Examination of Habitat Fragmentation and Effects on Species Persistence in the Vicinity of Naval Base Pt. Loma and Marine Corps Air Station Miramar, San Diego, CA and Development of a Multi-Species Planning Framework for Fragmented Landscapes

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List of Acronyms

oC	degrees Celsius
CALFLORA	http://www.calflora.org
CDF	California State Department of Forestry and Fire Protection
cm	centimeters
DoD	United States Department of Defense
DOE	United States Department of Energy
EMA	Expected Minimum Abundance
ESA	Endangered Species Act
FMMP	Farmland Mapping and Monitoring Program
GCGS1	Generic chaparral gap species 1
GCGS2	Generic chaparral gap species 2
GFDL	Geophysical Fluid Dynamics Laboratory
GIS	Geographic Information System
HSM	Habitat Suitability Model
ha	hectares
IPCC	Intergovernmental Panel on Climate Change
MCAS	Marine Corps Air Station
m	meters
MTE	Mediterranean-type ecosystem
NCAR	National Center for Atmospheric Research
NOAA	National Oceanic and Atmospheric Administration
PCM	Parallel Climate Model
QER	Quasi-extinction risk
ROW	Right of way
SANDAG	San Diego Area Governments
SDSU	San Diego State University
SERDP	Strategic Environmental Research and Development Program
UC	University of California
US	United States

Keywords

Ceanothus verrucosus; *Quercus dumosa; Chorizanthe orcuttiana; Neotoma macrotis;* multi-species management; chaparral; climate change; global change; wildfire; habitat fragmentation; Mediterranean systems; obligate seeding shrub; obligate resprouting shrub, population model; habitat suitability model

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Abstract

Objective

Develop methods to identify optimal management for metapopulations of sensitive species occurring in highly fragmented landscapes where subpopulations may be isolated and not functioning as true metapopulations. Use the best available data or data that can be assembled within a short period of time so that options are not foreclosed by land use conversion before decisions can be made. This project will help sustain military missions by linking habitat preservation and management on and off military installations so that species persistence can be maximized and the Department of Defense's (DoD's) proportion of the responsibility for management does not increase over time.

Technical Approach

We developed a multi-species planning framework for fragmented landscapes using population viability analysis and habitat suitability modeling. Climate change was incorporated through habitat suitability projection. Quantitative conservation objective functions were used to select among management scenarios. Metapopulation models were used in a functional assessment approach to evaluate whether dispersal dynamics were likely to be operative in the landscape and thus inform management and reserve design. The test case involved four species of the maritime chaparral in coastal southern California with different population responses to one of the primary ecosystem drivers, wildland fire, and with different hypothetical responses to fragmentation. The species were *Ceanothus verrucosus*, a long-lived obligate seeding shrub; *Chorizanthe orcuttiana*, an annual plant; *Neotoma macrotis*, big-eared woodrat; and *Quercus dumosa*, a long-lived obligate resprouting shrub. Coastal southern California is a biodiversity hot spot with high levels of habitat loss and fragmentation.

Results

A multi-species planning framework was developed entailing four phases: 1) identification of the species and landscape, 2) modeling, 3) selection of objective functions and ranking management scenarios, and 4) implementation in an adaptive management framework. Specific recommendations for the San Diego region included maintaining longer average fire intervals. The specific objective in terms of percent decline from initial population influenced which fire management scenarios ranked highest. Climate change was included through projected changes in species abundance and distribution in the landscape. For the most part, the patterns in management rankings established for the current climate were maintained under future climates. The species modeled, even those with greater dispersal ability, have few connections between populations; consequently, removal of dispersal from the models has little to no effect on model results. This result indicates that patch connectedness is less important than total habitat area in prioritizing habitat configurations for conservation in the highly fragmented landscape of coastal southern California. If dispersal is not effective, future management may require translocations to reestablish extirpated populations and maintain genetic diversity.

Benefits

Specific conservation recommendations are presented for the target species throughout their geographic ranges. In addition, a multi-species conservation planning framework is presented that explicitly considers species tradeoffs in response to multiple threats and management. The

resulting methods rely on a combination of single patch and metapopulation models, habitat suitability models, and quantitative conservation objective functions to explicitly address species tradeoffs under multiple threats from global climate change.

1.0 Objectives

Key challenges to conservation decision making in rapidly developing regions are the paucity of data and the rapid foreclosure of conservation opportunities as land is appropriated for agricultural and urban uses. This circumstance necessitates basing decisions on available data or on data that can be quickly collected. Consequently, it is important to establish methods to develop conservation priorities in spite of uncertainty caused by sparse data. Our objective was to use the best available data supplemented with what could be collected in a short time to develop a framework for conservation decisions.

Coastal southern California is a recognized biodiversity hotspot, exhibiting high levels of endemism and supporting species characterized by limited ranges. To address the ongoing threats to biodiversity in this region, in 1991 stakeholders in San Diego County initiated the first multi-species planning efforts in California as part of the Natural Community Conservation Planning program. Department of Defense (DoD) lands were not included in this regional planning; instead DoD has developed parallel conservation planning and management through their natural resources conservation programs.

This project will help sustain military missions by linking habitat preservation with management both on and off military installations so that species persistence can be maximized and DoD's proportionate responsibility for management does not increase over time. Detailed analyses of four species were conducted, and conservation recommendations were developed to promote long-term stability in metapopulations of these species. All four species occur on Naval Base Pt. Loma; two of the species also occur on Marine Corps Air Station (MCAS) Miramar.

The Statement of Need specified the objective of developing methods to identify the most ecologically important parcels on and near DoD installations for which land protection could provide long-term species conservation benefits while avoiding additional restrictions on military training. This project integrates population viability analyses with habitat suitability models to identify parcels and management actions necessary to maintain stable metapopulations of the target species. We address habitats that are highly fragmented by development to a degree that seriously disrupts ecosystem processes and makes some or all of the fragments function in isolation. We evaluated management actions to maintain ecosystem and demographic processes and studied species at multiple scales in coastal scrub habitats, which exhibit hypothesized differential responses to fragmentation.

The specific objectives of this project are to develop methods to identify optimal regional habitat configurations for metapopulations of sensitive species occurring on Naval Base Pt. Loma and MCAS Miramar, San Diego County California (Figures 1 and 2). The subpopulations in this landscape may be isolated and therefore may not function as true metapopulations. If the subpopulations are not reliably connected by dispersal, *artificial dispersal*—or periodic recolonization—may be necessary to perpetuate species in this landscape. The entire U.S. range for three of our four study species occurs in the small, highly fragmented landscape within our study area. It is possible that conservation as artificial metapopulations is our only choice for perpetuation of these species.

Metapopulation modeling approaches have value for conservation planning even for populations so fragmented that metapopulation theory may not apply. These models allow the examination of what levels of process (e.g., fire return interval) and function (e.g., dispersal) may need to be artificially implemented to maintain sufficient subpopulations within the species' range in

perpetuity to ensure species persistence (Scott et al. 2005). Costs and feasibility can be evaluated and informed decisions can be made on the basis of such analyses. For example, if dispersal is not functioning or is only partially functioning, patches of habitat that are easier to manage in other respects may be selected for conservation in light of a fuller understanding of the periodic management input that may be required to compensate for insufficient dispersal.

The analysis identifies subpopulation characteristics (i.e., size and connectedness) most important to the perpetuation of the target species in this landscape and evaluates management actions needed to sustain subpopulations. We developed a framework to prioritize management actions and highlight how they might influence optimal habitat configuration for persistence of a selected group of species. This approach has the additional advantage of addressing management issues that may be important for engaging potential partners in ventures to protect habitat across ownership and political boundaries. This project makes specific recommendations for the San Diego region that have the best chance of avoiding future Endangered Species Act (ESA) listings. In addition, because the approach is general, it is applicable in other highly fragmented landscapes. Through the evaluation of risk, identification of sensitive parameters, and assessment of data uncertainty, these models facilitate the integration of an adaptive management framework into the process of conserving important habitat (Beissinger 2002).

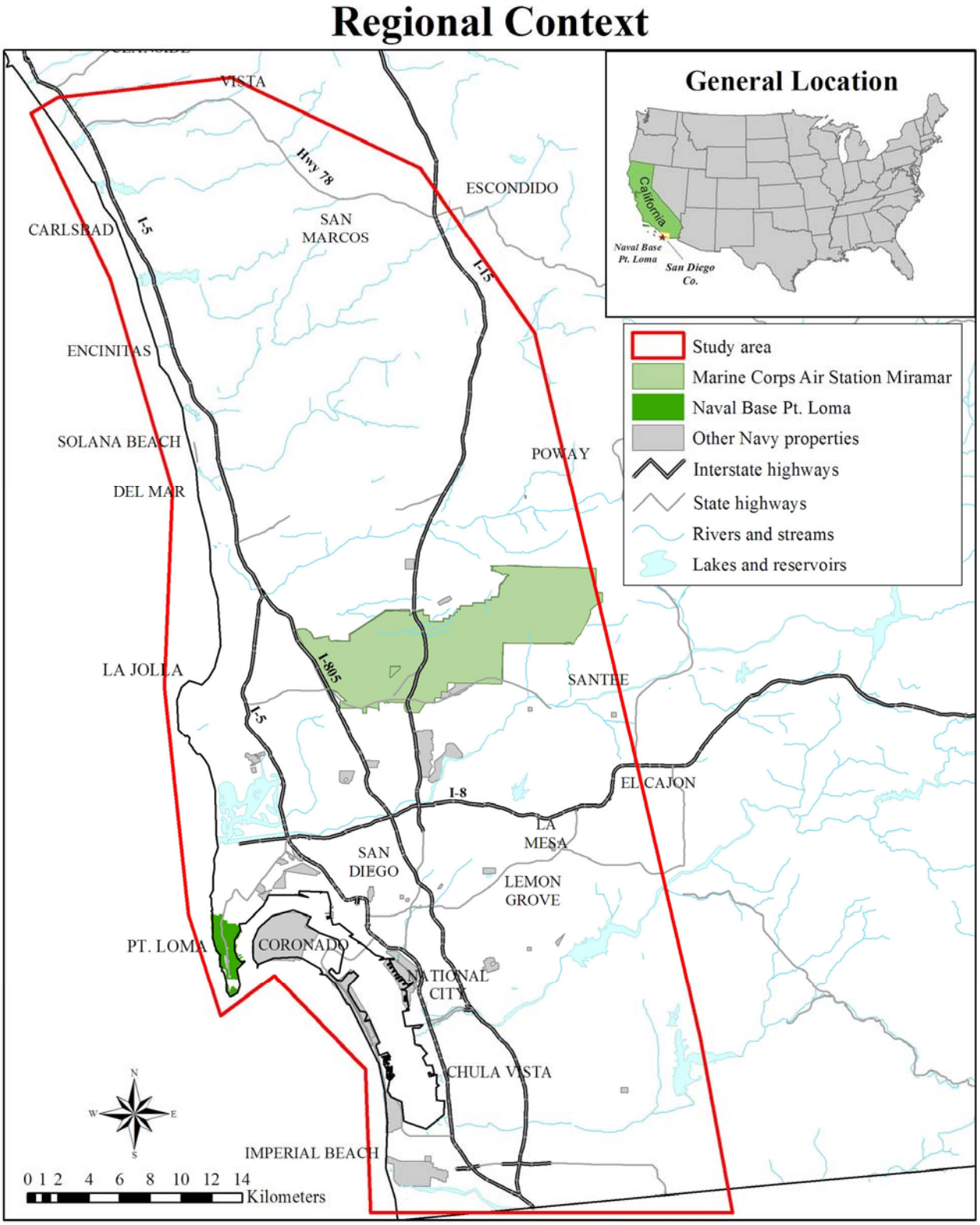


Figure 1. Regional context.

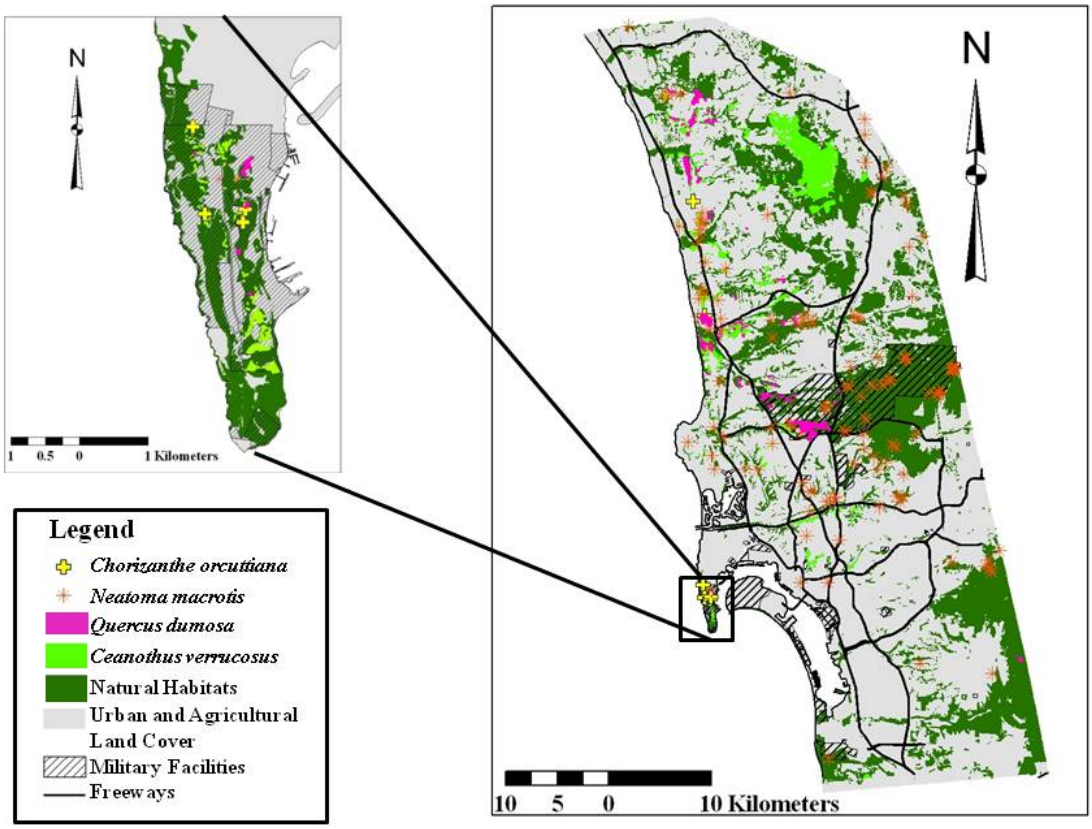


Figure 2. Study area showing military installations and distribution of study species.

2.0 Introduction

Although natural populations have always experienced fragmentation to varying degrees, human activities in North America in recent centuries have greatly increased the extent of fragmentation for nearly all native species. Since the persistence of local populations is a function of population size (Elphick 2001), such fragmentation has significantly raised the probability of local—and therefore global—extinction for many species (Henle *et al.* 2004). The likelihood of species persistence is decreased directly through reductions in available resources such as food, breeding locations, and territorial home ranges; and indirectly through higher susceptibility of smaller populations to environmental variability such as drought years, storms, and unexpected low breeding events. Additionally, fragmentation can reduce the potential for recolonization of habitat patches where subpopulations have become extirpated. Fragmentation can also disrupt ecosystem processes on which species and communities depend. For example, when habitat is fragmented by urbanization or other changes in land use that disrupt fuel continuity, fragments can no longer burn with historic frequency or patterns.

DoD lands support more than 350 federally listed species—the highest density of threatened and endangered species of any federal landowner (Stein 2008). Military use of the land can cause threats to listed species but does not, in general, result in the complete conversion of suitable habitat to unsuitable habitat, as has been the case on lands surrounding many DoD installations. Consequently, as habitat is lost and fragmented around installations, DoD carries an increasing responsibility for conservation of listed species.

Some of the measures necessary to conserve listed species restrict military land uses, potentially compromising DoD's mission (GAO 2003). DoD needs to develop methods to identify the most ecologically important land parcels and conservation strategies on and near its installations to facilitate long-term species conservation benefits and avoid additional military training restrictions.

2.1 Conservation Planning

Conservation planning addresses fragmentation in part through habitat linkages (Beier and Noss 1998; Hanski 2002). In many cases, however, both natural and anthropogenic fragmentation can lead to systems where habitat linkages are not feasible and there is no alternative to a having a set of small unconnected preserves (Schwartz 1999). This is the case around many DoD facilities, where urbanization has permanently fragmented habitats. This situation is apparent in our study area, which is focused on species occurring on Naval Base Pt. Loma and MCAS Miramar (Figure 2).

Naval Base Pt. Loma lies within the City of San Diego. Urbanized areas are shown in grey: only a small fraction of natural habitats remain. This project specifically addresses habitats that are highly fragmented by development to a degree that seriously disrupts ecosystem processes and makes some or all of the fragments function in isolation. In these situations it is unclear whether populations function as metapopulations, exhibiting equilibrium of colonization-extinction dynamics (With 2004). With highly variable dispersal abilities among species, it is likely that some species maintain metapopulation function in at least portions of these fragmented systems, while others do not.

Unfortunately, habitat loss and fragmentation are not the only problems. Natural systems face an array of anthropogenic threats that also include altered disturbance regimes and climate change

interacting at different spatial and temporal scales (Rosenzweig 2005). Understanding the effects of these threats and their interactions on species persistence is crucial to developing timely, cost-effective management strategies to conserve biodiversity.

In addition, because species have different ecological requirements and are limited by different factors, it is critical to consider tradeoffs among species in response to threats and management when making conservation decisions (Lindenmeyer 2002 and Roberge and Angelstam 2004).

The imperative of multi-species management operates even in the realm of managing at-risk species. In some ecosystems, so many species have become imperiled that the density of federally listed species on military lands has put the military in the position of managing multiple listed species, in some cases with unavoidable tradeoffs between them due to conflicting habitat or management requirements (U.S. Navy 2007).

2.2 Case Study

The case study is set in coastal southern California, a Mediterranean-type ecosystem (MTE).

MTEs world-wide are high in species richness and endemism and are considered biodiversity hotspots of global significance (Cowling *et al.* 1996; Myers *et al.* 2000). They are also among the most threatened ecosystems in the world because they are particularly sensitive to the most prevalent and dominant threats: habitat loss, altered natural disturbance regimes, invasive species, and climate change (Cincotta *et al.* 2000; Sala *et al.* 2000; Underwood *et al.* 2009).

Authorities generally agree that anthropogenic warming started in the twentieth century and that average temperatures and climatic variability will continue to increase (Christensen *et al.* 2007). During the twentieth century, California's climate has become hotter and wetter (Smith *et al.* 2004)—trends also reflected in our study area (Western Regional Climate Center 2009a and 2009b). Future projections show continued temperature increases, though precipitation projections are less certain (Cayan *et al.* 2008).

Fire is an important driver of ecosystem processes in MTEs (Dallman 1998), but fire regimes altered by anthropogenic influences threaten species persistence (Zedler 1995). Humans alter fire regimes in MTEs primarily through increased ignitions leading to shortened fire intervals, but also through fire suppression or reduction in ignitions (Zedler *et al.* 1983; Keeley and Fotheringham 2003; Syphard *et al.* 2007a). A number of studies also implicate climate change (Piñol *et al.* 1998; Pausas 2004; Westerling and Bryant 2008). While weather—both climate averages and extreme events—is a significant determinant of fire regimes, it is not necessarily clear how fire regimes will change with changing climate. Because fire regimes can be determined by extreme events (Littell *et al.* 2009) and because extreme events are poorly modeled by global climate models (Field *et al.* 1999), the effects of climate change on fire regimes are difficult to predict (Smith *et al.* 2004). MTEs are particularly useful as a case study to evaluate tradeoffs among species because fire is a primary driver of ecosystem processes and these systems consist of assemblages of species with different population responses to fire.

Species with restricted ranges are highly threatened by climate change (Thomas *et al.* 2004). Hence, such species are useful subjects for evaluating climate change impacts because significant population declines, subsequent extinctions, or range shifts are projected to occur sooner for rare species than for more widespread species (Schwartz *et al.* 2006). Because of the regional scale at which threats such as climate change, altered fire regimes, and urban development act, rare species with restricted ranges are more likely to be affected by a

confluence of threats. Consequently, focusing our study on rare species allows us to evaluate the relative and cumulative significance of different threats.

Our study species are all dependant on scrub habitats of California and northern Baja California, Mexico (Hickman 1993). The four species represent different ecosystem process requirements, dispersal abilities and threat levels, as shown below.

1. *Ceanothus verrucosus* Nutt. is a long-lived shrub that is killed by fire, is dependent on fire for stand reestablishment, and has limited dispersal abilities (Lawson *et al*. 2010; Quinn unpublished data). It is endemic to coastal scrub habitats of southern California and northern Baja California (Hickman 1993) and has a global conservation status ranking of G3 (vulnerable) (NatureServe 2010). Our study area contains the entire U.S. range.
2. *Quercus dumosa* Nutt. is a long-lived shrub that resprouts after fire and establishes seedlings in the absence of fire (Keeley 1992). It is capable of medium to long-distance dispersal facilitated primarily by small mammals and birds (den Ouden 2004). It is endemic to coastal scrub habitats of southern California and northern Baja California (Hickman 1993) and has a conservation ranking of G1G2 (critically imperiled to imperiled) (NatureServe 2010). Our study area contains 99% of the U.S. range.
3. *Chorizanthe orcuttiana* Parry is an annual plant that does not exhibit known fire adaptations and occurs in sandy gaps in the maritime chaparral (Bauder 2005). Its dispersal mechanisms are not well understood but are thought to be limited (Kluse and Doak 1999; Bauder 2005; Fox *et al.* 2005). It is endemic to coastal scrub habitats in southern California (Hickman 1993, Bauder 2005) and has a conservation status of G1 (critically imperiled) (NatureServe 2010). Our study area contains the entire U.S. range.
4. *Neotoma macrotis,* a widespread woodrat species with a conservation status of G5 (secure) (NatureServe 2010), is typically extirpated by fire and must recolonize after fire (Wirtz *et al.* 1988; Schwilk and Keeley 1998). It occurs in coastal central and southern California and in the Sierra Nevada below 5000 ft. (Kelly 1990; Matocq 2002; Braswell 2007). Woodrats have good dispersal abilities in natural landscapes (Smith 1965), but roads in anthropogenically fragmented landscapes serve as barriers (Bolger *et al.* 1997; McGregor *et al.* 2008).

One of the main methods used to assess the impact of climate change on biodiversity is the projection of species distributions, or habitat suitability models (HSMs). HSMs estimate realized niches using climatic and sometimes other habitat predictor variables, such as soils (Pearson and Dawson 2003; Thomas *et al.* 2004). These statistical models are then linked with future climate scenarios to project range shifts. While climatic factors are clearly important in influencing species distributions, shifts and contractions of suitable climates do not easily translate into extinction risks because they do not take into account demographic processes.

Keith *et al.* (2008) addressed this challenge by linking predicted shifts in habitat suitability under climate change to population viability models. This strategy has the advantage of integrating projected spatial changes in habitat suitability at the landscape level with demographic dynamics at the population level. These models have a wide range of utility from evaluating the effects of threats and management strategies on species persistence at varying spatial and temporal scales, to informing priorities for further data collection. To date, however, most of the existing research has focused on a threat-by-threat analysis for single species (Anderson *et al.* 2009; Firth *et al.* 2010; Yates and Ladd 2010).

