a). Because the urban core landtypes were parameterized to be non-active, any vegetated areas that became urbanized during the tight coupling simulations were excluded in future time steps, thereby ceasing all successional processes in those areas. This simulated the direct loss of habitat because the newly urbanized areas were excluded from the calculation of vegetated area in later time steps.

5.2.6 Analysis

Before analyzing the simulation results, the area and percent change of the WUI and non-WUI landtypes were calculated for years 2000 and 2050. Then, the model
runs were analyzed by comparing the loosely and tightly coupled results to those of the results using LANDIS alone for the different fire regime treatments.

The effect of model coupling on the fire regime was analyzed by calculating the simulated fire rotation intervals for all of the model runs. The spatial pattern of fire was analyzed by comparing maps of fire frequency, derived from overlaying GIS output maps of fire from the 50 years of simulations. Fire frequency patterns were only analyzed for the short treatments because they experienced the most fire. To better visualize the locations where high frequency fire was being simulated on the landscape, areas that experienced five or more fires were selected and mapped. In addition to calculating fire rotation intervals (again, the length of time required to burn a specified area) fire return intervals were also calculated. Unlike the fire rotation interval, the fire return intervals indicated the average number of years between two successive fire events at specific locations. Therefore, they revealed whether the total area burned was composed of fires spread widely across landscape, or whether certain portions of the landscape were being burned repeatedly.

To evaluate the effect of model coupling on the vegetation, the extent and spatial pattern of dominant plant functional types were compared. Most of the analysis focused on the two functional types that best represented the different post-fire response strategies characteristic of the chaparral (obligate seeders and obligate resprouters) and the dominant sub-shrub vegetation type, coastal sage scrub.

Obligate seeder species recruit from long-lived dormant seed banks that are cued by fire to germinate, but these species 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 (Zedler 1995). On the other hand, obligate resprouters do not produce new individuals following fire; instead, these species vigorously resprout, which can begin 2-3 years following fire (Keeley 1992). 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). The other chaparral functional type, facultative seeders, can both resprout and produce seeds that are cued by fire to germinate. Facultative seeders are also sensitive to high fire frequency (e.g. Zedler et al. 1983).

The coastal sage scrub species are drought-deciduous subshrubs that occupy lower-elevations than chaparral on coastal mountains and inland valleys (Malanson and O’Leary 1995). Coastal sage scrub is shorter-lived and less shade tolerant than chaparral, but these species also mature early and recruit continuously between fires (Westman 1982). Although they don’t have a fire-cued seed bank, all of the coastal sage scrub species simulated were able to resprout following fire, but at variable 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, coastal sage scrub can also start to decline (Haidinger and Keeley 1993, Minnich and Dezzani 1998).
The model runs using LANDIS alone (Chapters 3 and 4 and Syphard et al. in prep a and b) effectively simulated these different sensitivities to fire, and the obligate seeders and facultative seeders declined substantially under the shortest fire rotation intervals; however, the obligate resprouters were most abundant under the shortest and longest fire rotation intervals.

The coastal sage scrub species were more resilient to frequent fire than the obligate seeders and facultative seeders, but they did decline when fire frequency was extremely high (Syphard et al. in prep a and b). Also, exotic grass was favored by the high fire frequency.

5.3 Results

Although the total edge calculated between urban land and natural habitat increased by approximately 80 percent over the course of the simulations (Chapter 2 and Syphard et al. in press), the resulting increase in WUI area from 2000 to 2050 was only approximately 35 percent. However, the percent change to the WUI was disproportionate between landtypes (Figure 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 simulated fire rotation intervals, averaged across 10 replicates, for the non-WUI and WUI landtypes differed only slightly when LANDIS was coupled with the UGM, but they became slightly longer in the medium and long treatments (Figure 4). Also, the fire rotation intervals were slightly longer in the tightly coupled runs than
in the loosely coupled runs. The fire rotation intervals were the same for the WUI and non-WUI landtypes for all model runs in the short treatment.