Nicholson and Possingham (2006) developed multi-species objective functions that combined estimates of species extinction risk for individual species to quantify different objectives (such as minimizing the expected number of extinctions) for biodiversity conservation. They used one of these functions (minimize the expected number of extinction) to find the optimal reserve system in a 10-species, 36-patch landscape constrained by a land acquisition budget (Nicholson and Possingham 2006). They found this method—*maximizing persistence*—to outperform two traditional area-based reserve selection methods aimed at maximizing habitat area and effective habitat area across species. They did not, however, evaluate selecting the best management scenario for biodiversity conservation using species chosen to represent different process requirements across the landscape.

Our study extended these approaches to develop methods to identify the best management and reserve design strategies to maximize persistence of biodiversity in highly fragmented landscapes, considering a suite of current and projected future threats to species persistence: habitat loss, altered fire regime, and climate change. We selected a set of focal species to represent the range of fire responses to allow a comprehensive evaluation of species tradeoffs with regard to fire return interval, and we evaluated the effect of habitat loss and projected climate change on the best management strategy for multiple species. We considered two options for reserve design, based in ecological theory. One focuses on patch size, targeting the largest patches for the reserve; the other focuses on patch connectedness, targeting the least isolated patches. We used spatially explicit metapopulation models and multi-species objective functions (Nicholson and Possingham 2006) to synthesize estimates of extinction risk from the models. Realistic problems that require decisions typically include some level of subjectivity (Drechsler and Burgman 2004). While subjectivity is often viewed negatively, all values are inherently subjective. The choice of objective function influences which scenario is judged to be “best”. We employ multiple objective functions and discuss species trade-offs resulting from the rankings of the scenarios.

3.0 Materials and Methods

The study species were selected to include species with hypothesized differential probabilities of surviving in anthropogenically fragmented landscapes and exhibiting varying responses to fire. We also developed two generic chaparral gap species based on the *Chorizanthe orcuttiana* model with different responses to fire that were not included in the current set to examine the effects of different combinations of species on multi-species priorities. While the ranges of all of the study species except *C. orcuttiana* extend into Baja California, the study is limited to the U.S. portion of the ranges due to a paucity of species distribution and environmental data for Baja California. Figure 2 shows the distribution of the study species within the study area. Sections 4.1.1–4.1.4 present summaries of the study species' ranges and life histories; for more details, see Appendices A–D and F.

3.1 Study Species

3.1.1 *Ceanothus verrucosus*

C. verrucosus Nutt. (Figure 3) is a long-lived shrub of the coastal chaparral of southern California and northern Baja California. Figures 4–6 show diagnostic vegetative and floral structures. Globally, it is ranked as a vulnerable species (G3) (CNPS 2009). Like many narrow-niche endemics in MTEs, it is threatened by high levels of development, and its restricted range likely reflects adaptation to a narrow niche characterized by climatic factors and possibly soils (Nicholson 1993; Keeley 2000). Our study focuses on the U.S. portion of the range (Figure 2), which extends approximately 70 kilometers (km) north of the U.S. border with Mexico and includes 151 subpopulations (greater than 0.25 hectare [ha] and separated by more than 44 meters) totaling 4,311 ha (California Department of Fish and Game 2005) (Appendix E). We updated habitat maps (California Department of Fish and Game 2005) using aerial photography and field surveys, and we estimated population sizes through direct counts or density estimates, resulting in a complete inventory of the known U.S. population.

The distribution of *C. verrucosus* is very limited and likely to be controlled by climate based on physiological and biographical data regarding congeners (Nicholson 1993; Davis *et al.* 1999; Ewers *et al.* 2003;). *C. verrucosus* is an appropriate species for evaluating the effects of climate change because its distribution is correlated with climate variables (winter lows and summer highs) that are likely to change within its range (Nicholson 1993; Smith *et al.* 2004). Physiological evidence also indicates that climate strongly influences distributions within the *Ceanothus* genus, especially winter low temperatures (Ewers *et al.* 2003) and drought severity (Davis *et al.* 1999), which is closely related to temperature. However, abrupt species turnover with little comingling between species in the genus suggests that competition is also important in determining species distributions (Nicholson 1993).

Seed production begins at 3–6 years and is a curvilinear function of age peaking around age 50 (Zammit and Zedler 1993; Lawson 2010). The species has a long-lived, persistent seedbank. Some age diversity is introduced by occasional germination between fires and by vegetative establishment (Zedler 1995). Average peak production is estimated to be on the order of 300 seeds per plant (Keeley 1987; Zammit and Zedler 1993). Seeds are initially dispersed ballistically an average of about 1 meter (m) (Quinn unpublished data) and secondarily by animal vectors including harvester ants, small mammals, and birds (Davey 1982; Quinn 1994).

Herbivory and drought drive mortality in the first year or two (Kummerow *et al.* 1985; Moreno and Oechel 1991; Quinn 1994) and density-dependent thinning occurs for approximately the first 15 years (Horton and Kraebel 1955; Schlessinger and Gill 1978). Mortality rates decline through these phases, remaining at very low levels in mature stands. Plant longevity exceeds 95 years but an upper bound is unknown (Lawson 2010).

Figure 3. *Ceanothus verrucosus* (white flowers) and *Quercus dumosa* (rust hue).

Figure 4. *Ceanothus verrucosus*—characteristic warts on stem from which it gets its common name, wart-stemmed Ceanothus. Note alternate leaves characteristically reflexed against the stem.

Figure 5. Note three-part seed cup characteristic of many species in the genus *Ceanothus.*

Figure 6. *Ceanothus verrucosus*—five-part axillary flowers.

3.1.2 *Quercus dumosa*

Quercus dumosa Nutt. (Figure 3), a very long-lived shrub, occurs in the coastal chaparral of southern California and northern Baja California (Hickman 1993; Keeley 1993). Figures 7 and 8 show leaves, flowers, and fruit. Globally, it is ranked as a critically imperiled to imperiled species, intermediate between G1 and G2 (CNPS 2009). Like many narrow-niche endemics in MTE, it is threatened by high levels of development. Our study focuses on the U.S. portion of the range, which extends approximately 85 km north of the U.S. border with Mexico and 20 km inland from the coast (Figure 2), and comprises 188 subpopulations (greater than 0.01 ha and separated by more than 44 meters) totaling 671 ha. We used detailed population maps with

population counts for most of the U.S. range (Roberts unpublished data) supplemented by location-specific survey reports for some conservation lands and military installations (Dossey and Associates 2006; TDI 2007, CNLM unpublished data). We updated these maps using aerial photography and field surveys, and we estimated population sizes through direct counts or density estimates where sizes were not included in survey results and added several unrecorded populations, resulting in a complete inventory of the known U.S. population.

The species' restricted range likely reflects both biotic and ecophysiological limitations. Climate, based on its effect on seedling establishment, has been identified as differentially limiting the distribution of three Mediterranean oaks and is also likely to influence the range of *Q. dumosa*. Drought length, summer precipitation and temperature have been identified as influential climatic variables (Sharp and Sprague 1967; Purves *et al.* 2007). In addition, dispersal dynamics are thought to be an important influence in the size of oak range, which is correlated with acorn size (Aizen and Patterson 1990; Purves *et al.* 2007). Indeed, like its range, *Q. dumosa's* acorns are small (http://efloras.org).

Q. dumosa occupies the persistence niche with a strong resprouting response to disturbance (Bellingham and Sparrow 2000; Keeley *et al.* 2006). Because the persistence niche is associated with low post-disturbance mortality and low reliance on seedling establishment, species in this niche are more influenced by processes that affect adult survival than recruitment (Bond and Midgley 2001). In keeping with ecological theory that suggests that strong resprouters should perform best under high severity disturbances with intermediate to high frequency (Bellingham and Sparrow 2000), *Q. dumosa* has been shown to be resilient to high severity fires under a wide range of fire intervals (Keeley 1992).

For long-lived species such as *Q. dumosa*, resprouting sustains population sizes during long periods of poor or no recruitment (Bond and Midgley 2001; Abrahamson and Layne 2003). As would be expected for such species, mortality rates are high for juveniles but decline to very low levels in adults. Mature *Q. dumosa* resprout vigorously after fire and experience very low fire-related mortality. Individual stems turn over regularly, typically living less than 100 years (Keeley 1985). Due to resprouting, this individual *Q. dumosa* have lifespans on the order of centuries (Keeley 1993) and may live much longer (May *et al.* 2009).

When seedlings do establish, as has been shown for other oak species (Lawson *et al.* 1997), they tend to form a long-lived persistent seedling bank (Keeley 1992). Seedling establishment is most likely to occur under canopies in very old stands, but recruitment of saplings to the canopy requires the opening of a canopy gap through the mortality of individual stems or entire plants. Consequently, seedlings can persist for decades suppressed by the canopy until they die or a canopy gap forms (Keeley 1992; Lawson *et al.* 1997). Even though stand-replacing fires typical of chaparral can kill mature individuals (Keeley 2006), fire intensity varies significantly over relatively short distances (3–5 m) and mortality is correlated with soil heating (Odion and Davis 2000). The variation in fire intensity combined with the presence of well-developed basal burls allows survival and resprouting after fire. Because of this ability to survive fire, and the need for post–seedling establishment gap formation to allow recruitment to the canopy, it has been hypothesized that scrub oak species may require fires to recruit saplings to the canopy (Keeley 2000).

Figure 7. *Quercus dumosa* leaves—upper side shiny, lower side covered in trichomes.

Figure 8. *Quercus dumosa*—acorns, 10–20 mm in length (Hickman 1993), and catkins or male flowers.

3.1.3 *Chorizanthe orcuttiana*

Chorizanthe orcuttiana Parry (Figure 9) occurs in the coastal chaparral of southern California and northern Baja California (Hickman 1993). Globally, it is ranked as G1, a critically imperiled species (CNPS 2009), and is listed as endangered under the ESA. It is a winter annual that occurs in sandy gaps in the maritime chaparral and Diegan coastal sage scrub. It experiences periodic recruitment failures due to drought (Bauder 2005) and appears to have a persistent seedbank, based on reports of populations appearing after the removal of long-established ice-plant cover (Bauder 2005).

C. orcuttiana experiences highly variable climatic conditions. The coefficient of variation of January and February precipitation within its range was 67% over the last century. This variability is similar to that of coastal habitats of other *Chorizanthe* species (Fox *et al.* 2006), as well as southwestern deserts, which are known for their high environmental variability (Clauss and Venable 2000). Long-lived seeds create a storage effect, buffering the population from

environmental variation and allowing the species to persist under unpredictable conditions (Fox *et al.* 2006). Annual population counts are highly correlated with climate variables, in particular winter precipitation and winter average maximum temperature (r^2=0.94, p<0.0073) (Appendix B).

How and when the sandy openings that comprise its habitat form, and how long they persist, are important questions because *C. orcuttiana* does not grow under shrub canopies. Consequently, changes in the spatial extent of these openings are important to population persistence. Recently at Pt. Loma, the size of one subpopulation expanded after nonnative *Acacia* shrubs were removed (Bryan Munson pers. comm.). The expansion, on the order of meters, may have resulted from either dispersal or a dormant seedbank. *C. orcuttiana* does not require fire for any part of its life cycle; because the openings where it occurs are sparsely vegetated (Bauder 2005), fire likely skips over them, or they are subject to low-intensity patchy fire (Davis *et al.* 1989).

Generic chaparral gap species 1 (GCGS1) was developed to consider a hypothetical scenario where fire has positive indirect effects on *C. orcuttiana* by influencing gap formation. Fires increase suitable habitat for GCGS1 adjacent to existing populations or remove canopy cover that suppresses undetected populations present only as seed. Seed survival after fire was parameterized based on other herbaceous chaparral gap species (Davis *et al.* 1989).

Two nonnative species, ice-plant (*Mesembryanthemum* spp.) and *Acacia* spp., threaten *C. orcuttiana* through encroachment into the canopy gaps where it occurs (Kimberly O'Connor pers. comm.). In addition, exotic annual grasses may pose a risk (CBI 2000). In southern California, *Chorizanthe* species tend to occur in sandy openings with few nonnative grasses (CBI 2000; Bauder 2005). However, if climate change results in increased rainfall, habitat suitability could increase for competitors, especially annual plants that may already be present in the ecosystem, and *C. orcuttiana* could be harmed by competition even if the new conditions are within its fundamental niche (Brooks 2000; Brooks and Berry 2006).

Generic chaparral gap species 2 (GCGS2) was developed to consider a hypothetical scenario where annual grasses compete with *C. orcuttiana*, restricting habitat area. In coastal scrub habitats in northern California, *Vulpia myuros,* an exotic annual grass, has been shown to compete heavily with other *Chorizanthe* species (Zador 1993 in Kluse and Doak 1999). While ice-plant and acacia effectively close canopy gaps and exclude *C. orcuttiana*, annual grasses coexist as competitors to congenerics (Kluse and Doak 1999). Fires results in a short-term increase carrying capacity for GCGS2.

Unlike many narrow-niche endemics in MTEs, *C. orcuttiana* is not currently threatened by high levels of development because its current distribution (there are only six known subpopulations) occurs entirely within park or military lands not at risk of land use conversion. It is likely that there are few if any undetected populations, as thorough efforts have been recently made to survey additional suitable habitat (Bauder 2005). However, if unknown populations exist, they may be threatened by development.

Our study includes all known populations, which extend approximately 40 km from Point Loma, near downtown San Diego, north to Encinitas. Known populations occur within 3 km of the coast and comprise six subpopulations separated by more than 175 meters. The populations range from around 10 m^2 to 1,000 m^2 in area and total 0.25 hectare. We used detailed population maps with population counts (Bauder 2005; Department of the Navy unpublished data) as a complete inventory of the known U.S. population.

Figure 9. *Chorizanthe orcuttiana*.

3.1.4 *Neotoma macrotis*

Neotoma macrotis is a widespread species occurring in woody habitats including chaparral, coastal sage scrub, oak and riparian woodlands, and coniferous forests in coastal central and southern California and in the Sierra Nevada at elevations less than 5,000 ft. (Kelly 1990; Matocq 2002; Braswell 2007). Figure 10 is a picture of a typical woodrat stick house. *N. macrotis* is widespread in our study area, occurring mainly in chaparral, and is associated with *Malosma laurina* (Schwilk and Keeley 1998; G. Fleming unpublished data). Globally, it is ranked as G5, a secure species (NatureServe 2009). Our study focuses on species distribution within the study area (Figure 2). We did not have detailed population maps as were available for the other species.

Figure 10. Woodrat house in a stand of *Quercus dumosa* Naval Base Pt. Loma.

Woodrats are nocturnal rodents active year-round. They are small, with an adult weight of 200–350 grams (g) (McEachern *et al.* 2007), and typically produce between one and five litters per year. Juveniles mature in 9–12 months and live for an average of 1.6 years with (Matocq 2002) and a maximum of 3–4 years (Lee and Tietje 2005). *N. macrotis* was previously considered part of *N. fuscipes* and was only recently separated (Matocq 2002). Our study area is well within the the species' range, which extends approximately 120 km inland from the coast in San Diego County, approximately 50 km south of the U.S.-Mexico border, and almost 500 km north.

Precipitation, through its effect on food resources, has been shown to be important to small mammal population dynamics (Meserve *et al.* 2001; Lima *et al.* 2002). Annual precipitation is thought to drive population dynamics through its influence on food availability in our study area (Dana Morin pers. comm.). Although small mammals are expected to increase in abundance in response to extreme precipitation associated with El Niño Southern Oscillation events (Jaksic 2001; Braswell 2007), woodrat populations in coastal southern California did not show a response (Braswell 2007).

Woodrats are very sensitive to fire. In fact, unburned refugia appear to be required for woodrats to survive the moderate to hot fires typical of chaparral (Wirtz *et al.* 1988; Schwilk and Keeley 1998). Wirtz *et al.* (1988), in a study of four chaparral burns, found that no marked woodrats

survived experimental fires. It can take up to 2 years for woodrats to colonize new habitat after fire (Wirtz 1982; Wirtz *et al.* 1988), but this is dependent on the location of source populations and can be impeded by habitat fragmentation (McGregor *et al.* 2008).

Woodrats are highly affected by habitat fragmentation. Bolger *et al.* 1997 concluded that rodents in fragmented habitats in San Diego were incapable of colonizing fragments where populations had been extirpated. This may be because they generally do not cross roads even if traffic is light (McGregor *et al.* 2008). In a study of small mammal use of road rights of way (ROWs) and adjacent habitats, *N. fuscipes* presence was negatively correlated with ROWs (possibly due to lack of woody cover), and they were not found road-killed (Adams and Geis 1983). Rather than being killed crossing roads, they may be avoiding them, as small mammals have been shown to avoid the road surface itself independent of the amount of traffic or noise (McGregor *et al.* 2008).

The combination of fire sensitivity and road avoidance may mean that this species, which is thought to be secure, may not be able to persist within the study area without periodic reintroduction due to high levels of fragmentation from land conversion and road development and the presence of catastrophic wildfire. In other words, the threat from habitat loss for this species is not so much the direct loss of habitat but the disruption of landscape-level processes—specifically colonization of extirpated patches after fire.

The preservation of woodrat middens in desert regions from the Pleistocene and Holocene has facilitated detailed documentation of woodrat response to climate change, including rapid climate change (Wells 1976; Smith and Betancourt 2003). Documented responses include adaptation through change in body mass as well as range shifts and extirpations. While individual species of *Neotoma* respond in different degrees to changes in summer and winter temperature, body size in this genus generally decreases as temperature increases (Smith and Betancourt 2003; Smith *et al.* 2009). As would be expected, demographic rates reflecting climatic parameters and fecundity in *N. macrotis* have been shown to be correlated with the preceding winter's low temperature (Lee and Tietje 2005).

3.2 Landscape Data

3.2.1 Current Climate and Future Climate Projections

The climate in the study area is a typical Mediterranean-type climate characterized by hot dry summers and cool wet winters. For the period 1970–1999, the average winter temperature in the study area (December–January) was 17.8^{o}C, and the average summer temperature (July–September) was 22.0^{o}C (Western Regional Climate Center 2009a). Average annual precipitation during this period was 27.5 centimeters (cm) (Western Regional Climate Center 2009b).

During the twentieth century, the climate in California has become hotter and wetter (Smith *et al.* 2004) (trends also reflected in our study area) (Western Regional Climate Center 2009a and 2009b). Future projections show continued temperature increases, though precipitation projections are less certain (Cayan *et al.* 2008). We used two future climate scenarios, based on the Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment medium-high emissions scenario, produced by two different global climate models and shown to realistically simulate California's climate (Cayan *et al.* 2008). Each scenario exhibited differing sensitivity to greenhouse gas forcing. The projections run through 2099. For our study area, the National Center for Atmospheric Research (NCAR) and the Department of Energy's (DOE's) Parallel

Climate Model (PCM) projects a slightly wetter and hotter climate (2.5°C increase in temperature and 8% increase in precipitation), while the National Oceanic and Atmospheric Administration (NOAA) Geophysical Fluid Dynamics Laboratory CM2.1 model (GFDL) predicts a much hotter and drier climate (4.4°C increase in temperature and 26% decrease in precipitation).

We used downscaled (1 km grid) GFDL data provided by the Sustainability Solutions Institute (http://ssi.ucsd.edu/) and averaged the predictions for the years 2070–2099 to reach an estimate of the projected future climate at the end of the twenty-first century. To represent the PCM model projections, we modified the GFDL predictions based on the model comparisons in Cayan *et al.* (2008) for summer and winter averages; we lowered the projections in each grid cell by 2.5° C for the July maximum temperature and increased the projections in each grid cell by 2.1° C for the January minimum temperature. The HSM developed using the existing climate variables was then applied to the climate variables averaged from the 2070–2099 PCM and GFDL projections.

3.2.2 Future Habitat Loss and Fragmentation

Even within areas targeted for conservation, habitat loss will continue under existing multi-species conservation plans. For example, the City of San Diego's Multi-Species Conservation Program (City of San Diego 1997) allows development on private lands up to 25% of the parcel, with an overall goal of 90% preservation considering strategic acquisitions to augment publicly owned lands. As an example for a single species (*Ceanothus verrucosus*), the San Diego Association of Government's assessment of developable land identifies approximately 33% of the occupied habitat as developable (http://www.sandag.org/resources/maps_and_gis/gis_downloads/land.asp).

To compare results across species, we evaluated the loss of 20% of the habitat area for each of the four study species. We implemented two scenarios representing widespread conservation strategies: 1) preserving the most connected habitat, and 2) preserving the largest habitat patches. The most connected patches were determined based on distance to the nearest patch. All populations identified for loss under both scenarios were removed from the models. This is a worst-case scenario, as all converted habitat is removed at the onset of the simulation (rather than incrementally).

3.2.3 Fire Regime and Fire History

Fire is an important driver of ecosystem processes in MTEs (Dallman 1998), but fire regimes altered by anthropogenic influences threaten species persistence (Zedler 1995). Humans alter fire regimes in MTEs primarily through increased ignitions leading to shortened fire intervals, but also through fire suppression or reduction in ignitions (Zedler *et al.* 1983; Keeley and Fotheringham 2003; Syphard *et al.* 2007a). Syphard *et al.* (2009) found in MTEs worldwide that fire occurrence increased with human population density until it reached a threshold from where it declined with further increases in population density, due in part to habitat fragmentation disrupting fuel continuity. This is the case within our study area. Even though the study area is only about 20 km east to west and 70 km north to south, the inland portion faces the risk of shortened fire return intervals, while the coastal portion faces risks of extended fire return intervals.

Increased ignitions and fire suppression are unmistakably important in explaining changing fire regimes, but a number of studies implicate climate change as well (Piñol *et al.* 1998; Pausas

2004; Westerling and Bryant 2008). While weather—both climate averages and extreme events—is a significant determinant of fire regimes, it is not necessarily clear how fire regimes will change with changing climate. Pausas (2004) and Piñol *et al.* (1998) have documented increased fire frequency with increasing temperatures and decreasing summer rainfall (while average annual precipitation stayed the same). Westerling and Bryant (2008), on the other hand, concluded that where fire regimes are dependent on the rate of accumulation of biomass, fires can occur more frequently with greater rainfall. Extreme weather (low humidity and high winds) is a major predictor of fire size in southern California chaparral, but the effect of antecedent weather is less clear (Keeley 2004; Littell *et al.* 2009). While drought severity and precipitation are important predictors, extreme weather may explain more of the variability in annual area burned (Littell *et al.* 2009), and extreme events are poorly modeled by global climate models (Field *et al.* 1999). Because of this dependence on extreme events, the effects of climate change on fire regime are difficult to predict; in other words, while fire risks are expected to be altered, the specific alterations of fire regimes remain unclear (Smith *et al.* 2004).

Fire is the primary disturbance regime in the shrubland systems of southern California (Syphard *et. al.* 2006). Fire intervals in chaparral vary widely, and the community type is thought to be resilient to a wide range of fire intervals, with historic intervals ranging from 30 to more than 100 years depending on the life history of the species involved (Keeley 1992; Zedler 1995; Keeley 2007). Fires that burn very frequently (fire return interval less than 5 years) are likely to be patchy and are not considered to represent the typical stand-replacing chaparral fire (Sampson 1944; Hedrick 1951; Zedler *et al.* 1983). Human activities are correlated with significant changes in the historic fire regimes of southern California's wildland urban interface (Syphard *et. al*. 2007); it is this matrix that characterizes the study area. The management of fire, through suppression or prescribed burning, is the primary management action in this habitat (Cabrillo National Monument 2008). Accordingly, a range of fire-return-interval scenarios were tested to evaluate altered fire regimes and proposed management. The average 35-year interval reflecting existing conditions (Polakaw *et al.* 1999) was used to represent the management recommendation for this habitat type by the Park Service and Navy (Cabrillo National Monument 2008). To evaluate a range of conditions representing shortened and extended fire return intervals, six average intervals were tested in addition to the existing conditions: 10, 20, 50, 65, 80, and 120 years.

The fire history of the study landscape came from the California Department of Forestry and Fire Protection's (CAL FIRE's) compilation of a 94-year interagency fire history. The minimum mapping unit for CAL FIRE fires is 300 acres; the minimum mapping unit for the U.S. Forest Service and other federal agencies is 10 acres (Fire and Resource Assessment Program). GIS coverages of time since last fire and total fires in the period of record extracted by the San Diego State University Geography Department were provided for our use (Caitlin Chason unpublished data). Statistics quantifying fire frequency and time since last fire were developed for our habitat patches.

3.2.4 Vegetation Data

The most recent vegetation maps available for the study area were developed in 1995 (http://www.sandag.org/resources/maps_and_gis/gis_downloads/senlu.asp). Rapid development in the study area necessitated map updates to reflect land use conversion, but based on the accuracy assessment of the 1995 vegetation map for coastal scrub habitats (Stow *et al.* 1993), no further field verification of vegetation classification was done.

All polygons of natural habitats from the 1995 vegetation coverage larger than 4 ha were evaluated against current aerial photography and updated to reflect land converted to development or agricultural uses (Fig 11). We used vegetation data to update historic population maps for *Ceanothus verrucosus* by removing developed land and in defining habitat for *Neotoma macrotis* by limiting suitable habitat to woody habitat types.

Figure 11. Vegetation map update. Vegetation polygons over 2005 aerial imagery. Light green polygons were mapped as natural habitat in 1995 and were shown as developed on the 2005 imagery.

3.2.5 Patch Isolation

To develop patch isolation data, we reviewed records from the County of San Diego, University of California (UC) San Diego, UC Santa Barbara, San Diego State University (SDSU), San Diego Historical Society, and the State of California Farmland Mapping and Monitoring Program (FMMP) to identify potential data sources. We considered both maps and aerial photography.

Sources were found for 1953 (photo mosaic, University of California, Santa Barbara Map and Imagery Library); 1974 (Orthophoto mosaic, County of San Diego); 1984 (GIS maps, California Farmland Mapping and Monitoring program); and 1995 (GIS map, SANDAG).

We developed GIS layers for each year identifying natural habitats, agricultural lands, and urban development. We determined time since isolation, defined as the number of years since patches encompassed 100 ha or more, by overlaying the current vegetation map with GIS layers for 1953, 1974, 1984, and 1995.

3.3 Habitat Suitability Models—Current and Future Spatial Distributions

Knowledge of past, present, and future species distribution is fundamental to conservation planning (Elith *et al.* 2010). Such planning must consider both occupied habitat (current species distribution) and suitable habitat (both occupied habitat and unoccupied habitat with the same

physical environmental characteristics). We used both in our spatially explicit metapopulation models. Consideration of suitable habitat (both occupied and unoccupied) allowed us to evaluate the effects of existing stressors such as habitat loss and fragmentation and altered fire regimes, which may increase the likelihood of patch extirpation, while altered suitable habitat configurations may compromise a species' ability to recolonize habitat patches.

In a few cases, particularly for rare species, comprehensive distribution information may be known and mapped. More commonly, however, species distribution information is incomplete. The development and application of models to predict species distributions has expanded greatly over the last 20 years (Franklin 1995; Guisan and Zimmerman 2000; Guisan and Thuiller 2005).

We developed suitable habitat predictions using HSMs, which use known locations of species occurrence, and sometimes known absences, along with environmental predictors, such as soils, slope, and climatic variables (Franklin 1995), to estimate a species-realized niche (Hutchinson 1957). We used species survey data, land use change scenarios, and HSMs linked to future climate projections to project current and future spatial distributions of our study species (Lawson *et al.* 2010). The species occurrence data came from a number of sources (Table 1) including recent surveys, historical surveys, and museum specimens. The distribution of the woodrat was based entirely on HSM results because we had only occurrence locations and not habitat maps, while for the other species we used HSM results to identify potentially suitable unoccupied habitat. The study area contains the entire U.S. range of *Chorizanthe verrucosus* and *Chorizanthe orcuttiana* and more than 99% of the range of *Quercus dumosa*. *Neotoma macrotis* is much more widespread. While the ranges of all four study species except *C. orcuttiana* extend into Baja California, our study is limited to the U.S. portion of the ranges due to a paucity of species distribution and environmental data for Baja California. Figure 2 shows the distribution of the study species within the study area.

Table 1. Sources for species occurrence data and the number of subpopulations or, in the case of *N. macrotis*, species occurrence points from museum specimens.

Species	Source	n subpopulations[a]/ data points[b]
Ceanothus verrucosus	1. California Natural Diversity Database (CNDDB) (California Department of Fish and Game 2005) 2. Field Surveys (Appendix E)	151[a]
Chorizanthe orcuttiana	1. Bauder 2005 2. Dept. of Navy unpublished data 3. San Diego Natural History Museum unpublished data	6[a]
Quercus dumosa	1. Fred Roberts unpublished data 2. CNLMN unpublished data 3. TDI 2007 4. Dossey and Associates 2006 5. Field Surveys (Appendix E)	188[a]
Neotoma macrotis	1. San Diego County Mammal Atlas, unpublished data 2. Scott Tremor, personal communication	251[b]

The HSMs were developed using Maxent software (Phillips *et al.* 2006). Maxent uses maximum entropy to develop a probability distribution, which is an index of habitat suitability. We chose Maxent because it more effectively discriminates between suitable and unsuitable habitat using only species presence data than do other modeling techniques (Elith *et al.* 2006). In our HSMs we used explanatory variables to represent resource gradients and environmental regimes embodying the following limiting factors shown to be important predictors of species distributions in southern California (Franklin 1998). Resolution and source of these variables are shown in Table 2.

- Summer and winter topographically distributed potential solar insolation (summer insolation and winter insolation).
- Slope.
- January average minimum temperature.
- July average maximum temperature.
- Average annual precipitation.
- Soils.
- Available water holding capacity.
- Topographic moisture index (Syphard and Franklin 2010).

Table 2. Resolution and source for variables used in the HSMs.

Description	Resolution	Source	
Elevation, aspect, slope, topographic moisture index	30 m^2	U.S. Geological Survey Digital Elevation Model (DEM)	http://eros.usgs.gov/products/elevation/dem.php
Annual precipitation, minimum January and maximum July temperature	1 km^2	Interpolated from climate station data 1966-1995	J. Michaelsen (UCSB) unpublished data
Soil order	1:20,000	Natural Resources Conservation Service (NRCS) digital maps	http://soils.usda.gov/survey/online_surveys/california/
Available water holding capacity	1:250,000	State Soil Geographic Data Base (STATSGO) NRCS	http://soils.usda.gov/survey/geography/statsgo/

The topographic moisture index is based on the summed area of upslope pixels that drain into a given cell in a digital elevation model scaled by the slope of the pixel (Beven and Kirkby 1979). Elevation, aspect, and slope are often important in predicting plant species distributions, but because they represent indirect resource gradients they generally have less explanatory power than variables that are more directly tied to resource availability, such as the topographic moisture index (Miller and Franklin 2002). The spatial extent of the models—an area of approximately 15,532 km^2—is shown in Figure 12 with reference to the study area. To evaluate the potential effects of projected future climate change we first modeled habitat suitability under the current climate; then we used that model as the basis for predicting the distribution of suitable habitat under alternative future climate projections using Maxent (Phillips & Dudik 2008). The specifics for each species follow.

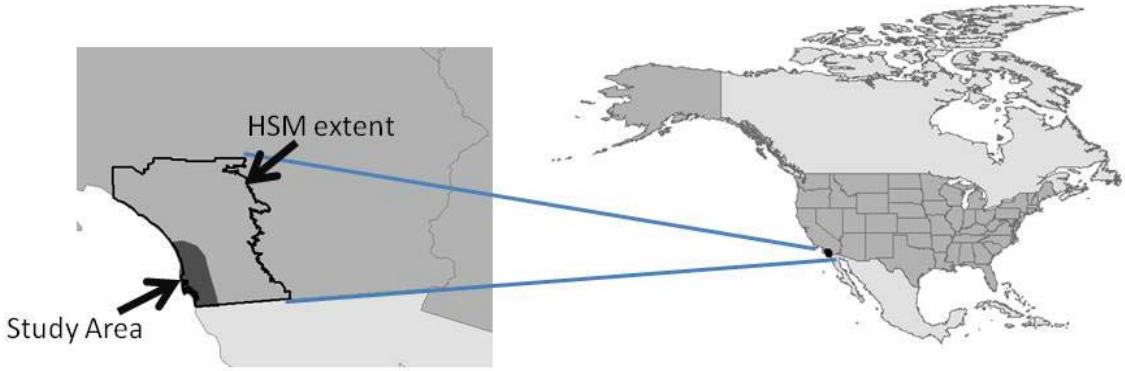


Figure 12. Location of study area in southwestern California and the spatial extent of the habitat suitability models (HSMs).

One problem that arises with modeling coastal populations with distributions right along the coast is that, if the environmental data are of low resolution and the coastline is angled, the cells that make up the raster files of the explanatory data may form a stair-step pattern and leave data gaps, resulting in missing data values for some species observations. Some of the data points representing occurrences of all four study species were in areas affected by this problem, resulting in missing environmental data and making it impossible to use a given data point for modeling. Excluding these data points alters the results of the models (unpublished data). We manually moved data points to the nearest location with coverage of all environmental layers (e.g., one grid cell inland) or manually added the values of the missing environmental data from the nearest pixel with coverage to the presence data using the "samples with data" input format (Phillips 2006). Moreover, when using the projections of habitat suitability under future climate scenarios, habitat patches included in the models based on direct mapping along the coast—but that could not be modeled due to missing data—were manually ranked as suitable or unsuitable based on the adjacent habitat that was modeled.

We used the area under the curve (AUC) for receiver-operating characteristic (ROC) plots, a common measure of model accuracy, to evaluate model performance. ROC plots graph true positives against false positives. The AUC value is the proportion of the time that a randomly selected group from the positives scores higher than a randomly selected group from the negatives. Values range from 0.5 to 1 (Fielding and Bell 1997).

A logistic threshold was used to distinguish suitable from unsuitable habitat. The Maxent model produces continuous output representing probability of species occurrence or habitat suitability. Consequently, a threshold must be selected to distinguish between suitable and unsuitable habitat for use in our population demographic models. For all species we selected a threshold that maximized the sum of model sensitivity (true positives) and specificity (background) estimated from the training data (Allouche *et. al*. 2006). Because we had no observations of absence, "negatives" actually represented background.

To evaluate which variables are most important in explaining the species distribution, we used the percent contribution to model gain from the Maxent results. The percent contribution is

estimated by adding the regularized gain (average log probability of the presence samples minus a constant) or subtracting the loss in each of the model iterations as the model is being trained, and converting these to percentages at the end. We looked at natural breaks in the range of percent contribution to model gain and included variables that contributed more than 3%.

3.3.1 *Ceanothus verrucosus* HSM

The U.S. portion of the range (Figure 2) extends approximately 70 km north of the U.S. border with Mexico and includes 151 subpopulations (greater than 0.25 ha and separated by more than 44 meters) totaling 4,311 hectares (California Department of Fish and Game 2005; Lawson 2009). We updated habitat maps (California Department of Fish and Game 2005) using aerial photography and field surveys and estimated population sizes through direct counts or density estimates, resulting in a complete inventory of the known U.S. population.

The HSM for the current distribution was based on a total of 88 presence-only data points; 75% were randomly selected for training and 25% were used for testing the Maxent model (Lawson *et al.* 2010). The data points were generated by randomly selecting points within existing patches averaging one per 5 ha with a minimum of one point per patch. Populations in close proximity to each other—derived from the fragmentation of larger natural populations—were grouped based on population boundaries in the California Natural Diversity Database (California Department of Fish and Game 2005) so that highly fragmented populations were not overrepresented in the model. To represent extirpated stands, we included documented historic locations more than 100 m from extant populations (Taylor 2004). This added 19 data points.

To evaluate the potential effects of projected future climate change, we used the Maxent models developed above to estimate habitat suitability under the current climate as the basis for predicting the distribution of suitable habitat under alternative future climate projections (Pearson and Dawson 2003; Thomas *et al.* 2004; Lawson *et al.* 2010).

3.3.2 *Quercus dumosa* HSM

Our study focuses on the U.S. portion of the range, which extends approximately 85 km north of the U.S. border with Mexico and 20 km inland from the coast (Figure 2), and comprises 188 subpopulations (greater than 0.01 ha and separated by more than 44 meters) totaling 671 ha. We used detailed population maps with population counts for most of the U.S. range (Roberts unpublished data) supplemented by location-specific survey reports for some conservation lands and military installations (Dossey and Associates 2006; TDI 2007, CNLM unpublished data). We updated these maps using aerial photography and field surveys, and we estimated population sizes through direct counts or density estimates where sizes were not included in survey results and added several unrecorded populations, resulting in a complete inventory of the known U.S. population.

The HSM for the current distribution was a presence-only model based on a total of 83 data points; 75% were randomly selected for training and 25% were used for testing the model. The data points were generated by randomly selecting points within existing patches averaging one per 5 ha with a minimum of one point per patch. Populations within 250 meters of each other were grouped so that highly fragmented populations were not overrepresented in the model.

3.3.3 *Chorizanthe orcuttiana* HSM

Our study includes all known populations, which extend approximately 40 km from Point Loma, near downtown San Diego, north to Encinitas. Known populations occur within 3 km of the

coast and comprise six subpopulations separated by more than 175 meters. The populations range from around 10 m^2 to 1,000 m^2 in area and total 0.25 hectare. We used detailed population maps with population counts (Bauder 2005; Department of the Navy unpublished data) as a complete inventory of the known U.S. population.

The HSM for the current distribution was a presence-only model based on a total of 17 data points; 75% were randomly selected for training and 25% were used for testing the model. The data points were generated using the center point of existing populations and documented historic locations more than 100 m from extant populations (California Department of Fish and Game 2005; SDNHM unpublished data).

3.3.4 *Neotoma macrotis* HSM

The HSM for the current distribution was a presence-only model based on a total of 251 occurrence points; 75% were randomly selected for training and 25% were used for testing the model. The occurrence points were compiled by the San Diego Mammal Atlas from existing information and field surveys (San Diego County Mammal Atlas unpublished data; Scott Tremor pers. comm.). This dataset predicted a very widespread distribution, but because the species is known primarily from woody habitats (Schwilk and Keeley 1998; Kelly 1990; Matocq 2002; Braswell 2007), we constrained its distribution to the current distribution of woody habitats.

3.4 Population Demographic Models

We developed stochastic age- and stage-based matrix population models and linked them to the spatial arrangement of patches and stochastic fire functions using RAMAS GIS® (Akçakaya 2005). Stochasticity was incorporated through Monte Carlo simulations for 1,500 replications over a 100-year time period to account for natural variation in the fire events and the demographic rates of the population. Single population models were used with the artificial landscape and metapopulation models to evaluate metapopulation function in terms of dispersal in the real landscape. Expected minimum abundances (EMAs) across the 1,500 replications and average population trajectories and risk (probability) of quasi-extinction (QER) were used to compare across treatments (McCarthy and Thompson 2001).

Sensitivity analyses were performed on model parameters or groups of parameters generated by the same function from the stage matrix by perturbing their values. The model was deemed sensitive to a parameter if the relative difference in model output was greater than the initial extent of perturbation. Sensitivity analyses were performed using single population models except for features (e.g., dispersal) that required metapopulation models.

We incorporated stochastic fire using a Weibull function (equation 1) to model the probability of fire as a function of time since fire (Moritz 2003):

$$f(\mathrm{t}) = ct^{c-1}/b^{c}(\exp(-(t/b)^{c})) \qquad (1)$$

The b parameter is a scale parameter related to the fire return interval. c is the shape parameter, which reflects the degree to which fire hazard changes with time since fire. The shape parameter c equals 1 when fire hazard is not related to time since fire. We used parameters developed by Polakaw *et al.* (1999) for mixed chaparral along the southern California coast using data from the Santa Monica Mountains (c =1.42; b=40.26). Their b parameter reflects a 35-year fire return interval, which we used as the existing condition in our model. We calculated the other fire return intervals used with the c value of 1.42. Fire is modeled as a catastrophe. When fire occurs,

depending on the species, carrying capacity and/or vital rates are modified; summary model descriptions are provided in sections 4.4.1–4.4.1 below, and detailed descriptions are presented in Appendices A–D.

3.4.1 *Ceanothus verrucosus* Demographic Model

The model is a spatially explicit stochastic age-based matrix model using available data (Zedler *et al.* 1995; Cummins 2003), supplemented with data collected in field studies and published data for congeners. The model structure is depicted in Figure 13. *Ceanothus* is a diverse genus that includes numerous closely related species. The six congeners used to help parameterize the model are members of the subgenus *Cerastes*; all have similar life history characteristics including shade sensitivity, refractory seed, and limited seed dispersal (Conard *et al.* 1985; Keeley 2000). A biogeographical study that examined three of the congeners, *C. megacarpus, C. crassifolius* and *C. cuneatus,* identified them as ecological equivalents (Nicholson 1993). Age classes ranged from seeds to plants 92+ years old.

Initial population sizes of patches were estimated using average densities from field surveys (Lawson 2010). Stand age is equal to time since last fire. Because *C. verrucosus* primarily forms even-aged cohorts, the age class of the initial population reflected the last recorded fire. Initial seedbank abundance was estimated by multiplying the average number of seeds per individual for each age class by the population size. Seed numbers were excluded from simulated population totals.

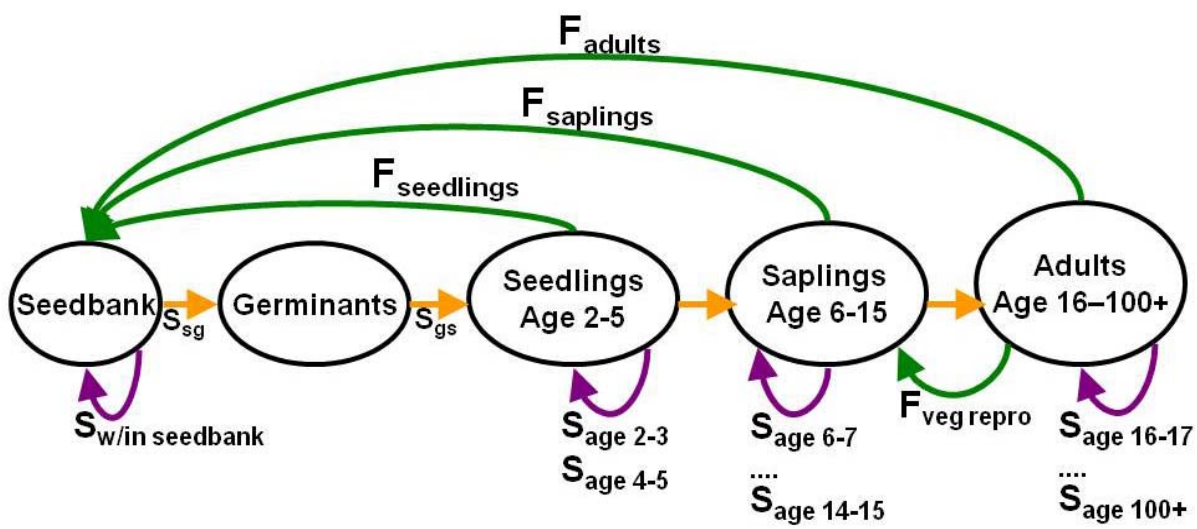


Figure 13. *Ceanothus verrucosus* demographic model structure. F=fecundities; S=survivals.

3.4.2 *Quercus dumosa* Demographic Model

The model was constructed with data from congeners. *Quercus* is a diverse genus comprising 23 species in California (CALFLORA) and is divided into three subgenera. Data from nine oak species (four from California, three from the Mediterranean, and two from Florida) and one obligate seeding shrub (*Malosma laurina*) were used to parameterize this model. The historical literature does not distinguish *Q. dumosa* from several other California scrub oaks: *Q. turbinella,*

Q. john-tuckeri, Q. cornelius-mulleri, Q. berberidifolia, and *Q. pacifica* (http://www.efloras.org). As a result of this lack of distinction and *Q. dumosa's* very small range, there are virtually no vital rate data published for the currently recognized taxon. Most of the data reported from the literature as *Q. dumosa* are likely to be from the taxon currently recognized as *Q. berberdifolia*.

We prioritized the data from the white oak subgenus, scrub oaks, and oaks from MTEs for use in our model. However, with the exception of fecundity and adult mortality, all the data we used were from tree oak species. To gain some compatibility between the tree oak data and *Q. dumosa* for our transitions between subadult stages, we utilized portions of datasets—those individuals growing under canopies and those severely burned by fire—that best represent closed canopy shrublands, which burn in high-intensity stand-replacing fires (Keeley *et al.* 2008).

The model is a spatially explicit stage-based matrix model structured with a 2-year time step and incorporating dispersal. Model structure is depicted in Figure 14. The first two stages are age-based and the remaining four are size-based. The model includes acorns, germinants (year of germination plus the next year), small seedlings (<15 cm height), seedlings (15–49.99 cm height), saplings (>49.99 cm height), and adults (>149.99 cm height). This structure reflects the high and variable mortality in acorns and germinants, which declines and becomes more stable in older individuals where fecundity and mortality are related more to size than to age (Silvertown and Charlesworth 2001).

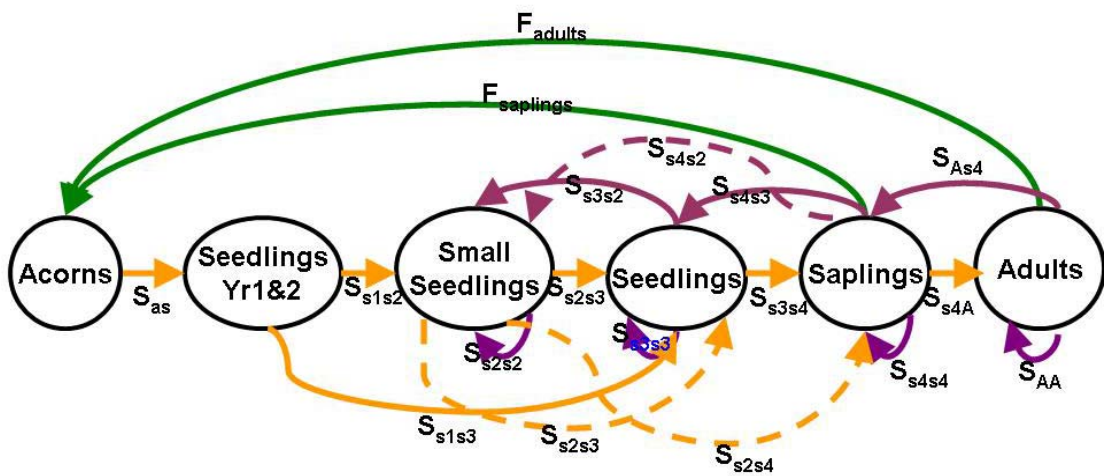


Figure 14. *Quercus dumosa* demographic model structure.