In the model runs using LANDIS alone, most of the landscape burned at fire return intervals from 25 to 17 years (Figure 5). In the loosely coupled model runs, the fire return intervals were slightly shorter, with the greatest proportion of area burning at return intervals of 17 to 10 years. The fire return intervals for the tightly coupled model runs were different from those using LANDIS alone and the loosely coupled runs because a substantially larger proportion of the landscape only burned once in the 50-year simulations. Also, a lower proportion of the landscape burned at the shortest fire return intervals (17 – 6 years) than the runs using LANDIS alone or loosely coupled model runs. The overall spatial pattern of high fire frequency areas was similar for all of the model runs, even in the loose treatment that was heavily urbanized for the entire duration of the simulations (Figure 6). Generally, the areas that burned five or more times were located all along the coast and in the western end of the study area. The northeast part of the landscape was devoid of high fire frequency in all the model runs.

Although the final extent (area of cover) was substantially lower in the coupled runs than in the runs using LANDIS alone for all five of the simulated functional types, there was little difference between the loosely coupled and the tightly coupled runs for all three of the fire regime treatments (Figure 7). However, by looking at the functional types’ extent over the course of the simulations, there was a distinct difference between the loosely coupled and tightly coupled runs, and the slight
differences in final extent, particularly for the coastal sage scrub, species became more apparent (Figure 8). 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 in approximately 30 years in all of the runs and treatments. Generally, there were smaller differences in extent between the runs using LANDIS alone and the coupled model runs when the overall area of the functional type was smaller. This was most apparent for the obligate seeders in the short treatment (Figure 8).

Although there were numerous localized differences, the overall spatial pattern of the functional types’ extent was similar between the runs using LANDIS alone and both of the coupled model runs (Figures 9 – 11). In all of the runs, the obligate seeders gained the most cover in the west and lost the most cover in the southeast in the long treatment, and they lost substantial area along the coast in the short treatment, where the fire frequency was highest (Figure 9).

The extent of the obligate resprouters changed less than the obligate seeders, and the locations of gain and loss of cover were also patchier and more evenly dispersed (Figure 10). Across all treatments 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 treatment. Most of the loss occurred in the interior portions of the study area in locations that favored other functional types.

For the coastal sage scrub species, a substantial portion of the area that was lost to urbanization in the coupled model runs was also lost for other reasons in the runs
using LANDIS alone for the long treatment (in the interior and northwestern parts of the landscape) (Figure 11). Also in the long treatment, coastal sage scrub gained several patches in the middle of the landscape in the coupled model runs that were not gained in the runs using LANDIS alone. In the short treatment, the areas that were lost to urbanization in the coupled model runs remained on the landscape in the coupled runs. For all the short treatment runs, most of the loss occurred along the west and east sides of the coast.

5.4 Discussion

The relationship between human activities and increased ignitions (and fire frequency), particularly along roads and the WUI, has been documented in the coastal shrublands of southern California (e.g. Keeley et al. 1999, Keeley and Fotheringham 2003, Wells et al. 2004) and in other regions (e.g. Cochrane et al. 1999, Cardille et al. 2001). Therefore, one of the primary expectations of this research was that high probabilities of ignitions at the WUI would lead to increased fire frequency in the LANDIS simulations. The premise of this expectation was the assumption that urban development would grow in a sprawling pattern that expanded the WUI (Johnson 2001). In addition to direct habitat loss, this effect of urban growth on the fire regime was expected to further impact the vegetation, particularly those functional types that are sensitive to repeated fires (Keeley and Fotheringham 2003).
Although the WUI area increased by 35%, more of it was consumed by development than was created across a large portion of the landscape, due to high rates of infill in the pattern of growth predicted by the UGM. Therefore, the increase in the WUI was disproportionately lower than the increase in total urban edge because some of the WUI area was shared between urban pixels that were located close to each other. Likewise, the change in WUI among landtypes strongly reflected the type and amount of urban growth on the landscape. For example, although the low coast landtype lost the greatest proportion of WUI, a substantial proportion 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, which gained the greatest proportion of WUI, gained most of its urban land from expansion of developed areas in the low coast and from growth along roads. Therefore, less infill occurred because much of the growth occurred in an area that had only been sparsely developed in 2000.