Initial population sizes of patches were estimated using average densities from field surveys to represent adults and the number of juveniles per adult from the literature to represent the other stages. Acorn numbers were excluded from simulated population totals.

In addition to the stage matrix, sensitivity analyses were performed on: 1) the maximum dispersal rate evaluating values of 0.05 and 0.15, 2) post-fire adult survival evaluating values of ±0.5% (corresponding to catastrophe matrix multipliers for adult survival of 0.9951 and 0.9850),

and 3) plant lifespan, which (adult to adult survival) was evaluated at 250 years (2-year survival of 0.9763) and 400 years (2-year survival of 0.9851).

3.4.3 *Chorizanthe orcuttiana* Demographic Model

The model was constructed with available field data for this species: 8 years of population counts, seed counts from a single year, and one set of germination trials (Bauder 2005). The model is a spatially explicit stage-based matrix model structured with a 1-year time step. Seed dispersal is assumed not to occur between subpopulations. The relevant life history characteristics for this annual plant are germination, survival to seed production, seed production, seed viability, seed predation, annual germination from the seed bank, and annual seed bank mortality. Our model is limited to two stages: a seedbank and an adult stage (Figure 15).

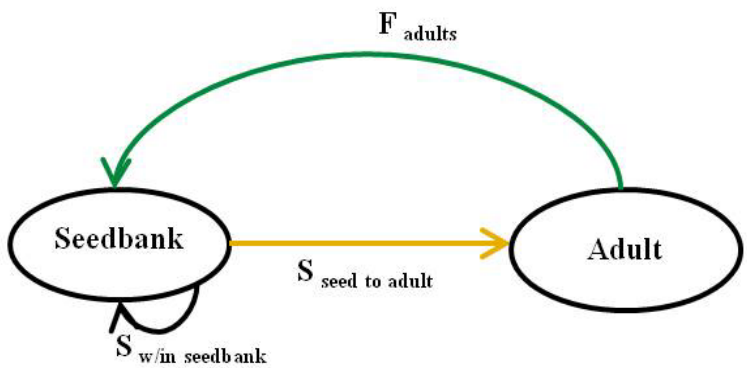


Figure 15. *Chorizanthe orcuttiana* demographic model structure.

For the model of GCGS1 (reflecting the effects of post-fire shrub canopy closure), we parameterized a decline in carrying capacity. In the simulations, carrying capacity was gradually reduced to zero over an 80-year period. When a fire occurs, the woody canopy is removed and germination of seeds from the seedbank can occur. In the model, the carrying capacity is reset to its maximum amount to reflect habitat for GCGS1 (open sandy sites) increasing immediately after fire and then decreasing over time as the canopy closes. We selected 80 years because, based on the absence of dead stems within the openings occupied by *Chorizanthe orcuttiana* on Pt. Loma, it is likely that the openings can persist this long. Fire last burned on Pt. Loma in approximately 1912 (Zedler 1995). The canopy likely closed 10–20 years later (Hanes 1971). If the canopy openings were a result of shrub ramet or genet mortality, we would expect to see the dead remnants (Keeley 1992). Indeed, we sampled stems of *Ceanothus verrucosus* at Pt. Loma that, based on ring counts, persisted for more than 70 years after death. Consequently, the lack of dead woody stems in the openings occupied by *Chorizanthe orcuttiana* means that the gaps likely date to sometime around the last fire.

For our model of GCGS2 (reflecting the effects of annual grass invasion), the initial carrying capacity was set to 10% of modeled carrying capacity to reflect a population where annual grasses are already established. As in the canopy closure scenario, fire is modeled as a catastrophe. Annual grasses are typically reduced by fire for 1–2 years, but the effects largely disappear 2–3 years after a burn (Klinger *et al.* 2006). In the time step after fire occurs, carrying capacity is restored to 100%. It is subsequently reduced in the model over a 2-year period to 10%

to reflect the temporary nature of exotic annual grass control by fire. We used 90% reduction in carrying capacity as Brooks and Berry (2006) found that annual grasses can account for up to 91% of the biomass of an annual community in an arid environment.

Initial population sizes of adults were estimated at 8.5 plants per m^2 based on observed average densities in extant populations. The number of seeds was estimated using the relative final stage abundances after a 50-year initialization period (seedbank=0.989; adults=0.011). Seed numbers were included in simulated population totals.

3.4.4 *Neotoma macrotis* Demographic Model

The model was constructed with data from a mark and recapture study of *N. macrotis* (Kelly 1990). It is a spatially explicit age-based matrix model structured with a 1-year time step and includes dispersal. It includes four 1-year age classes with a maximum age of 4 years (Figure 16). The model includes only females. Initial population sizes of 19/ha were estimated based on the literature (Kelly 1990; Matocq and Lacey 2004; Lee and Tietje 2005). We used the stable age distribution to allocate initial abundances across the stages.

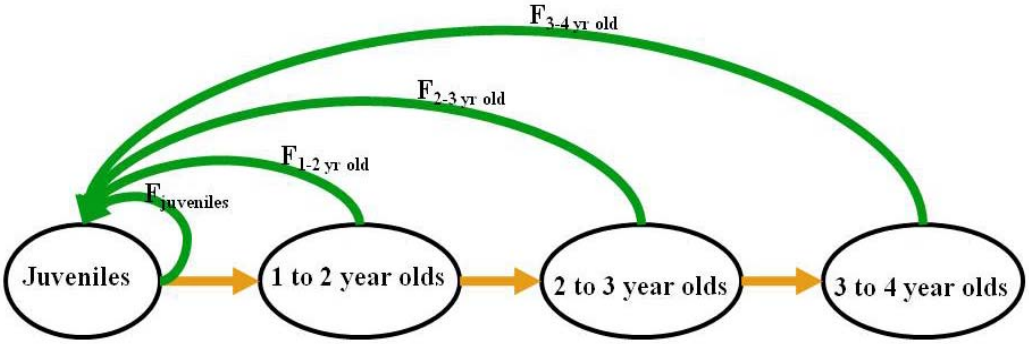


Figure 16. *Neotoma macrotis* demographic model structure.

3.5 Multi-Species Analysis

There are many well-documented problems with single species approaches to conservation (Franklin 1993; Lambeck 1997). However, integrating the information we have from single species into a standard currency to allow for multi-species approaches is problematic. Due to problems with model accuracy, it is generally accepted that results can be compared within scenarios from a given model but not between species (McCarthy *et al.* 2001; Brook *et al.* 2002; Lindenmayer *et al.* 2003; McCarthy *et al.* 2003). Nevertheless, Nicholson and Possingham (2006) have addressed this obstacle by developing multi-species objective functions that use extinction risk estimates from stochastic population models to inform multi-species management. The use of extinction risk estimates is not, however, without problems. The risk of actual extinction from models might be very rare and may not distinguish well among alternative scenarios. There are no accepted criteria for selection of thresholds to define extinction risk. We use a range of QER estimates from our models to explore the influence of different thresholds on conservation decisions. We start with the results from single population models in an artificial landscape. We then test those results in a real landscape.

3.5.1 Artificial Landscape

The artificial landscape consists of 100 cells. Each cell represents a subpopulation or habitat patch that contains one to four species. The number of cells occupied by each set of species represents the proportion of the study area occupied by that species combination when the HSM results for each species were overlaid. We created artificial landscapes for the present climate, the PCM projection for 2070–2099, and the GFDL projection for 2070 to 2099. The artificial landscape does not account for the change in the amount of habitat under future climate projections, but rather represents the relative amount of habitat occupied by each species. Because the species respond differently to fire, this variation in proportion of the landscape occupied by each species could mean that the optimal management strategy will be different under different climate scenarios. The artificial landscape provides a simplified way to consider how changes in the relative abundance of species across the landscape influences selection of the best management plan.

3.5.2 Real landscape

For the real landscape we used a portion of our study area (Figure 17) because of the need to use a scale that reflects dispersal processes and to limit the analysis to 500 populations in the study area. We configured the study area to include 100% of occupied *Chorizanthe orcuttiana* habitat, 99% of occupied *Quercus dumosa* habitat, and 96% of occupied *Ceanothus verrucosus* habitat.

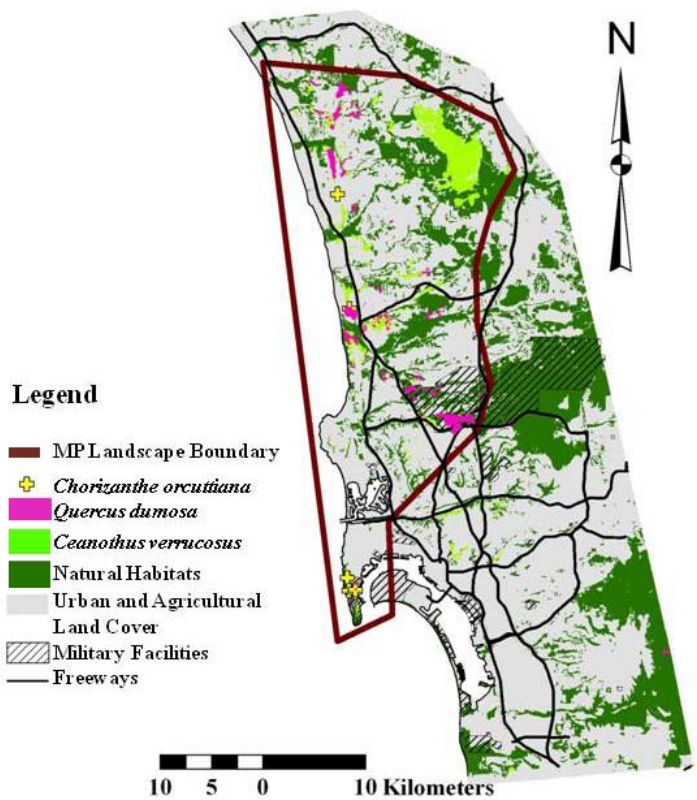


Figure 17. Boundary of the landscape (brown line) used for metapopulation models within the study area. Natural habitats within the study area = dark green; *Ceanothus verrucosus* = light

green polygons; *Chorizanthe orcuttiana* = yellow crosses; *Quercus dumosa* = polygons with magenta crosshatching.

3.5.3 Biodiversity Objective Functions

There are multiple possible formulations of conservation objectives that meet the general goal of *biodiversity conservation*. The choice can influence the rankings of management scenarios (Nicholson and Possingham 2006). We evaluated management scenarios using four different objective functions (Table 3.1) to reveal tradeoffs among objectives. Two use absolute estimates of extinction risk (equations 1 and 2), and two use values relative to the scenario with the lowest extinction risk per species (equations 3 and 4). Only equation 1 takes overlap among species distributions into account. The simplest computationally was minimizing the expected number of extinctions. For this we summed QERs within a patch and then summed the patches across the landscape. The second, reflecting the species composition of each patch, minimized the joint probability of all species going extinct. This involved calculating the product of the QERs within a patch and then summing those values across the landscape. The third, minimizing the increase in expected extinctions, used the difference in QER between the scenario under evaluation and the best scenario for that species and summed these within patches and then across the landscape. The fourth, minimizing the proportional increase in extinction risk, involved calculating the quotient of the QER of the scenario under evaluation and the best scenario for the species and then summing these within a patch and across the landscape. These functions assume that extinction risks are independent across patches and species. However, while it is unlikely that extinction risks are completely uncorrelated, incorporating dependencies is problematic because they are unknown for most systems (Sarkar *et al.* 2004) and not feasible in this case.

We compare three species sets: 1) *Ceanothus verrucosus, Quercus dumosa, and Neotoma macrotis*; 2) GCGS1 added to set 1; and 3) GCGS2 added to set 1. Because *Chorizanthe orcuttiana* does not have a known fire response, set 1 represents the complete existing set of species.

In the following functions, $p_i(x)$ is the QER across the landscape from the metapopulation models where i is the species and x is the scenario (fire return interval and present or future climate).

Table 3. Biodiversity objective functions: $p_i(x)$ is the QER for the patch in the single-species models and for the landscape in the metapopulation models, where i is the species and x is the scenario (fire return interval and present or future climate). $p_i(1)$ is the QER for the best scenario for a given species.

Description	Function
Minimize the joint probability of all species going extinct.	$minimize \prod_{i=1}^{n} p_i(x)$
Minimize the expected number of extinctions.	$minimize \sum_{i=1}^{n} p_i(x)$
Minimize the increase in the expected number of extinctions.	$minimize \sum_{i=1}^{n} [p_i(x) - p_i(1)]$

Minimize the proportional increase in extinction risk.	$minimize \sum_{i=1}^{n} \frac{p_i(x)}{p_i(1)}$

We compare management rankings using seven fire management scenarios, expressed as average fire return interval (FRI), for each of three climate scenarios and each of three species sets (Table 4).

Table 4. Scenarios evaluated.

Scenarios																				
Species set 1	***Ceanothus verrucosus, Quercus dumosa, Neotoma macrotis***																			
Climate scenarios	Present							PCM (2070-2099)							GFDL (2070-2099)						
Average fire return intervals	10	20	35	50	65	80	120	10	20	35	50	65	80	120	10	20	35	50	65	80	120
Species set 2	***Ceanothus verrucosus, Quercus dumosa, Neotoma macrotis,* Gap-Closure**																			
Climate scenarios	Present							PCM (2070-2099)							GFDL (2070-2099)						
Average fire return intervals	10	20	35	50	65	80	120	10	20	35	50	65	80	120	10	20	35	50	65	80	120
Species set 3	***Ceanothus verrucosus, Quercus dumosa, Neotoma macrotis,* Exotic-Competition**																			
Climate scenarios	Present							PCM (2070-2099)							GFDL (2070-2099)						
Average fire return intervals	10	20	35	50	65	80	120	10	20	35	50	65	80	120	10	20	35	50	65	80	120

4.0 Results and Accomplishments

4.1 Vegetation Map and Patch Isolation

In 1995, 40,122 ha of vegetation were mapped as sage and scrub habitats within the study area. Between 1995 and 2005, 2704 ha of natural habitats within the study area had been converted to development or agriculture. Figure 18 shows the updated vegetation map.

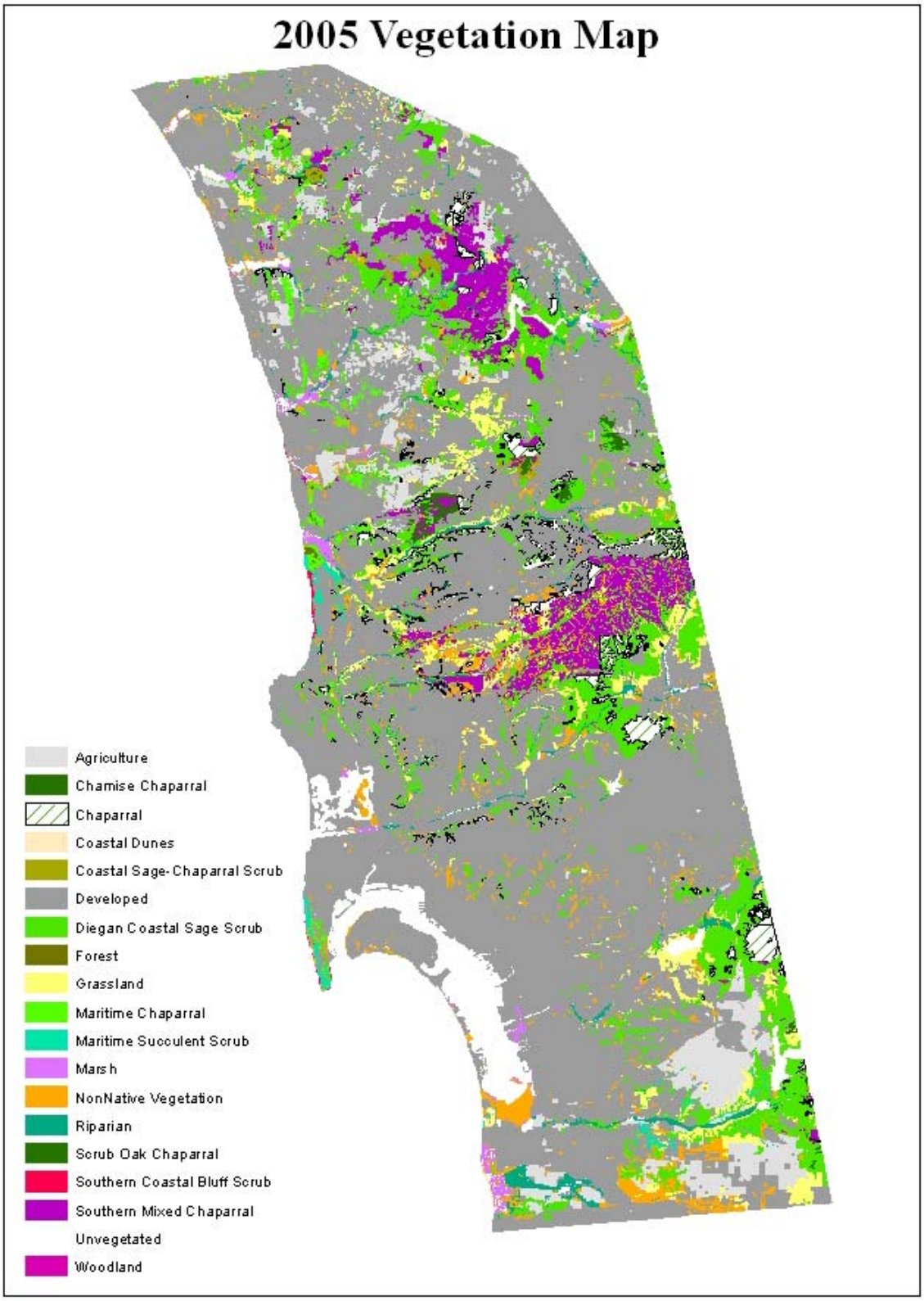


Figure 18. Vegetation map of study area 2005.

Figure 19 shows the increasingly fragmented natural habitats from 1953 to 2005; Table 5 shows patch statistics for each of the years. The area of natural habitats was reduced by approximately half over this time period, while the number of patches increased by a factor of almost 40. Mean patch size decreased by a factor of almost 70, and the perimeter-to-area ratio increased by an order of magnitude. The lack of a sizable difference between the 1984 and 1995 estimates of natural areas is likely due to errors in the 1984 map. Small polygons—often canyons or other unbuildable slopes—were not differentiated in the Farmland Mapping and Monitoring data. In addition, several large polygons were mapped as developed or agriculture in 1984 and as natural vegetation in 1995. These were either mapping errors or agricultural areas that recovered to natural vegetation. Figure 20 depicts isolation of landscape elements by showing the length of time that patches of vegetation in the current landscape have existed as patches smaller than 100 hectares in size. Approximately 30% of the patches in this landscape have been smaller than 100 ha for more than 54 years. *Neotoma macrotis* does not appear to exist in long-isolated patches; this may be due to dispersal barriers preventing the reestablishment of extirpated populations in suitable habitat (Bolger *et al.* 1997), given that 30% of the landscape consists of habitat fragments that have been smaller than 100 ha for more than 50 years.

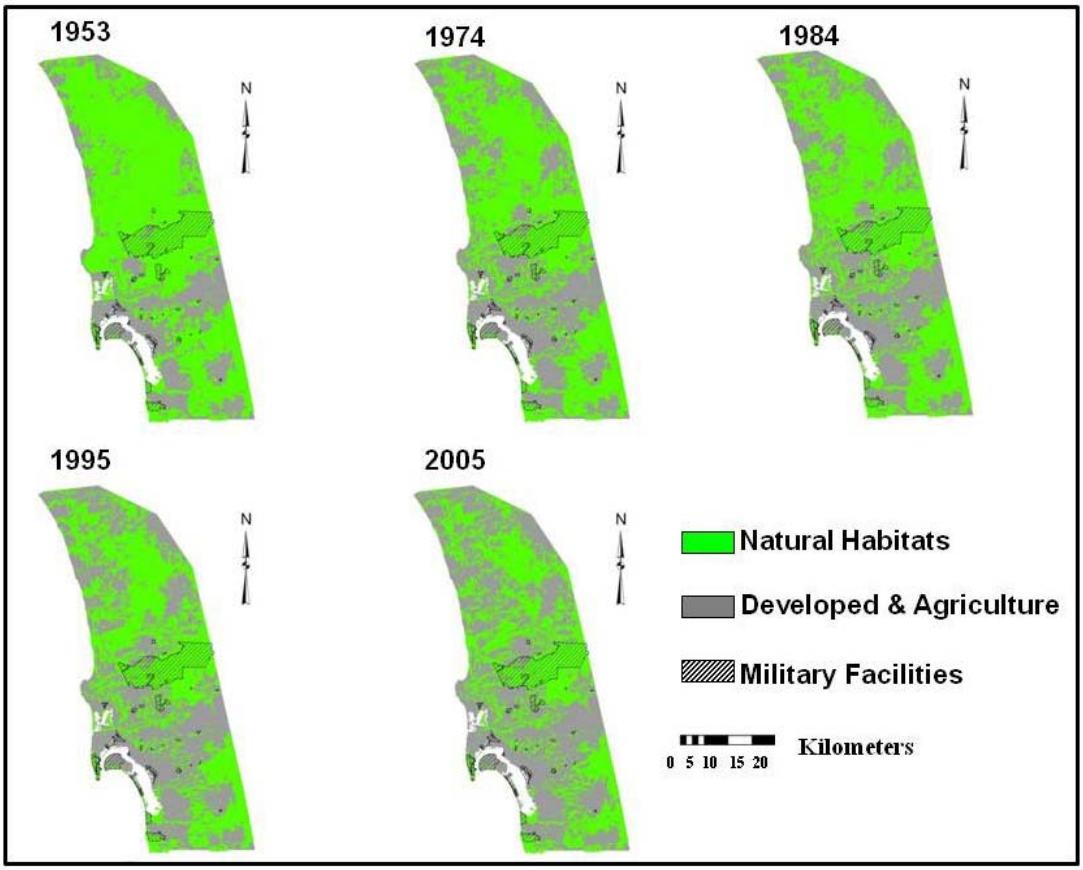


Figure 19. Natural habitat maps of study area—1953, 1974, 1984, 1995, and 2005.

Table 5. Patch statistics by year of mapping.