Because urban growth did not increase the WUI as much as expected, increased ignition probabilities parameterized for the WUI areas had little influence on the fire regime, explaining why the fire rotation interval differed little between the runs using LANDIS alone and the coupled model runs. The fact that the aggregated pattern of predicted growth resulted in minimal increase of the WUI and no increase in the fire rotation interval suggests that intermediate levels of urbanization may actually create the highest fire risk. In other words, this type of development, while resulting in the
greatest amount of direct habitat loss, actually reduced the amount of interface
between areas of human activity and the fire-prone chaparral vegetation.

Therefore, there may be a threshold at which urban infilling starts to contribute to
better fire suppression in wildland fragments on certain parts of the landscape.
Suppression of fires is more effective in accessible areas and can be aided by highly
fragmented fuels (Cardille et al. 2001, Prestemon et al. 2002), even in the fire-prone
shrublands of southern California that are difficult to suppress in high wind
conditions (Radtke et al. 1982). This phenomenon, in which increased fire frequency
levels off, was observed in the East Bay region of San Francisco, CA, which also has
an anthropogenic fire regime with few lightning-ignited fires. In this region, 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 in review).

The hypothesis that intermediate levels of urbanization may create the greatest
fire risk may also be a function of scale, or the overall proportion of a landscape that
becomes urbanized. Percolation theory describes how a landscape's connectivity
undergoes an abrupt transition from connected to unconnected at critical thresholds,
and these thresholds of connectivity 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; however, below 30%
cover, connectivity is lost and the spread of disturbance may be retarded. The actual
relationship between landscape heterogeneity and fire spread is also a function of
other factors, including the fire regimes that are characteristic of different ecosystems (Turner 1989).

To test the hypothesis that intermediate levels of urbanization create the highest fire risk, it would be useful to compare fire frequency across different patterns and levels of development. Ignition data would also be helpful in better understanding the spatial relationship between humans and the fire regime, and could illustrate different patterns of ignitions based on land use types or other areas of human activity such as roads and hiking trails. If these types of data were available, it would be possible to run alternate scenarios with the simulation models based on patterns observed on the landscape. For example, the size of the WUI buffer or the ignition frequency in the WUI could be altered to reflect different characteristics of the landscape.

Although the overall amount of fire was similar among the model runs (as expressed by the fire rotation interval), there was a difference in the pattern of fire frequency. Specifically, more of the landscape burned at shorter fire return intervals in the loosely coupled (and using LANDIS alone) model runs than the tightly coupled runs. This difference can be explained by the fact that fires were able to burn on portions of the landscape that would then become urbanized during the course of the simulations in the tightly coupled runs. Those previously burned areas that became urbanized were thereby prevented from experiencing repeated fires, leading to a broader distribution of fire events on the landscape.
Although the fire rotation interval is a frequently used statistic to describe fire frequency on a landscape scale, the fire return interval combined with the spatial pattern of fire frequency on the landscape can help identify which parts of the landscape are burning at higher frequencies than others. The implications of fire return intervals are important with regards to high frequency fire and type conversion of shrublands that need a certain length of time to recover until the next fire comes through. If certain portions of the landscape are burning with very short return intervals, these areas may be most at risk for type conversion if they also correspond with the distribution of sensitive species. Therefore, the fact that a lower proportion of the landscape burned at short fire return intervals in the tightly coupled runs than in the loosely coupled runs could have biological implications that would make it preferable to use the tight coupling approach, despite the fact that the overall amount of fire on the landscape was similar to the loosely coupled runs.

Similar to the difference in fire, the loosely coupled and tightly coupled model runs resulted in very similar final extent of functional cover after 50-year simulations. However, if land managers are concerned about vegetation change in the next 30 years (the duration of the simulations when the extent was different in the runs), it might be important to use the tightly coupled approach because it more realistically simulated incremental growth over time; and, there were substantial differences in functional type extent between the loosely coupled and tightly coupled runs in that time frame. Intellectually, for the loosely coupled approach to represent reality, the “futures” influence would have to expand backward in time, similar to the
concept of “transaction time” in database theory. This does not seem as satisfying a solution as annual feedbacks that allow immediate response, be it positive or negative in amplitude.

Furthermore, although the UGM predicted that growth would slow down and become “saturated” after approximately 30 years, the predictions were also based on a number of assumptions; therefore, the rate of growth over time could vary based on a number of factors that can’t be accounted for in the simulations. For example, we assumed that the land currently protected as state or national park (approximately 50% of the landscape) would remain excluded from development in the simulations. However, it is also possible that 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 actually be faster or slower than what was predicted by the model.

The coastal sage scrub species appeared to be the most affected by the model coupling in that more area was directly lost to urbanization, but also because there were more differences between loose and tight coupling for this functional group. The primary reason for this is that a large proportion of the distribution of coastal sage scrub species occurs in locations that are favorable for development (e.g. along the coast or in low-slope areas), which is also why coastal sage scrub has already lost a substantial proportion of its original extent (O’Leary 1995). Although coastal sage scrub species are sensitive to extremely short fire return intervals, the simulations
suggest that direct habitat loss will likely be more of a threat to these species than altered fire regimes.

On the other hand, the obligate seeders were the functional type that was most sensitive to high frequency fire; yet, they also lost less area directly to urbanization than the other functional types. Therefore, increased fire frequency appears to be the primary threat to the obligate seeders. Furthermore, the future scenario in the Santa Monica Mountains will probably resemble that of the short treatment based on current and projected fire frequencies on the landscape (Keeley et al. 1999, NPS 2004). The obligate resprouters are very resilient to high frequency fire (Keeley 1986), so they will also be most at risk to direct habitat loss than to an altered fire regime.

5.5 Conclusion

Due to the complex interactions and feedbacks in processes that contribute to global change, model coupling (with a GIS or another model) has been used as a tool to broaden the scope of analysis beyond the capacity of one particular model (Nyerges 1992, Park and Wagner 1997, Westervelt and Hopkins 1999, Stocks and Wise 2000, Candau et al. 2000, Frysinger 2002). Despite the advantage of simulating a coordinated system, disadvantages of model coupling may include added accumulation of uncertainty, the necessity to ensure compatible assumptions and scales, and difficulties in calibrating and validating results from an integrated system (beyond the evaluation of the models in isolation) (Frysinger 2002).
When focusing on research questions dealing exclusively with urban growth on habitat patterns or with the effects of altered fire regimes on plant species distribution, the UGM and LANDIS were suitable to use by themselves. However, to fully capture the interactions between these disturbances (particularly with urban growth as the primary driver of ignitions in southern CA), there were clear benefits to integrating the models together, particularly using the tight coupling approach. Despite the minimal impact on the overall fire frequency, incorporating the UGM predictions into the LANDIS simulations revealed differences in the spatial pattern of change in the WUI in combination with differential impacts of direct habitat loss and altered fire regimes (alone and in combination) on the plant species in the simulations. Also, despite the fact that the coupled simulations only included feedbacks in one direction (LANDIS simulations receiving feedback from the UGM), the integrated results nevertheless informed the UGM predictions as well as the LANDIS predictions. For example, including the UGM predictions in the LANDIS simulations provided a dynamic context for the landtype properties, fire regimes, and vegetation types that were being urbanized.