		Size(Ha)			Perimeter/Area Ratio	
Year	N	Sum	Mean	StdDev	Mean	StdDev
2005	2,047	58,265	28.5	330.9	0.022	0.055
1995	1,655	68,568	41.4	554.7	0.017	0.022
1984	313	68,019	217.3	1,393.0	0.046	0.071
1974	396	86,716	219.0	2,503.2	0.020	0.012
1953	54	102,888	1,905.3	11,336.7	0.005	0.005

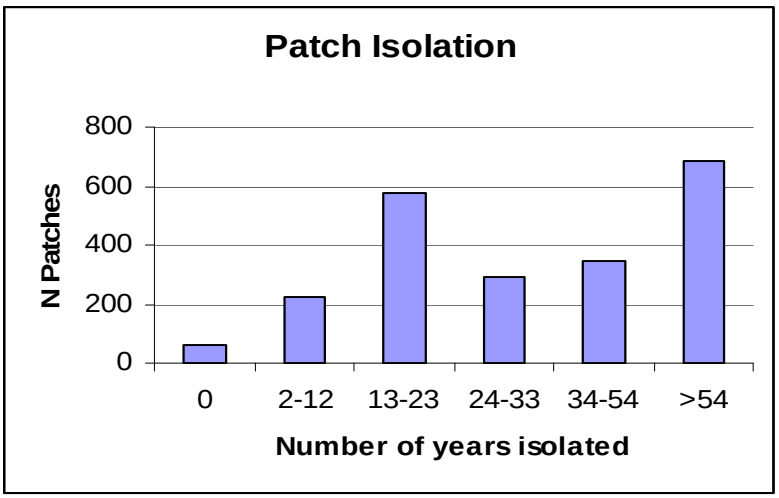


Figure 20. Isolation of patches of habitat in the current landscape in terms of the number of years since the patches were 100 hectares or more in size.

4.2 Habitat Suitability Models

The HSMs predicted habitat contractions and virtually no habitat shifts (habitat predicted suitable in presently unsuitable locations) for three of the four study species (Table 6). Only the predictions for *Chorizanthe orcuttiana* show expanding and shifting habitat.

Table 6. Habitat predictions. The upper half of the table shows habitat predictions under the present climate and future climate change projections. The lower half of the table shows predictions of future habitat shifts, where habitat not predicted suitable under the present climate is predicted suitable under future climate scenarios. These projections use the logistic threshold that maximizes the sum of model sensitivity (true positives) and specificity (background) estimated from the training data for each species.

	Ceanothus verrucosus		*Chorizanthe orcuttiana*		*Neotoma macrotis*		*Quercus Dumosa*	
Logistic threshold	*0.221*		*0.11*		*0.337*		*0.24*	
Habitat Projections within Study Area	Area (ha)	% of Area Predicted under Present Climate	Area (ha)	% of Area Predicted under Present Climate	Area (ha)	% of Area Predicted under Present Climate	Area (ha)	% of Area Predicted under Present Climate
Present Climate	37,727		22,075		34,202		23,908	
PCM Climate Scenario 2070-2099	6,107	16%	28,153	128%	266	1%	9,893	41%
GFDL Climate Scenario 2070-2099	830	2%	8,039	36%	64	0%	1,164	5%
Habitat Shifts								
Suitable under PCM climate scenario but not under Present Climate	34	0%	6366	29%	55	0%	225	1%
Suitable under GFDL climate scenario but not under Present Climate	1	0%	8	0%	10	0%	3	0%

It is interesting to note that *Chorizanthe orcuttiana*—the species considered the most endangered at this time (critically imperiled) (NatureServe 2010)—is projected to benefit under these models, while *Neotoma macrotis*—the least endangered species at this time (secure) (NatureServe 2010)—is expected to decline the most (Table 6). The other two species projections reflect projections contracting up against the coastline (Figures 16 and 18, a pattern projected for other coastal MTE species (Loarie *et al.* 2008). Examination of the temperature variables underlying the Maxent prediction for *Neotoma macrotis* reveals the reason for its predicted contraction. In this case, the overlap between suitable minimum January and maximum July temperatures is dramatically reduced (Figure 21). In our study area the summer is too hot except on the coast and in the mountains, and the winter is too hot except in the mountains.

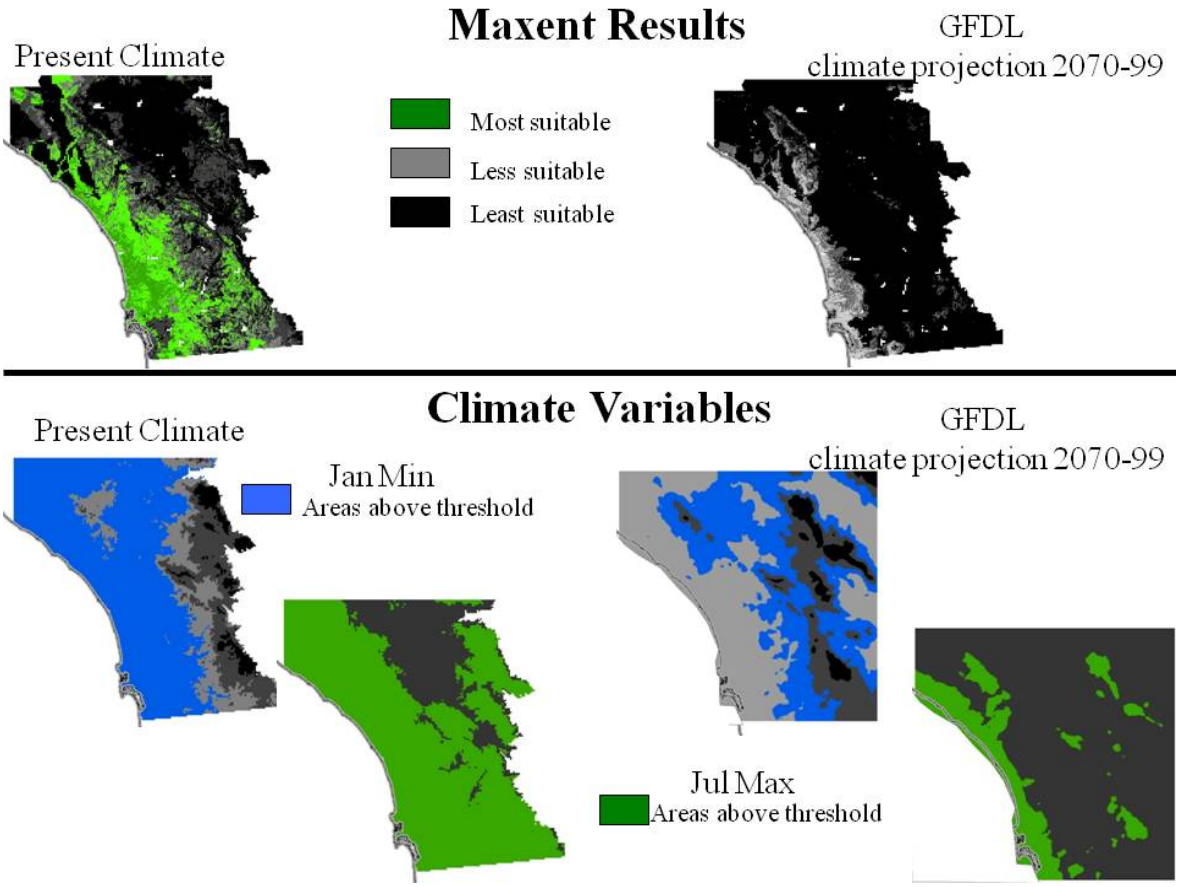


Figure 21. Maxent projections for *Neotoma macrotis* and underlying climate variables using a 0.337 logistic threshold for habitat suitability for the present and future climate projected under the GFDL model. Shows declining overlap in climate variables required for suitable habitat predictions.

4.2.1 *Ceanothus verrucosus*

Figure 22 shows habitat suitability predictions for the current climate and for the two alternative climate change models. Five variables—January minimum temperature, July maximum temperature, soil, available water holding capacity and slope—were important in predicting the distribution of the species (Table 2). Three variables were dropped: precipitation and winter insolation contributed less than 1% to the model and topographic moisture index contributed nothing. The model rerun with the most important variables had an AUC value for the test data of 0.944 and resulted in the values of percent contribution to model variance listed in Table 7.

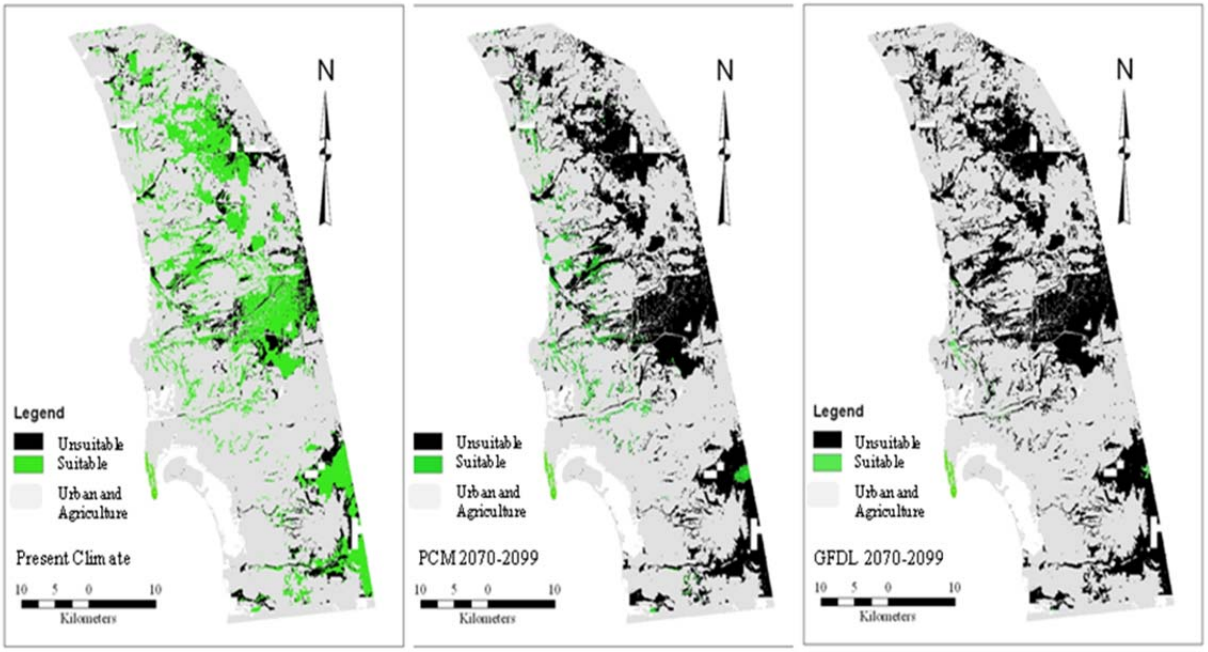


Figure 22. Suitable and unsuitable *Ceanothus verrucosus* habitat under the current and two projected future climate scenarios using a threshold of 0.221 with the Maxent output.

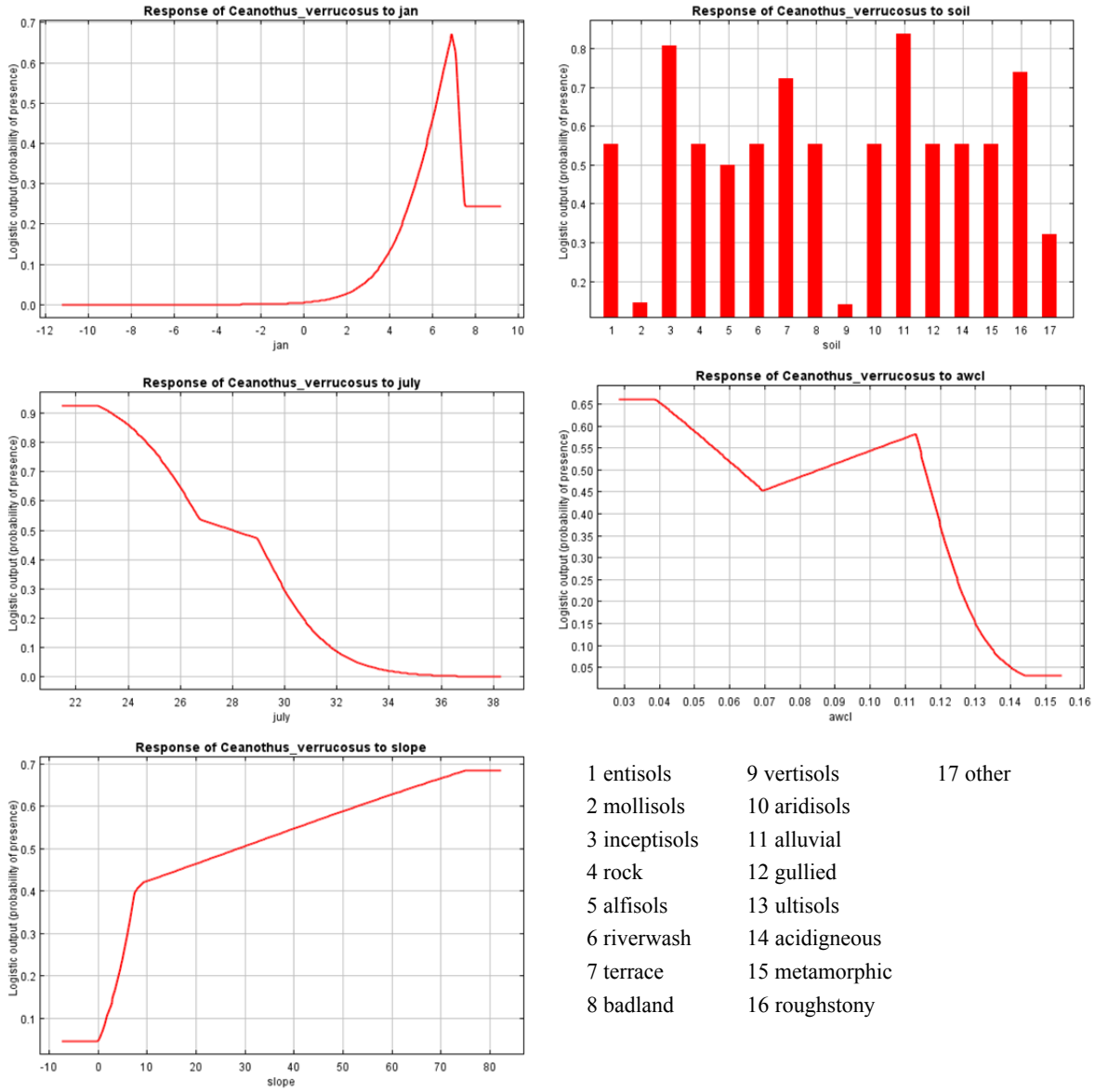
Table 7. Influential variables in predicting habitat suitability for *C. verrucosus* and their relative contribution to model gain (average log probability of the presence samples minus a constant) during the model run.

Variable	Percent Contribution
Minimum January Temp	42.3
Soil type	23.9
Maximum July Temp	21.8
Slope	7.5
Soil Water Holding Capacity	4.5

Both climate change models result in a predicted loss of suitable habitat for this species. Suitable habitat, estimated using the thresholds described in Table 6, declined by 84% under the PCM climate scenario and 98% under the GFDL scenario (Table 6 and Figure 22).

The response curves (Figure 23) show how the habitat suitability prediction changes with changes in each predictor variable as the others are held at their average values. *C. verrucosus* is predicted to occur in a narrow minimum January temperature range with an optimum around 7°C, and habitat suitability declines rapidly above and below the optimum. The soil orders associated with the highest habitat suitability include inceptisols, terrace soils, alluvial soils, and rough stony land. Mollisols and vertisols are associated with very low habitat suitability. Habitat suitability is highest where July temperatures are lowest—around 22°C—and declines steadily

approaching zero suitability around 35°C. The response curves show high suitability over a broad range of the soil water holding capacity within the landscape (0.03–0.11), but suitability drops precipitously after that. *C. verrucosus* is predicted to occur on slopes from 10 to 80° with habitat suitability increasing with slope.



1 entisols	9 vertisols	17 other
2 mollisols	10 aridisols	
3 inceptisols	11 alluvial	
4 rock	12 gullied	
5 alfisols	13 ultisols	
6 riverwash	14 acidigneous	
7 terrace	15 metamorphic	
8 badland	16 roughstony	

Figure 23. Response curves for each variable in the *C. verrucosus* habitat suitability model with the other variables held at their average values.

Seedlings of *C. verrucosus* are likely to be the most vulnerable life stage to climate change (Morris *et al.* 2008); due to the infrequent, episodic nature of recruitment tied to fire, habitat may become unsuitable long before a population is extirpated. This has two important implications for HSMs and their use in forecasting species distributions. The first is that due to climate change within the species' range during the twentieth century (Western Regional Climate Center

2009a), this HSM may be based on presence locations that are no longer suitable. The second is that there may be a lag in patch extirpation so that the patch may persist long after it is projected to be unsuitable habitat, causing the projections to appear incorrect when they are not. One of the shortcomings with HSMs is that they do not account for competition; however, interspecific competition is likely to be important within the *Ceanothus* genus (Nicholson 1993) and is anticipated to influence its response to climate change.

4.2.2 Quercus dumosa

Figure 24 shows habitat suitability predictions for the current climate and the two alternative climate scenarios. Both climate change scenarios result in a predicted loss of suitable habitat for this species. Suitable habitat declined by 59% under the PCM climate scenario and 95% under the GFDL scenario compared to the suitable habitat predicted under the current climate (Table 6). Neither of the climate projections resulted in habitat shifts; only a negligible amount of suitable habitat emerged on sites that did not previously support it (Table 6).

It is less clear for this species than for *Ceanothus verrucosus* that its distribution is controlled by climate variables, although a number of climate variables have been shown to be important to Mediterranean oaks, including drought length, summer precipitation, and temperature (Sharp and Sprague 1967;Purves *et al.* 2007). However, *Q. dumosa* is likely to be much less vulnerable to climate change than *Ceanothus verrucosus* because of its longevity, fire survival, and lack of reliance on seedlings for stand regeneration after fire (Keeley 1992, 1993).

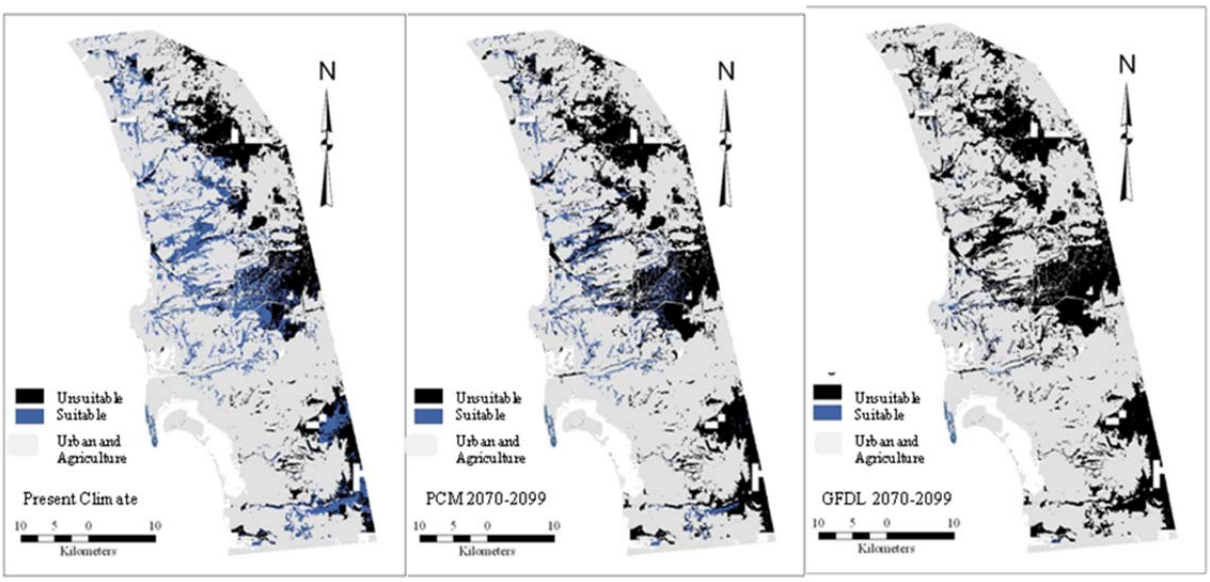


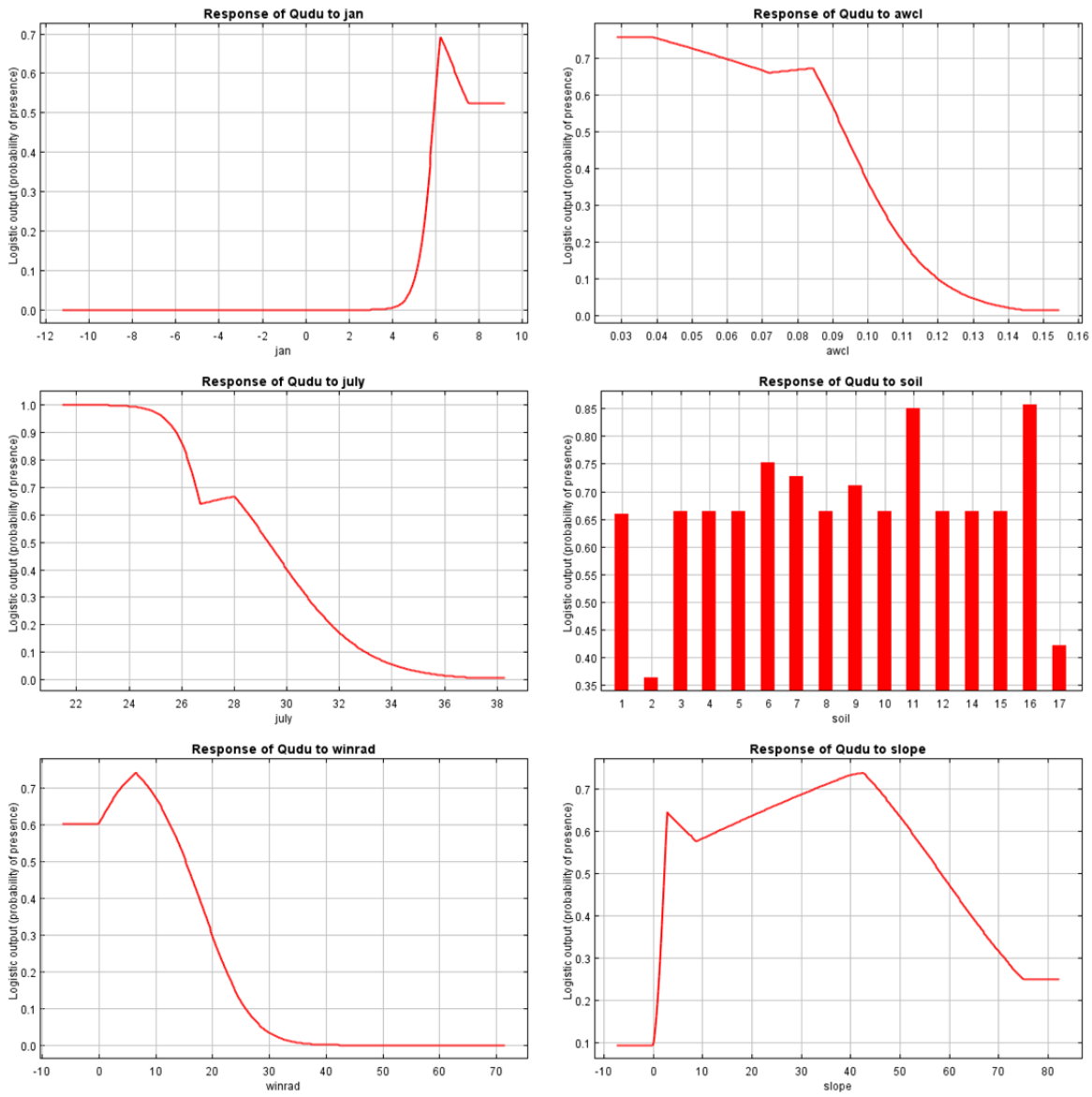
Figure 24. Suitable and unsuitable *Quercus dumosa* habitat under the current and two projected future climate scenarios using a threshold of 0.240 with the Maxent output.