Before we selected the urban growth model to integrate with LANDIS, we carefully considered the compatibility of the two simulation models with regard to temporal and spatial scale, as well as model assumptions. Therefore, we believe that the additional information gained from simulating urban growth and altered fire regimes as an integrated system outweighed the disadvantages of added uncertainty associated with combining the models together.
There has also been debate regarding tradeoffs between loose and tight model coupling, particularly dealing with the lower data requirements and software development required for loose coupling versus the added complexity that yields potentially higher realism in tight coupling (Park and Wagner 1997, Frysinger 2002). Although there were a number of similarities between the loosely coupled and tightly coupled simulation results, including the general spatial pattern of species extent and fire frequency, and the final extent of species’ cover, we believe the differences in results are important enough to recommend the tightly coupled approach over the loosely coupled approach, at least for these two models. The tightly coupled simulations resulted in notably different proportions of the landscape burning at different fire return intervals, which could have biological implications due to the fact that the risk of vegetation type conversion for obligate and facultative seeders increases at shorter fire return intervals. Also, the tightly coupled approach provided a temporal signature to landscape change that wasn’t possible to detect with the loosely coupled approach, which could be important for land managers who are interested in rates of habitat change over time. Version 4.0A of the LANDIS model now includes the functionality to update landtype maps and/or disturbance regime maps at every time step. Therefore, the preparation is in place for future research that involves tightly coupling LANDIS with urban growth predictions.
5.6 References


Conard, S. G. and Weise, D. R. 1998. Management of fire regime, fuels, and fire effects in southern California chaparral: lessons from the past and thoughts...
for the future. Tall Timbers Fire Ecology Conference. Tall Timbers Research Station. Tallahassee, FL.

Fabritus, S. and Davis, S. D. Is increasing fire frequency causing vegetation-type conversion among chaparral plant communities of the Santa Monica Mountains? Manuscript in preparation.


Franklin, J., Syphard, A. D., He, H. S., and Mladenoff, D. J. in press. The effects of altered fire regimes on patterns of plant succession in the foothills and mountains of southern California. Ecosystems.


254


National Park Service. 2000. Fire regime, fire management and the preservation of biological diversity in the Santa Monica Mountains N.R.A.


Syphard, A. D., Clarke, K. C., and Franklin, J. in press. Using a cellular automaton model to forecast the effects of urban growth on habitat pattern in southern California. Ecological Complexity.


Syphard, A. D., Yang, J., Franklin, J., and He, H. S. in prep a. Calibrating a forest landscape model to simulate high fire frequency in Mediterranean-type shrublands.


Figure 5-1: The Santa Monica Mountains in southern California
Figure 5-2: Landtype maps for the Santa Monica Mountains depicting urban land and WUI in 2000 (LANDIS alone) 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.
Figure 5-3: Percent change in area of landtypes and their respective WUIs from 2000 – 2050
Figure 5-4: Average simulated fire rotation intervals in the non-WUI and WUI landtypes for the long, medium, and short fire regime treatments of the LANDIS alone, loosely coupled, and tightly coupled model runs. The expected fire rotation intervals for the non-WUI and WUI landtypes were 60 and 45 for the long treatment, 30 and 22 for the medium treatment, and 15 and 11 for the short treatment.
Figure 5-5: Distribution of total area burned across fire return interval classes for the short fire regime treatment of the LANDIS alone, loosely coupled, and tightly coupled model runs.
Figure 5-6: Maps illustrating locations that burned five times or more (black) for the short fire regime treatment of the LANDIS alone, loosely coupled, and tightly coupled model runs. White represents urban area at year 2000, and gray represents areas that burned fewer than five times.
Figure 5-7: Final extent (ha) of functional types after 50 years of simulation for the long, medium, and short fire regime treatments of the LANDIS alone, loosely coupled, and tightly coupled model runs. OR = obligate resprouters; OS = obligate seeders; FAC = facultative seeders; CSS = coastal sage scrub species; GRASS = non-native annual grass.
Figure 5-8: 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 treatments of the LANDIS alone (NC), loosely coupled (LC), and tightly coupled (TC) model runs.
Figure 5-9: Distribution of areas lost, areas gained, and areas that maintained cover by the obligate seeders from 2000 – 2050 for the long and short fire regime treatments in the LANDIS alone, loosely coupled, and tightly coupled model runs.
Figure 5-10: Distribution of areas lost, areas gained, and areas that maintained cover by the obligate resprouters from 2000 – 2050 for the long and short fire regime treatments in the LANDIS alone, loosely coupled, and tightly coupled model runs.
Figure 5-11: Distribution of areas lost, areas gained, and areas that maintained cover by the coastal sage scrub species from 2000 – 2050 for the long and short fire regime treatments in the LANDIS alone, loosely coupled, and tightly coupled model runs.
Appendix 1. AML Script used to update landtype maps with annual urban growth predictions