Six variables—minimum January temperature, soil water holding capacity, maximum July temperature, soil type, winter insolation, and slope—were important in predicting the distribution of the species (Table 8). The model rerun with the most important variables had an AUC value for the test data of 0.980 and resulted in the variable importance values listed in Table 8.

Table 8. Influential variables in predicting habitat suitability for *Q. dumosa* and their relative contribution to model gain (average log probability of the presence samples minus a constant) during the model run.

Variable	Percent Contribution
Minimum January Temp	43.2
Available Water Holding Capacity	22.7
Maximum July Temp	17.8
Soil Type	7.6
Winter Insolation	5.5
Slope	3.2

The response curves (Figure 25) show how the habitat suitability prediction changes with changes in each predictor variable as the others are held at their average values. Q. *dumosa* is predicted to occur in a narrow minimum January temperature range, with the optimum around 6°C and habitat suitability declining rapidly above and below the optimum. Habitat suitability is highest for a range of values on the low end of the available water holding capacity curve, declining steadily at values above the middle of the range. Habitat suitability is highest where July temperatures are lowest—between 22°C and 25°C—and declines steadily above that, approaching zero suitability around 36°C. The highest habitat suitability values are associated with alluvial and rough stony soil orders, and the species is not predicted to occur on mollisols. Habitat suitability shows a peak at the low end of the winter insolation range (values that tend to occur on north-facing slopes) with lower suitability at lower (deeply shaded) and higher (sunny) values. *Q. dumosa* is predicted to occur on relatively flat to moderate slopes (2° to around 50°).



1 entisols	4 rock	7 terrace	10 aridisols	13 ultisols	16 roughstony
2 mollisols	5 alfisols	8 badland	11 alluvial	14 acidigneous	17 other
3 inceptisols	6 riverwash	9 vertisols	12 gullied	15 metamorphic	

Figure 25. Response curves of probability of presence for each variable in the *Q. dumosa* habitat suitability model with the other variables held at their average values. SeeTable F4 for the soil orders corresponding the numbers in the soil legend.

The logistic threshold used to distinguish suitable from unsuitable habitat for *Q. dumosa* was 0.240. Approximately 92% of the independently mapped habitat (California Department of Fish and Game 2005, unpublished data) was correctly identified as suitable using this threshold and 6.3% of the natural habitats remaining in the region were predicted suitable using it.

4.2.3 *Chorizanthe orcuttiana*

Figure 26 shows habitat suitability predictions for the current climate and the two alternative climate scenarios. Four variables—January minimum temperature, July maximum temperature, soil water holding capacity, and soil type—were important in predicting the species' distribution (Table 9); each of the remaining four variables contributed less than 1% to model gain. The model rerun with the most important variables had an AUC value for the test data of 0.988 and resulted in the percent contribution values to model gain listed in Table 9.

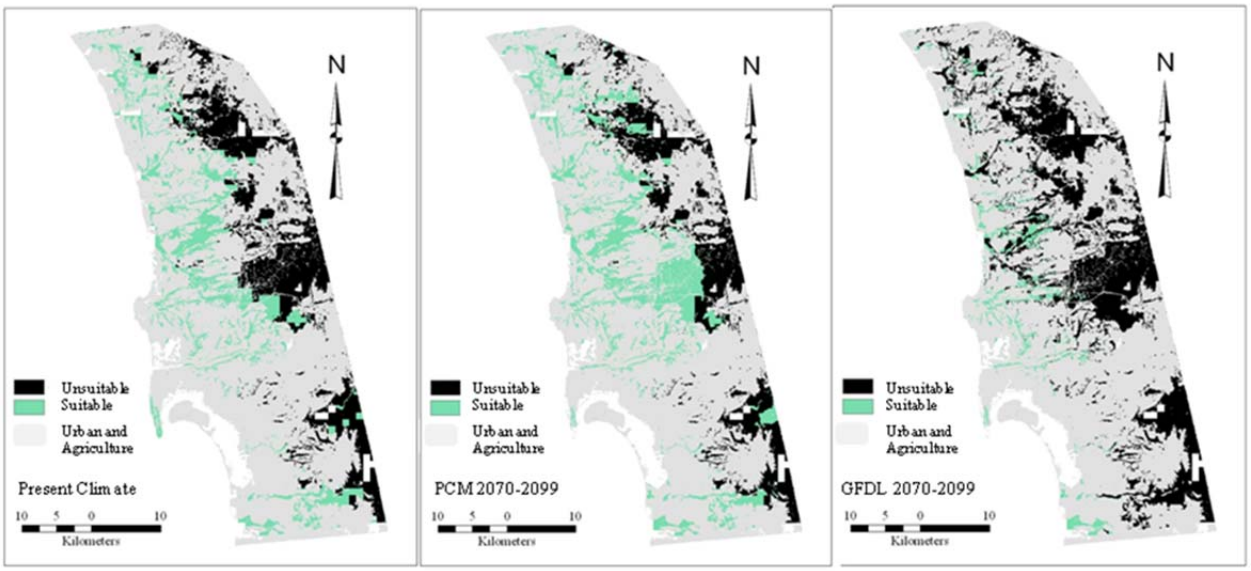


Figure 26. Suitable and unsuitable *Chorizanthe orcuttiana* habitat under the current and two projected future climate scenarios using a threshold of 0.110 with the Maxent output.

Table 9. Influential variables in predicting habitat suitability for *C. orcuttiana* and their relative contribution to model gain (average log probability of the presence samples minus a constant) during the model run.

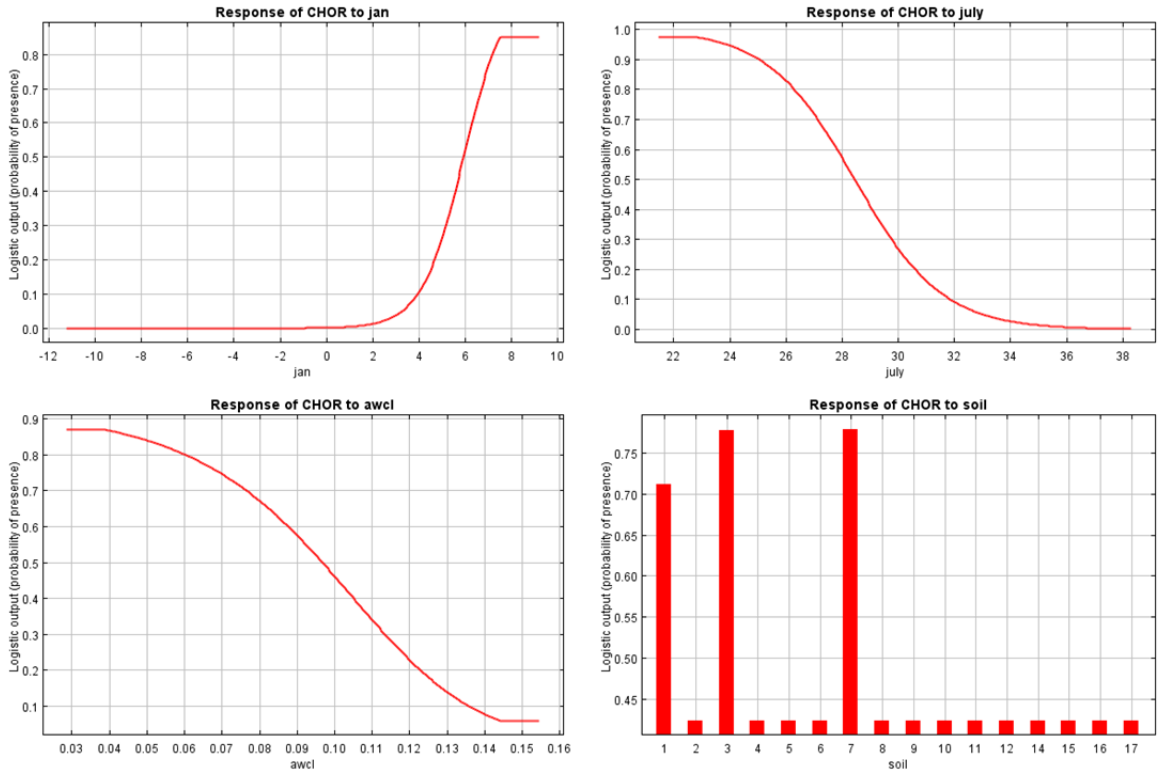
Variable	Percent Contribution
Minimum January Temp	54.6
Maximum July Temp	20.5
Soil Water Holding Capacity	16.4
Soil type	8.5

The PCM climate change scenario resulted in a predicted increase of suitable habitat for *C. orcuttiana*, while the more severe (hotter and drier) GFDL scenario resulted in a predicted loss of suitable habitat. Suitable habitat increased by 27% under the PCM climate scenario and declined by 64% under the GFDL scenario compared to the suitable habitat predicted under the current climate (Table 6).

Population demographics in *C. orcuttiana* are tightly linked to winter temperatures, which are projected to increase; and to winter precipitation, the projections of which, while less certain, are project to decrease (Appendix B) (Cayan *et al.* 2008). The reason that predicted habitat increases

under the PCM projection and decreases less than that for the other species modeled under the GFDL projection is that, based on data collected for this species under 8 years of high climate variability (Appendix B), *C. orcuttiana* does better under higher temperature regimes than those reflected by current conditions. However, like all HSM predictions, these do not consider competition, which could be an issue of some concern. *C. orcuttiana* habitat now consists of open sandy gaps containing few competitors (Bauder 2005); and although the species is projected to do better under higher temperatures, exotic herbaceous species may likewise benefit. Thus, the generic species GCGS2 modeled under this study may reflect a plausible future condition for *C. orcuttiana* where interspecific competition in its habitat increases.

The response curves (Figure 27) show how the habitat suitability prediction changes with changes in each predictor variable as the others are held at their average values. Habitat suitability increases steadily with minimum January temperature, with the highest suitability correlated with the highest minimum January temperature values. Habitat suitability is highest where maximum July temperatures are lowest—around 22°C—and declines steadily, approaching zero suitability around 35°C. Habitat suitability is highest were soil water holding capacity is lowest and declines steadily as it increases. The soil orders in suitable habitats include entisolos, inceptisols, and terrace.



1 entisols	4 rock	7 terrace	10 aridisols	13 ultisols	16 roughstony
2 mollisols	5 alfisols	8 badland	11 alluvial	14 acidigneous	17 other
3 inceptisols	6 riverwash	9 vertisols	12 gullied	15 metamorphic	

Figure 27. Response curves of probability of presence for each variable in the *C. orcuttiana* habitat suitability model with the other variables held at their average values.

The logistic threshold used to distinguish suitable from unsuitable habitat for *C. orcuttiana* was 0.110, predicting 3.3% of the region. All of the independently mapped habitat (California Department of Fish and Game 2005, unpublished data) was correctly identified as suitable using this threshold.

4.2.4 *Neotoma macrotis*

Figure 28 shows habitat suitability predictions for the current climate and the two alternative climate scenarios. Six variables—January minimum temperature, soil water holding capacity, July maximum temperature, slope, soil type, and precipitation—were important in predicting the distribution of the species (Table 10); winter insolation explained less than 3% of model gain and topographic moisture index explained 2%. The model rerun with the most important variables had an AUC value for the test data of 0.872 and resulted in the percent contribution values to model gain listed in Table 10.

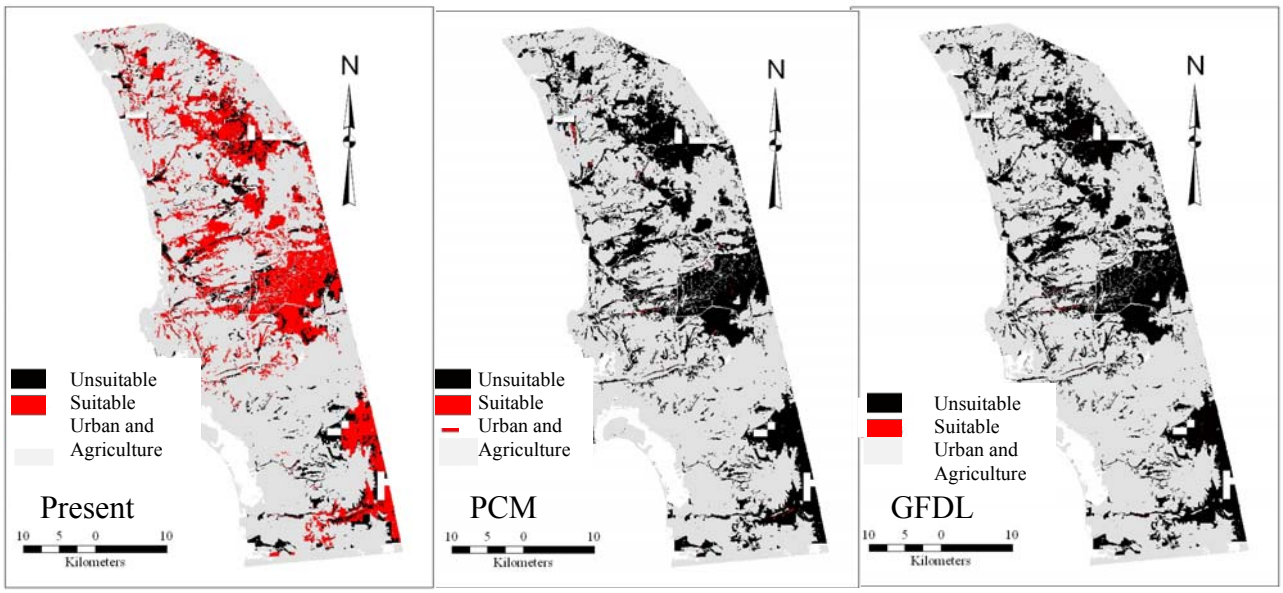


Figure 28. Suitable and unsuitable *N. macrotis* habitat under the current and two projected future climate scenarios using a threshold of 0.337 with the Maxent output. Suitable habitat has been constrained to the distribution of woody habitats under the present climate.

Since *N. macrotis* is known primarily from woody habitats (Kelly 1990; Schwilk and Keeley 1998; Matocq 2002; Braswell 2007), we constrained its distribution under the present climate to the current distribution of woody habitats by intersecting the Maxent output with an updated vegetation map for the study area (Figure 18). The resulting predicted distribution within the study is shown in Figure 29. We did not constrain future projected distributions using woody habitats because it is uncertain how they might change.

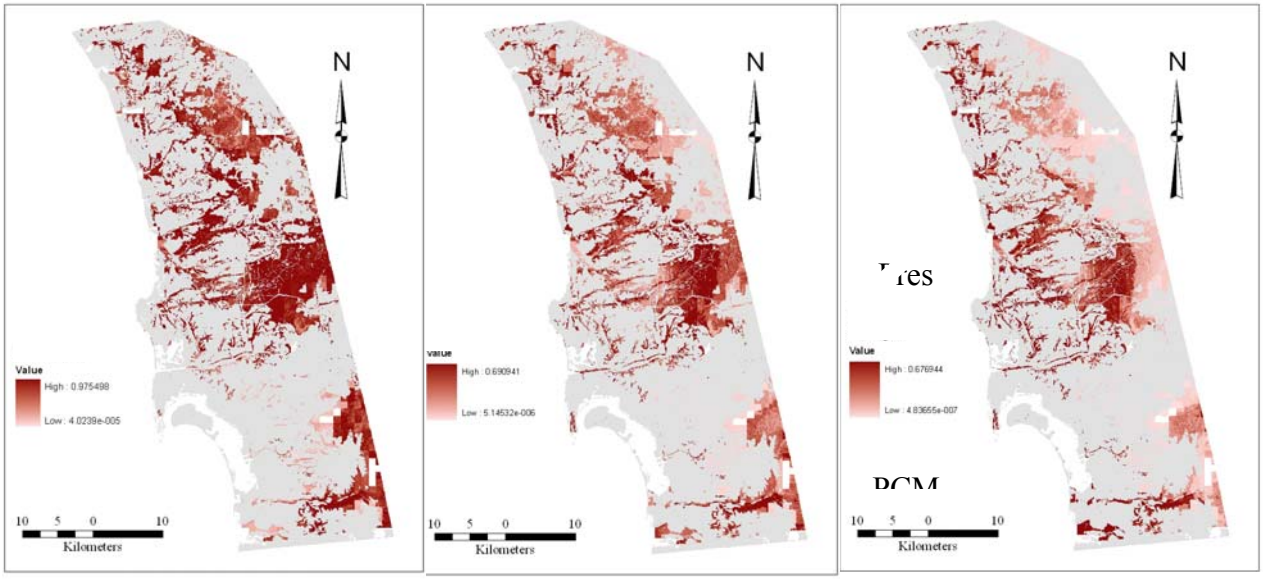


Figure 29. Predicted probability of *N. macrotis* occurrence under the current climate and two projected future climate scenarios. Dark brown is the most suitable habitat and light brown the least. Grey areas have urban and agricultural landcover.

Table 10. Influential variables in predicting habitat suitability for *N. macrotis* and their relative contribution to model gain (average log probability of the presence samples minus a constant) during the model run.

Variable	Percent Contribution
Minimum January Temp	30.7
Available Water Holding Capacity	24.8
Maximum July Temp	24.4
Slope	8.7
Soil	5.9
Precipitation	5.5

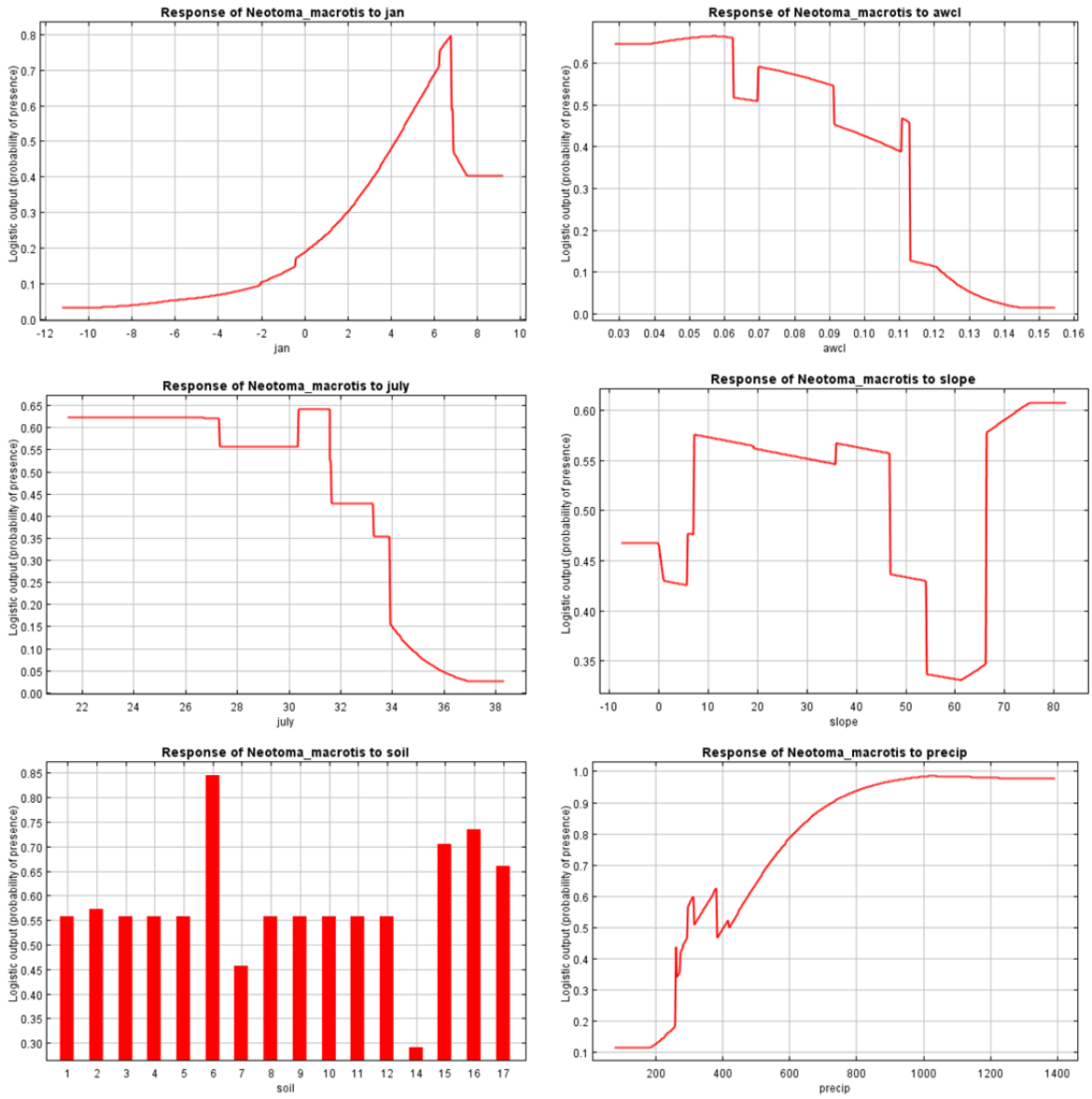
Both climate change scenarios result in a predicted loss of suitable habitat for this species. Suitable habitat declined by 99% under the PCM climate scenario, and virtually all the habitat was lost under the GFDL scenario compared to the predictions under the current climate (Table 6). Neither of the climate projections resulted in habitat shifts; only a negligible amount of suitable habitat emerged on sites that did not previously support it (Table 5).

The future for *Neotoma macrotis* may appear less dire in consideration of the genus' adaptive capacity; however, dispersal remains a problem for population reestablishment after fire.

Of the four species modeled, the clearest case for evolutionary adaptive capacity in the face climate change can be made for *Neotoma macrotis*. Woodrats have a well-documented response to climate change—even rapid climate change as evidenced by preservation of prehistoric middens in deserts (Wells 1976; Smith and Betancourt 2003). Documented responses include

adaptation through change in body mass as well as range shifts and extirpations; body size in this genus generally decreases as temperature increases (Smith and Betancourt 2003; Smith *et al.* 2009).

The response curves (Figure 30) show how the habitat suitability prediction changes with changes in each predictor variable as the others are held at their average values. They show that *N. macrotis* is predicted to occur in a narrow minimum January temperature range, with the optimum around 7°C; habitat suitability declines rapidly above and below the optimum. Habitat suitability is highest at the low end of the range of available water holding capacity, but it declines slowly to the upper third of the range, where it declines rapidly to very low levels. Habitat suitability is high for a range of maximum July temperatures (22°C to almost 32°C), declining rapidly to low levels after that. The highest habitat suitability was on riverwash soils and by far the lowest was on soils of metamorphic origin; suitability was similar among the rest of the soil types. Habitat suitability increases with precipitation, reaching its highest values at 900–1,400 mm annual precipitation.



1 entisols	4 rock	7 terrace	10 aridisols	13 ultisols	16 roughstony
2 mollisols	5 alfisols	8 badland	11 alluvial	14 acidigneous	17 other
3 inceptisols	6 riverwash	9 vertisols	12 gullied	15 metamorphic	

Figure 30. Response curves of probability of presence for each variable in the *N. macrotis* habitat suitability model with the other variables held at their average values.

The logistic threshold used to distinguish suitable from unsuitable habitat for *N. macrotis* was 0.337.Approximately 61.5% of the natural habitats remaining in the study area were predicted suitable using this threshold.

4.2.5 Artificial Landscape

Table 11 shows the artificial landscape constructed by overlaying the results of the HSMs above. The contraction in habitat predictions under the future climates (Table 6) is reflected in the shift to fewer patches with multiple species. Under the PCM projected climate—where suitable habitat for *Chorizanthe orcuttiana* increases and decreases for the other species—the proportion of patches where *C. orcuttiana* is present increases and the proportion of patches where others are present decreases. Consequently, it is anticipated that the changes in multi-species priorities will be driven by QER values for GCGS1 and GCGS2. Under the GFDL projected climate—where all species contract but where *C. orcuttiana* less than the others—multiple species combinations proportionally decline and patches with *C. orcuttiana* proportionally increase. As a result, it is anticipated that differences in multi-species priorities between the joint probability function and the expected number functions are expected to decrease and QER values for GCGS1 and GCGS2 should have more influence than under the present climate but less than under the PCM projected climate.

Table 11. Proportion of landscape in all possible combinations of the four species based on habitat suitability model results under the present and two future climate scenarios. These proportions were used to allocate cells in the 100 cell artificial landscape to various species combinations. : NEMA = *Neotoma macrotis,* CHOR=*Chorizanthe orcuttiana,* QUDU=*Quercus dumosa* and CEVE = *Ceanothus verrucosus*.

Species Combinations	% of Total Area Predicted Suitable for All Species Combinations		
	Present Climate	PCM Climate Scenario 2070-2099	GFDL Climate Scenario 2070-2099
NEMA CHOR CEVE QUDU	2	3	0
NEMA CHOR CEVE	4	3	0
NEMA CEVE QUDU	2	0	0
NEMA CHOR QUDU	4	3	3
CHOR CEVE QUDU	4	6	7
NEMA CHOR	7	3	3
NEMA CEVE	5	0	3
NEMA QUDU	7	3	3
CHOR CEVE	7	12	14
CHOR QUDU	7	12	14
CEVE QUDU	4	6	0
NEMA	15	9	7
CHOR	15	24	28
QUDU	5	9	7
CEVE	13	9	10

4.3 Population Demographic Models

4.3.1 Sensitivity Analyses

4.3.1.1 *Ceanothus verrucosus*

Table 12 shows the results of the sensitivity analysis for the parameters determined sensitive. A complete table for all parameters tested is provided in Appendix A. In contrast to the model for the obligate sprouter *Quercus dumosa*, this model for an obligate seeder is sensitive to longevity (both plant and seedbank), post-fire germination, and juveniles and up to 54 years old (sensitivity

declines with age). Vegetative reproduction, parameterized into the model, was also found to contribute little to the output; when it was removed entirely, expected minimum abundance declined less than 10%. In addition, dispersal, when removed from the model, did not influence metapopulation model output (Table 12).

Table 11. *Ceanothus verrucosus* sensitivity analysis results for model parameters determined sensitive (change in model output was greater than change in parameter). A complete table including parameters not found sensitive is provided in Appendix A.

Model	% change in parameter	Expected Minimum Abundance	% Change from Basic Model
Basic Model		2800	
Stage 1 (seedbank longevity) +10% yrs	1.1%	2946	5.2%
Stage 1 (seedbank longevity) +20% yrs	2.0%	3177	13.5%
Stage 1 (seedbank longevity) +30% yrs	2.8%	3446	23.1%
Stage 2	10%	3482	24.4%
Stage 2	-10%	2137	-23.7%
Stage 3	10%	3429	22.5%
Stage 3	-10%	2300	-17.9%
Stage 4	10%	3254	16.2%
Stage 4	-10%	2451	-12.5%
Stage 5	10%	3249	16.0%
Stage 5	-10%	2370	-15.4%
Stage 6	-10%	2227	-20.5%
Stage 7	10%	3257	16.3%
Stage 7	-10%	2365	-15.5%
Stage 8	10%	3096	10.6%
Stage 8	-10%	2212	-21.0%
Stage 9	-10%	2232	-20.3%
Stage 10 ***	-10%	2422	-13.5%
Stage 11	-10%	2437	-13.0%
Stage 12	-10%	2430	-13.2%
Stage 14	-10%	2427	-13.3%
Stage 16	-10%	2500	-10.7%
Stage 17	-10%	2308	-17.6%
Stage 18	-10%	2332	-16.7%
Stage 19	-10%	2513	-10.3%
Stage 21	-10%	2431	-13.2%
Stage 22	-10%	2514	-10.2%
Stage 23	-10%	2279	-18.6%
Stage 26	-10%	2393	-14.5%
Stage 27	-10%	2460	-12.1%

Model	% change in parameter	Expected Minimum Abundance	% Change from Basic Model
Germination (post fire)	10%	3353	19.8%
Germination (post fire)	-10%	2231	-20.3%
Germination (post fire)	20%	3620	29.3%
Germination (post fire)	-20%	1747	-37.6%
Germination (post fire)	30%	4284	53.0%
Germination (post fire)	-30%	1304	-53.4%
longevity +20% yrs	4.5%	2944	5.1%
longevity -30% yrs	5.6%	3013	7.6%
*** from stage 10 to 47 the modeled survival is 0.998 or higher so only a decrease was evaluated			

4.3.1.2 *Quercus dumosa*

Table 13 shows the results of the sensitivity analysis for parameters considered sensitive. Ecological theory predicts that obligate sprouters will be influenced by processes affecting adult survival but not recruitment (Bond and Midgley 2001). Our model reflects this in that results were sensitive to adult mortality (Table 13) but not to any of the other transitions or fecundities (Table 6, Appendix C).

Table 12. *Q. dumosa* sensitivity analysis results for model parameters determined sensitive. For the complete table, see Appendix C.

Model	% change in parameter	Expected Minimum Abundance	% Change from Basic Model
Stage Matrix			
Basic		59.1	0.0%
Transitions			
Adults to adults (+ 0.5% to a 400 yr lifespan)	0.50%	69.6	17.8%
Adults to adults (- 0.4% to a 250 yr lifespan)	-0.40%	52.4	-11.3%
Catastrophe Matrix			
Post-fire adult survival +0.5% (catastrophe matrix value 0.9951)	0.5%	59.6	0.8%
Post-fire adult survival -0.5% (catastrophe matrix value 0.9850)	-0.5%	59.8	1.2%

Dispersal only contributed a small amount to the EMA for *Q. dumosa* (2.1%); this was a best-case scenario. The model represents a maximum potential for dispersal because in the model, all suitable but unoccupied habitat was considered unoccupied; but in fact the niche that *Q. dumosa* would fill is likely occupied by long-lived woody species. Nevertheless, dispersal contributed very little to population abundance.

4.3.1.3 *Chorizanthe orcuttiana*

Table 14 shows the results of the sensitivity analysis. The model output is not sensitive to changes in fecundity or the seed to adult transition, but it is sensitive to seedbank longevity. The alternative fire catastrophes representing canopy closure (GCGS1) and annual grass invasion

(GCGS2) resulted in large changes. The model representing canopy closure was reduced by 71.5%, and the scenario representing annual grass invasion declined by 18%.

Table 13. *Chorizanthe orcuttiana* sensitivity analysis results for model parameters.

Model*	% change in parameter	Expected Minimum Abundance	% Change from Basic Model
Stage Matrix			
Basic (drought but no fire catastrophes)		525574.6	0.0%
Fecundity Adults +10%*	10%	562355.6	7.0%
Fecundity Adults -10%*	-10%	475081.9	-9.6%
Seedbank longevity =10 years; seed to seed transition= 0.6541	10%	225045.8	-57.2%
Seedbank longevity =30 years; seed to seed transition= 0.8180	-10%	615734.3	17.2%
Seed to adult +10%*	10%	540877.9	2.9%
Seed to adult-10%*	-10%	482210.1	-8.3%
Alternate Catastrophe Scenarios			
GCGS1 FRI=35 (reduce K to 0 over 80 years post fire catastrophe)		149842.2	-71.5%
GCGS2 FRI=35 (set K to 10%, increase to 100% after fire, decline to 10% within 2 years post fire catastrophe)		430973.2	-18.0%
* grayedgrayed stages are not sensitive to parameter changes.			

4.3.1.4 *Neotoma macrotis*

The model was sensitive to most of the parameters tested with the exception of survival in the oldest age class and longevity (addition of an extra age class) (Table 15). The model was not sensitive to the use of roads as barriers to dispersal.

Table 14. *N. macrotis* sensitivity analysis results for model parameters determined sensitive. For the complete table, see Appendix D.

Model	% change in parameter	Expected Minimum Abundance	% Change from Basic Model
Stage Matrix			
Basic Model		234	
Fecundity 0–1 year +10%	10%	319	36.3%
Fecundity 0–1 year -10%	-10%	178	-24.0%
Fecundity 1–2 year +10%	10%	360	53.7%
Fecundity 1–2 year -10%	-10%	88	-62.5%
Fecundity 2–3 year +10%	10%	292	25.0%
Fecundity 2–3 year -10%	-10%	175	-25.4%
Fecundity 3–4 year +10%	10%	259	10.6%
Fecundity 3–4 year -10%	-10%	206	-11.8%
Transition 0–1 to 1–2 +10%	10%	377	61.0%
Transition 0–1 to 1–2 -10%	-10%	44	-81.4%
Transition 1–2 to 2–3 +10%	10%	303	29.3%
Transition 1–2 to 2–3 -10%	-10%	151	-35.3%
Transition 2–3 to 3–4 +10%	10%	260	11.3%

4.3.2 Expected Minimum Abundance

4.3.2.1 Single Population Model Results

The expected minimum abundances for the species show four different patterns in response to varying fire return interval (Figure 31). For *Ceanothus verrucosus*, the best interval of those tested was 35 years. The EMA declined rapidly at intervals less than 35 years, reflecting immaturity risk (Zedler 1995). As fire intervals increased, the decline was slower, reflecting plant and seedbank longevity. GCGS1 showed the highest EMA at the lowest fire return intervals. The EMA declined as fire interval increased, reflecting long-term decline in carrying capacity after fire. GCGS2 showed little variation in response to fire interval, reflecting that the hypothesized response of annual competitors to fire is short (2 years) relative to the fire intervals possible in chaparral, which have a wide range (30–100 years) (Keeley 1992, 2007; Zedler 1995) but are rarely less than 5 years (Sampson 1944; Hedrick 1951; Zedler *et al.* 1983). The increase in EMA for *Q. dumosa* with time since fire likely represents the suppressed post-fire seedling establishment (Patric and Hanes 1964; Keeley 1992), while the EMA for *N. macrotis* likely reflects the species' inability to survive fire (Wirtz *et al.* 1988; Schwilk and Keeley 1998).

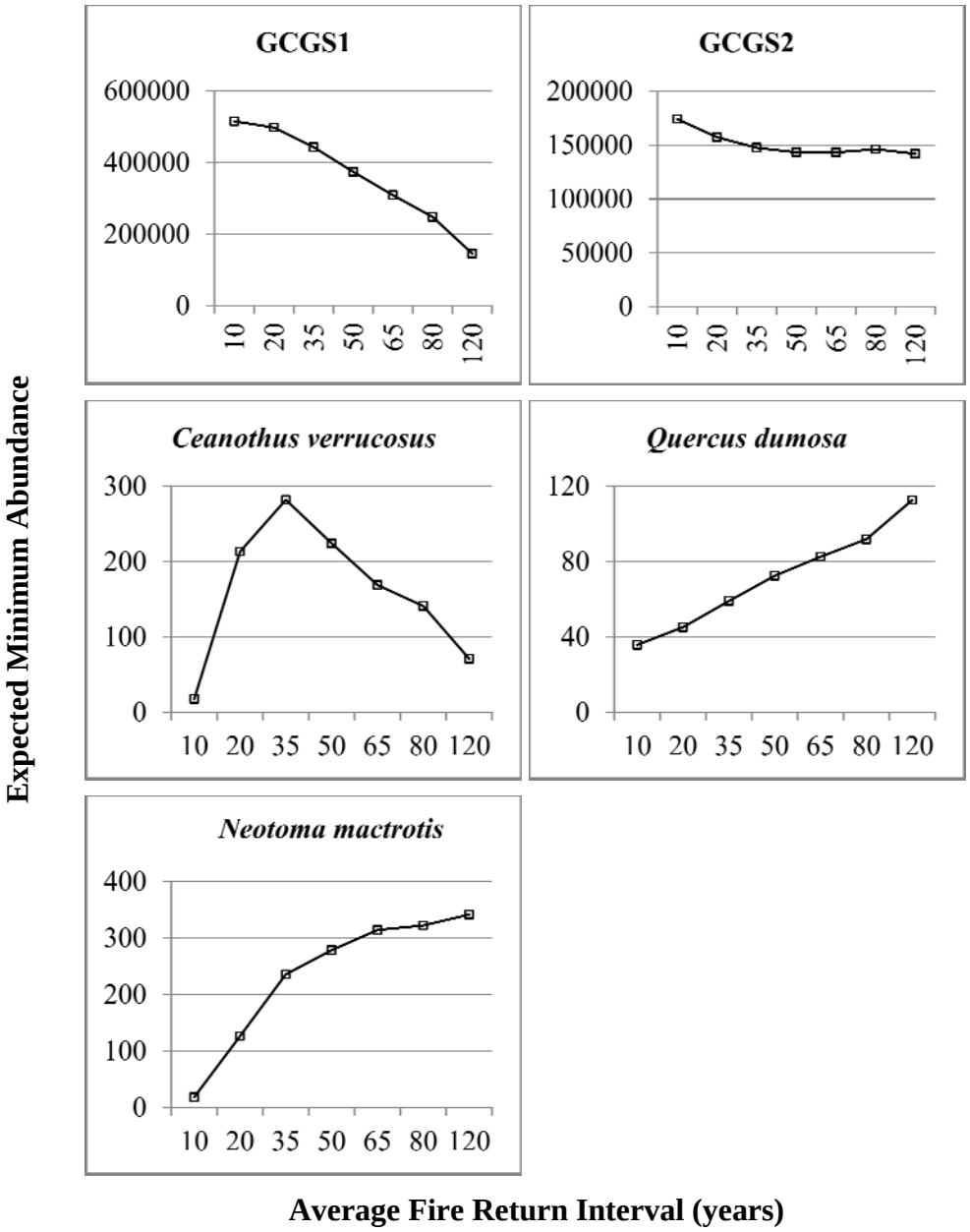


Figure 31. EMAs for single population models for each species for fire intervals from 10 to 120 years.

4.3.2.2 Metapopulation Model Results

The results from the metapopulation models (Figure 32) reflect similar but less distinct relationships. Particularly with respect to *Quercus dumosa* and *Neotoma macrotis*, it is difficult to distinguish between results for fire intervals greater than 50 years. This is interesting in light of the fact that one of the factors that would buffer the response to fire would be recolonization events, but dispersal for the study species is almost non-functional in this landscape.

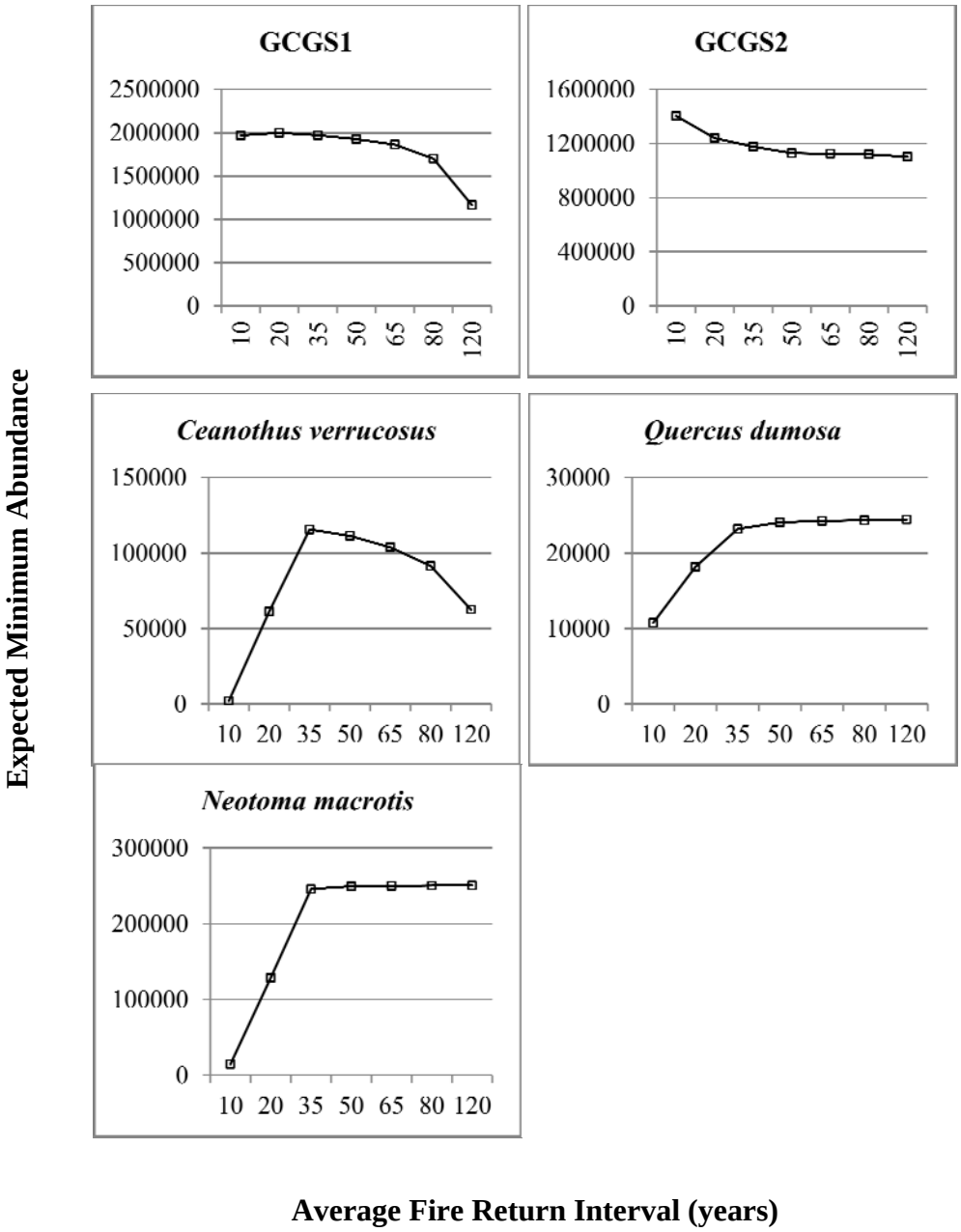


Figure 32. EMAs for metapopulation models for each species for fire intervals from 10 to 120 years.

4.3.3 Probability of Quasi-Extinction

We evaluated multiple quasi-extinctions levels using single species models. The quasi-extinction levels reflect the EMA for each species. The problem with threshold values is that there is no standard set of accepted criteria (Mace *et al.* 2008). Accordingly, we evaluated a range of thresholds (10%, 20%, 30%, 40% and 50%) based on the percentage of initial abundance an EMA represents. Figure 31 shows the single population model results. Reflecting Figure 31, four

response shapes emerged. The curves flatten, reflecting less distinction between alternatives for a quasi-extinction threshold of 50%, and for GCGS1, *Neotoma macrotis, and Quercus dumosa*, the threshold is too high to distinguish among all the alternatives (i.e., the QER=0). On the other hand, the 10% threshold results in QER values of 1 for the 10- and 20-year average fire return intervals for *Quercus dumosa*.

Probability

Figure 33. QER curves for thresholds of 10%, 20%, 30%, 40% and 50% of initial population numbers for single population models for each species for fire intervals from 10 to 120 years.

Like the EMA values from the metapopulation models, the QER thresholds (Figure 34) show less distinct differences among management scenarios. Accordingly, there appears to be an advantage in using single population models to simplify the system so that the best scenario can more clearly be distinguished.

Probability

Figure 34. QER curves for thresholds of 10%, 20%, 30%, 40% and 50% of initial population numbers for metapopulation models for each species for fire intervals from 10 to 120 years.

4.3.4 Dispersal

Quercus dumosa had the most dispersal connections: 4.1% of the possible connections based on number of patches (Table 16). This was not surprising given its long average dispersal distances—321 m for the portion of the crop dispersed by birds (Appendix C) (Gomez 2003). Dispersal barriers for *Neotoma macrotis* within the already fragmented habitat reduced dispersal connections by two-thirds: from 1.5% of the possible connections to 0.6 (average dispersal distance 62.3 m (Appendix D) (Matocq and Lacy 2004). *Ceanothus verrucosus* had few connections: 0.3% of the possible connections due to short average dispersal distances (8 m) (Appendix A) (Vander Wall 1994). Within the landscape for the metapopulation models, only *Quercus dumosa* exhibited a decline when dispersal was eliminated from the model; it was a very small decline of about 2%. However, dispersal appears to make a difference based on the habitat loss scenarios (Table 17). When 20% of the habitat was removed from the model, the most connected population scenario declined to about 80% of the EMA from the full model, but the largest patches scenario declined to 40%. There were only minor differences between the habitat loss scenarios for the other two species.

Table 15. Dispersal connections for each scenario.

	Neotoma macrotis		*Ceanothus verrucosus*	*Quercus dumosa*
	Modeled with Dispersal Barriers	Modeled without Dispersal Barriers		
n populations	359	359	132	482
dispersal connections	742	1,980	60	9,446
n possible connections	128,522	128,522	17,292	231,842
% of possible connections	0.6%	1.5%	0.3%	4.1%

Table 16. EMAs for metapopulation models with and without dispersal and habitat loss scenarios.

Scenario	Species					
	Neotoma macrotis		*Ceanothus verrucosus*		*Quercus dumosa*	
Entire landscape	EMA	% change	EMA	% change	EMA	% change
No habitat loss	245,865		115,662		23,189	
No dispersal	249,880	101.6%	115,741	100.1%	22,700	97.9%
Loss of 20% of habitat area						
Most connected populations	197,948	80.5%	85,385	73.8%	18,104	78.1%
Largest populations	199,156	81.0%	81,382	70.4%	9,132	39.4%

4.3.5 Habitat Loss Scenarios

The two habitat loss scenarios representing patch size and connectedness resulted in similar results for *Neotoma macrotis* and *Ceanothus verrucosus*. Therefore, neither species had an advantage in habitat protection. *Quercus dumosa* showed a large difference in model results, with the most connected population scenario generating double the EMA of the largest population scenario. It would seem that connectedness is important for *Q. dumosa*. Our measure

of connectedness was simply the distance to the nearest patch. It may be that smaller areas within the landscape, in particular within certain dispersal polygons, have functional dispersal for *Neotoma macrotis*, and that further investigations would be important for developing conservation priorities.