/* landtype.aml
/* modules: arc, GRID
/* date: December, 2003
/* creator: Alexandra Syphard
/* purpose: to overlay 50 urban growth predictions with original landtype map to produce updated landtype maps for tightly coupled LANDIS simulations

&do count = 2000 &to 2050 &by 1

&sv resolution = 90
/*for resampling at the end

&sv roadgrid = road90
/*name of grid to combine with resampled data at end of script

&sv buffsize = 2
/*number of pixels to buffer around urban areas

&sv clustsize = 3
/*number of pixels to designate cluster as having a WUI

GRID

region%count% = REGIONGROUP(urban%count%) /*clusters at 30m resolution

if(region%count%.link == 100 & region%count%.count > %clustsize%) cluster%count% = 1 else cluster%count% = 0 endif

/*above created grid with urban clusters greater than 5 pixels

expand%count% = EXPAND(cluster%count%,%buffsize%,list,1) /*buffers urban clusters by 4 pixels

combine1%count% = COMBINE(expand%count%, land17) /*combines expanded layer with original landtype map
if(combine1%count%.expand%count% == 1 && (combine1%count%.land17 < 8
&& combine1%count%.land17 > 0)) templand%count% =
combine1%count%.land17 + 7
else templand%count% = combine1%count%.land17
/*reclassifies the new landtype map

combine2%count% = COMBINE(urban%count%, templand%count%)
/*begin to dynamically combine new landtype maps with the urban maps

landtype%count% = con(combine2%count%.urban%count% == 100, 17,
combine2%count%.templand%count%)
/*reclassifies urban land into landtype classification

landtype0%count% = con(isnull(landtype%count%), 0, landtype%count%)
/*turns nodata into 0

lt%resolution%count% = resample(landtype0%count%, %resolution%)
/*resamples all landtype maps into desired resolution

combine3%count% = COMBINE(lt%resolution%count%, %roadgrid%)
/*begin to force the roads to become contiguous on the resampled grids with the
90m road grid

if(combine3%count%.%roadgrid% == 1 &&
combine3%count%.lt%resolution%count% == 17) ltr%resolution%count% = 17
else if(combine3%count%.%roadgrid% == 1 &&
combine3%count%.lt%resolution%count% == 0) ltr%resolution%count% = 0
else if(combine3%count%.%roadgrid% == 1) ltr%resolution%count% = 15
else ltr%resolution%count% = combine3%count%.lt%resolution%count%
endif
/*reclassification so that urban has precedence over road, but new road has
precedence over other landtypes

expand2%count% = EXPAND(ltr%resolution%count%,1,list,15)

combine4%count% = COMBINE(expand2%count%, ltr%resolution%count%)

if(combine4%count%.expand2%count% == 15 &
&combine4%count%.ltr%resolution%count% < 8 &
&combine4%count%.ltr%resolution%count% > 0)) lt%count%fin =
combine4%count%.ltr%resolution%count% + 7
else lt%count%fin = combine4%count%.ltr%resolution%count%
endif

kill expand2%count% all
kill combine4%count% all
kill lt%resolution%count% all
kill combine3%count% all
kill region%count% all
kill expand%count% all
kill combine1%count% all
kill combine2%count% all
kill cluster%count% all
kill templand%count% all
kill landtype%count% all

q

gridimage lt%count%fin none landtype%count%.gis ERDAS

&type end loop%count%
&end

&return