4.4 Multi-Species Analysis

The three sets of species used in the multi-species analysis vary by one species that either shows little difference in QER between management scenarios or is favored by the lowest fire return interval (Figure 33). The three-species set without *Chorizanthe orcuttiana* (Table 18) produces similar results to the set with GCGS2 (Table 19) representing annual grass invasion. This is because contributing a relatively constant value (GCGS2) across scenarios has the same effect as adding nothing (three-species set).

As was expected, the set with GCGS1 (Table 20) has a stronger effect on scenario ranking than GCGS2 (Table 18). GCGS1, however, does not have an effect on the best management scenario for three of the four objective functions at the 10% QER level. Including GCGS1 results in a decrease in the optimal fire interval by 55–70 years at the 30% QER threshold. At the 50% QER threshold, including GCGS1 reduces the best average fire interval from 120 years to 35–65 years for 4 out of 12 of the biodiversity values calculated. None of the values calculated for "Increase in expected extinctions" changed at the 50% QER threshold. GCGS1 is the only species favored by the shortest fire interval.

For the most part, given climate and QER threshold, the objective functions identified similar scenarios as the best. There were differences, however. Because model results are more generally reliable for the relative rather than for the absolute accuracy of their results, the objective functions that use relative rates—"increase in expected extinctions" and "proportional increase in extinction risk"—are recommended. However, due to the ease of calculation it is recommended that multiple objective functions be used and their differences be evaluated before the best management scenario is chosen.

Table 17. Rankings of management scenarios based on biodiversity values for the present and two future climate scenarios and seven fire management scenarios for specified objective functions. The values were calculated with QER values for *C. verrucosus*, *Q. dumosa*, and *N. macrotis*. The yellow cells indicate the best management scenario for a given objective function and a given climate.

Three species																					
QER=10%	**Present Climate**							**PCM Climate (2070-2099)**							**GFDL Climate (2070-2099)**						
	Average Fire Intervals							**Average Fire Intervals**							**Average Fire Intervals**						
objective functions	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**
Joint *probability* all extinct	7	6	2	1	3	4	5	7	6	1	2	3	4	5	7	6	1	2	3	4	5
Expected number of extinctions	7	6	1	2	3	4	5	7	6	1	2	3	4	5	7	6	1	2	3	4	5
Increase in expected extinctions	7	6	1	2	3	4	5	7	6	1	2	3	4	5	7	6	1	2	3	4	5
Proportional increase in extinction risk	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1
QER=30%	**Present Climate**							**PCM Climate (2070-2099)**							**GFDL Climate (2070-2099)**						
	Average Fire Intervals							**Average Fire Intervals**							**Average Fire Intervals**						
objective functions	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**
Joint *probability* all extinct	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1
Expected number of extinctions	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1
Increase in expected extinctions	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1
Proportional increase in extinction risk	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1
QER=50%	**Present Climate**							**PCM Climate (2070-2099)**							**GFDL Climate (2070-2099)**						
	Average Fire Intervals							**Average Fire Intervals**							**Average Fire Intervals**						
objective functions	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**
Joint *probability* all extinct	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1
Expected number of extinctions	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1
Increase in expected extinctions	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1
Proportional increase in extinction risk	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1

Table 18. Rankings of management scenarios based on biodiversity values for the present and two future climate scenarios and seven fire management scenarios for specified objective functions. The values were calculated with QER values for *C. verrucosus*, *Q. dumosa*, *N. macrotis*, and the hypothetical annual plant with exotic invasion. The yellow cells indicate the best management scenario for a given objective function and a given climate.

Four species (including GCGS2)																							
QER=10%	**Present Climate**							**PCM Climate (2070-2099)**							**GFDL Climate (2070-2099)**						
	Average Fire Intervals							**Average Fire Intervals**							**Average Fire Intervals**						
objective functions	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**
Joint probability all extinct	7	6	1	3	2	4	5	7	6	1	3	2	4	5	7	6	1	2	3	4	5
Expected number of extinctions	7	6	1	2	3	4	5	7	6	1	2	3	4	5	7	5	1	2	3	4	6
Increase in expected extinctions	7	6	1	2	3	4	5	7	6	1	2	3	4	5	7	5	1	2	3	4	6
Proportional increase in extinction risk	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1
QER=30%	**Present Climate**							**PCM Climate (2070-2099)**							**GFDL Climate (2070-2099)**						
	Average Fire Intervals							**Average Fire Intervals**							**Average Fire Intervals**						
objective functions	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**
Joint probability all extinct	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1
Expected number of extinctions	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1
Increase in expected extinctions	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1
Proportional increase in extinction risk	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1
QER=50%	**Present Climate**							**PCM Climate (2070-2099)**							**GFDL Climate (2070-2099)**						
	Average Fire Intervals							**Average Fire Intervals**							**Average Fire Intervals**						
objective functions	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**
Joint probability all extinct	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1
Expected number of extinctions	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1
Increase in expected extinctions	7	6	5	3	1	4	2	7	4	1	2	3	5	6	5	2	1	3	4	6	7
Proportional increase in extinction risk	7	6	5	4	3	2	1	7	6	5	4	3	2	1	7	6	5	4	3	2	1

Table 19. Rankings of management scenarios based on biodiversity values for the present and two future climate scenarios and seven fire management scenarios for specified objective functions. The values were calculated with QER values for *C. verrucosus*, *Q. dumosa*, *N. macrotis*, and the hypothetical annual plant with canopy closure. The yellow cells indicate the best management scenario for a given objective function and a given climate.

Four species (including GCGS1)																								
QER=10%	**Present Climate**							**PCM Climate (2070-2099)**							**GFDL Climate (2070-2099)**						
	Average Fire Intervals							**Average Fire Intervals**							**Average Fire Intervals**						
objective functions	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**
Joint *probability* all extinct	7	3	1	2	4	5	6	5	2	1	3	4	6	7	5	2	1	3	4	6	7
Expected number of extinctions	7	3	1	2	4	5	6	6	2	1	3	4	5	7	6	2	1	3	4	5	7
Increase in expected extinctions	7	3	1	2	4	5	6	6	2	1	3	4	5	7	6	2	1	3	4	5	7
Proportional increase in extinction risk	7	6	4	1	2	3	5	7	6	4	1	2	3	5	7	6	3	1	2	4	5
QER=30%	**Present Climate**							**PCM Climate (2070-2099)**							**GFDL Climate (2070-2099)**						
	Average Fire Intervals							**Average Fire Intervals**							**Average Fire Intervals**						
objective functions	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**
Joint *probability* all extinct	7	6	3	1	2	4	5	6	3	1	2	4	5	7	5	2	1	3	4	6	7
Expected number of extinctions	7	6	5	2	1	3	4	7	6	2	1	3	4	5	7	4	1	2	3	5	6
Increase in expected extinctions	7	6	5	2	1	3	4	7	6	2	1	3	4	5	7	4	1	2	3	5	6
Proportional increase in extinction risk	7	6	5	3	1	2	4	7	6	3	1	2	4	5	7	5	2	1	3	4	6
QER=50%	**Present Climate**							**PCM Climate (2070-2099)**							**GFDL Climate (2070-2099)**						
	Average Fire Intervals							**Average Fire Intervals**							**Average Fire Intervals**						
objective functions	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**	**10**	**20**	**35**	**50**	**65**	**80**	**120**
Joint *probability* all extinct	7	6	5	2	1	4	3	4	2	1	3	5	6	7	3	2	1	4	5	6	7
Expected number of extinctions	7	6	5	3	1	4	2	7	4	1	2	3	5	6	5	2	1	3	4	6	7
Increase in expected extinctions	7	6	5	3	1	4	2	7	4	1	2	3	5	6	5	2	1	3	4	6	7
Proportional increase in extinction risk	7	6	5	4	2	3	1	7	6	2	1	3	4	5	6	4	1	2	3	5	7

5.0 Conclusions and Implications for Future Research/Implementation

5.1 Conservation Management Recommendations for the Study Area

5.1.1 Management

Our results rely on demographic models that provide insight into population demographics within the U.S. range of *Ceanothus verrucosus, Quercus dumosa,* and *Chorizanthe orcuttiana.* These results should be used to inform management—not as the sole basis for decisions. The decisions supported by these models and analyses should be implemented in an adaptive management framework—i.e., where information and models are updated and decisions revisited on a regular cycle (Holling 1978; Shea *et al*. 2002). It is unlikely that the Mexican portion of the ranges of these species will contribute significantly to their persistence because of habitat loss driven by climate change in northern Baja California (Loarie et al. 2008) and because coastal habitat (up to 25 km inland from the coast) has been essentially eliminated at the border, creating a significant habitat gap (a minimum width of 2.5 km) (Google Earth 2011). In addition, northern Baja California represents the more arid end of the gradient, where the stress of climate change is almost certainly going to be greater and aggressive actions to preserve small populations are less likely. Many species in MTEs are subject to combinations of these factors (Cowling et al. 1996; Sala et al. 2000).

While formal approaches to decision analysis clarify choices, when uncertainty is incorporated into the process, ambiguity regarding the best choice often remains (Lawson *et al.* 2008). This is reflected our analysis, which shows variation in rankings based on the choice of objective function, QER threshold, and species used to calculate the biodiversity values with the objective functions. We have shown this through our analysis of different species combinations and with the use of different objective functions. However, some generalities can be formulated from the analyses.

The longer average fire return intervals we tested consistently rank higher than the shorter ones, with the longest (the average 120 year fire return interval) ranking highest most often. However, the QER thresholds make a difference, with the 10% threshold resulting in higher rankings for intermediate fire intervals and the higher thresholds favoring longer fire intervals.

The most conservative approach—ensuring that the species do not fall below 50% of their initial populations—results in the longer intervals tested (65–120 years) being ranked the highest depending on the conservation objective selected. As the QER threshold declines to 10% of the initial population, the highest ranked scenario is most frequently identified as the average 35-year fire return interval.

With only a few exceptions involving GCGS1, the average 10- and 20-year fire return intervals ranked the lowest for all of the objective functions. GCGS1 is a hypothetical annual species based on the *Chorizanthe orcuttiana* model. For this hypothetical species, the canopy closes over an 80-year period in the absence of fire. Canopy closure drives the species response to fire and a steep decline in QER values. Furthermore, with GCGS1 in the mix, the mid-range average fire return intervals more often rank as the preferred scenario.

Climate change in our analysis is included through changes in species abundance and distribution within the landscape. For the most part, the patterns in management rankings are maintained under the future climates. This means that even with the increases we project in relative habitat suitability for *Chorizanthe orcuttiana*, the longer fire intervals remain favored.

5.1.2 Habitat Patch Value to Species Persistence

Habitat connectedness may be important at a local scale, but it does not contribute significantly to population persistence across the landscape. While this is likely not surprising to conservation managers, our models showed that for species across a range of dispersal abilities, dispersal does not make a significant contribution to the EMA across the whole landscape. However, when 20% of habitat is lost for *Quercus dumosa*, a reserve set up from the most connected patches performs much better than one containing the largest patches. Given *Q. dumosa's* life span, it is not clear that this will matter over the typical conservation horizon. Improvements in dispersal functions and analysis of subregional connected networks would be useful in ranking patch value for conservation.

5.2 Multi-Species Planning Framework

The following framework is based on the methods we developed for the case study. There are four phases in the framework: 1) identification of the species and landscape, 2) modeling, 3) selection of objective functions and ranking management scenarios, and 4) implementation in adaptive management framework.

Phase 1 – Species and Landscape Identification

- Step 1 – Identify species of concern.
- Step 2 – Identify landscape boundaries.
- Step 3 – Identify threats.
- Step 4 – Identify management alternatives.
- Step 5 – Review the species list from step one and develop a complete set of focal species that represent the range of species responses to threat processes and management alternatives.

Phase 2 - Modeling

- Step 6 – Develop single population demographic models (for QER values) and metapopulation demographic models for landscape functional assessment.
- Step 7 – Develop habitat suitability models to provide the patch structure for metapopulation models and the basis for projections of habitat change under climate change.
- Step 8 – Evaluate whether metapopulation dynamics are functional in landscape.
- Step 9 – Revisit management alternatives in light of metapopulation functional assessment.
- Step 9 – Construct artificial landscape.
- Step 10 – Conduct population model runs under suite of management scenarios.

Phase 3 – Selection of objective functions and ranking of management scenarios

- Step 11 – Calculate biodiversity values for each management scenario using multi-species objective functions.
- Step 12 – Rank management scenarios to prioritize management.
- Step 13 – Evaluate metapopulation function within landscape and use to inform habitat preservation priorities and conservation management.

Phase 4 – Adaptive management

- Step 14 – Implement management within adaptive management framework.

5.3 Implications for Future Research

Future research into identification of optimal management scenarios should include a more sophisticated evaluation of climate change—for example, greater spatial detail in the HSMs and the inclusion of adaptive capacity of the species considered. In addition, more realistic dispersal functions and a consideration of sub-landscape dispersal networks could help in identifying management and land conservation priorities. Finally, as theory and methods develop, identification of optimal management scenarios should include the influence of novel competitive interactions that are likely to occur under climate change.

Our evaluation of climate change is simplistic. While HSMs have been used broadly to assess climate change impacts (Thomas 2004), they have a number of shortcomings and caution should be taken in their use (Guisan and Thuiller 2005). HSMs do not consider adaptive capacity (a species' genotypic and phenotypic plasticity and ability to rapidly evolve), and at least one of the species, *N. macrotis*, is likely, based on data from prehistoric middens of congeners, to have a strong capacity to adapt to climate change (Smith and Betancourt 2003). In addition, the spatial scale of our HSMs (1 km^2) may miss important habitat distinctions. Recent studies have found that modeling habitat suitability at finer scales reveals spatial heterogeneity that results in microclimatic buffering and fewer predicted species extinctions (Randin *et al.* 2009; Willis and Bhagwat 2009).

As is true of MTEs worldwide, the landscape in our study area is spatially complex due to high levels of land use change resulting in habitat loss and fragmentation. The species we modeled, even those with greater dispersal ability, have few connections between populations (Table 12). The removal of dispersal from the models had little to no effect on model results (Table 12), indicating that patch connectedness is less important than total habitat area (Harrison and Bruna 1999) in our study system. If dispersal is not effective, future management may require translocations to reestablish extirpated populations and maintain genetic diversity. Assessment of dispersal could be improved by using more sophisticated dispersal functions. Additionally, a limitation of the case study is that functional sub-networks, which could be useful in prioritizing habitat protection, were not identified within the landscape.

Several limitations to the models we developed for this study can be attributed to uncertainties in ecological response to management under climate change and novel competitive environments that may form under future climates. One limitation—the assumption that management effectiveness does not change with changing climate—is unlikely to be true. For example, recruitment after fire is likely strongly linked to temperature and precipitation, but information was not available to assess this possibility. Likewise, altered interspecific competition may result in a change in risk of extinction under future climates. However, the hypothetical species GCGS2 provides a possible future scenario for *C. orcuttiana* based on an altered competitive environment. If climate change results in increased rainfall, habitat suitability could increase for competitors such as annual plants that may already be present in the ecosystem, and *C. orcuttiana* could be harmed by competition even if the new conditions are within its fundamental niche (Brooks 2000). Furthermore, while single patch models differentiate better among alternatives (Figures 33 and 34), they exclude an important process for species where dispersal plays a significant role in post-disturbance population reestablishment.

5.4 Conclusions

Our methods provide a framework for managing species in highly fragmented landscapes. Particularly in biodiversity hotspots, it is possible for the entire range of a rare species (or multiple rare species, as is the case in the study area) to exist within a highly fragmented landscape, with no possibility for conservation in other locations where landscapes may be more connected and support functional metapopulations. In such fragmented landscapes it is important to assess metapopulation function to inform conservation management and land conservation priorities. Scott *et al*. 2010 found in an analysis of species listed under the ESA that 84% are *conservation-reliant*—meaning that long-term management will be necessary to ensure their persistence. Management of listed species is time consuming and expensive, with little room for error (Wilcove and Chen 1998). Accepting the inevitability of long-term conservation needs and implementing management long before species decline to the point where they are listed may be a way of ensuring persistence without the cost associated with managing listed species. For highly fragmented landscapes this may include occasional artificial dispersal—or reintroduction after fire—to maintain species such as *Neotoma macrotis*, which can be extirpated by a single fire, or *Ceanothus verrucosus,* which can be extirpated by two fires in rapid succession. It is important to conduct evaluations and develop strategies early to have the best chance of forestalling future ESA listing. Furthermore, it is important to consider multiple species in concert because the threats that exist—habitat fragmentation, altered disturbance regime, invasive species, and climate change—confront ecosystems rather than individual species. Management designed to conserve a single species may not only not benefit another species, but may inflict harm.

The framework developed under this project provides a method for assessment of metapopulation function and prioritization of land conservation and management activities using stochastic population models for a set of focal species, HSMs, and multi-species conservation objective functions within a specified landscape. Metapopulation function is assessed by conducting population viability analyses with spatially explicit stochastic population models developed by linking actual occupied habitat maps or HSM-generated habitat suitability maps to population models. The extent of dispersal function in the landscape can be used to develop priorities for land conservation and management—for example, identifying if periodic artificial reintroductions are likely to be needed. Best management practices (aside from dispersal-related management) are evaluated in an artificial landscape, which represents the relative abundance and distribution of the focal species in the current and projected future landscapes using the results of single population models.

Our analyses highlight the complexities of managing biodiversity in a landscape fragmented by a long history of human use and facing projected changes in land use, climate, and natural disturbance events. Projecting the effects of climate change is difficult when species distributions are not strongly controlled by climate. For the case study, two species—*Chorizanthe orcuttiana* and *Ceanothus verrucosus*—are likely to be controlled by climate (Nicholson 1993; Davis et al. 1999; Ewers et al. 2003); but climatic controls on the other two—*Neotoma macrotis* and *Quercus dumosa*—are less clear. Where species are embedded in a highly fragmented landscape such that dispersal is not functioning, there are few if any opportunities for species to shift their ranges in response to climate change.

It is vitally important to protect remaining habitats and, where feasible, to protect natural areas in configurations that will allow species to shift their ranges in response to climate change in

addition to managing disturbance regimes to provide for species persistence. In spite of the high levels of habitat fragmentation and human disturbance in MTEs, locally endemic plant species are an important component of the biodiversity of such ecosystems (Cowling et al 1996). Such species are not necessarily more likely to decline than rare plant species in more intact landscapes and so can be viable conservation targets (Lawson et al. 2008). In addition, rare species whose distributions are limited by climate are likely to be important subjects to study the effects of climate change because they are likely to be affected first (Schwartz et al. 2006).

The degree to which species' responses to climate change vary increases the chance of novel community associations forming (Breshears et al. 2008). Because competition is important in defining a species' realized niche (Nicholson 1993), it is not clear how species such as our study species might fare competitively in novel ecological associations that may form. This uncertainty highlights these competitive interactions as an important avenue for future research. The fragmented landscapes of the world's MTEs leave few "stepping stones" for species with impaired dispersal to shift their ranges as climate changes. Unfortunately, artificial dispersal may become a cost of doing business to preserve conservation-reliant species in situ in these highly fragmented landscapes (Scott et al. 2010). Strategies for artificial reintroductions should be developed and implemented before the species have been reduced to just a few populations. Implementation will be less expensive if it is not critical that it always works.

DoD is appropriately reluctant to relinquish control of land management in view of the compelling nature of its national defense mission. However, when species are federally listed, options are constrained and the potential conflicts between conservation imperatives and training opportunities increase (U.S. Navy 2009). DoD should collaborate in identifying regional conservation objectives; however, collaboration does not necessarily mean giving up the right to implement management scenarios that best reflect military operational needs. Furthermore, DoD is likely not the only organization in these complex landscapes that desires to retain its autonomy. Conservation goals between organizations may differ, but our results suggest that while rankings of management scenarios vary for different objectives, the general directive (maintain or increase fire intervals) is robust for multiple objectives under the current and potential future spatial distributions. Land managers do not necessarily need to give up their autonomy to develop conservation objectives to contribute to the larger goal. While regions such as San Diego, long valued for their natural values, may have groups already working on multi-species conservation initiatives, newly formed Landscape Conservation Collaboratives could provide an ideal forum to initiate planning endeavors in other regions.

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Appendix A—*Ceanothus verrucosus* Life History and Population Demographic Model

Methods

Distribution and Life History

C. verrucosus Nutt. is a long-lived shrub of the coastal chaparral of southern California and northern Baja California. Globally, it is ranked as a vulnerable species (G3) (CNPS 2009). Like many narrow-niche endemics in MTEs, it is threatened by high levels of development, and its restricted range likely reflects adaptation to a narrow niche characterized by climatic factors and possibly soils (Nicholson 1993; Keeley 2000). Our study focuses on the U.S. portion of the range, which extends approximately 70 kilometers (km) north of the U.S. border with Mexico and includes 151 subpopulations (greater than 0.25 hectare [ha] and separated by more than 44 meters) totaling 4,311 ha (California Department of Fish and Game 2005) (Appendix E). We updated habitat maps (California Department of Fish and Game 2005) using aerial photography and field surveys, and we estimated population sizes through direct counts or density estimates, resulting in a complete inventory of the known U.S. population.

Seed production begins at 3–6 years and is a curvilinear function of age peaking around age 50 (Zammit and Zedler 1993; Lawson 2010). The species has a long-lived, persistent seedbank. Some age diversity is introduced by occasional germination between fires and by vegetative establishment (Zedler 1995). Average peak production is estimated to be on the order of 300 seeds per plant (Keeley 1987; Zammit and Zedler 1993). Seeds are initially dispersed ballistically an average of about 1 meter (m) (Quinn unpublished data) and secondarily by animal vectors including harvester ants, small mammals, and birds (Davey 1982; Quinn 1994).

Herbivory and drought drive mortality in the first year or two (Kummerow *et al.* 1985; Moreno and Oechel 1991; Quinn 1994) and density-dependent thinning occurs for approximately the first 15 years (Horton and Kraebel 1955; Schlessinger and Gill 1978). Mortality rates decline through these phases, remaining at very low levels in mature stands (Appendix E). Plant longevity exceeds 95 years but an upper bound is unknown (Appendix E).

Demographic Model Structure and Parameterization

We constructed a spatially explicit stochastic age-based matrix model using available data (Zedler *et al.* 1995; Cummins 2003), supplemented with data collected in field studies and published data for congeners. *Ceanothus* is a diverse genus including a number of closely related species. The six congeners used to help parameterize the model are members of the subgenus *Cerastes*; all have very similar life history characteristics including shade sensitivity, refractory seed, and limited seed dispersal (Conard *et al.* 1985; Keeley 2000). A biogeographical study that included three of the congeners, *C. megacarpus, C. crassifolius* and *C. cuneatus,* identified them as ecological equivalents (Nicholson 1993). Age classes ranged from seeds to plants 92+ years old.

Fecundity and seed survival were estimated from published data for congeners using seed production in five stands of differing ages (Zammit and Zedler 1993) adjusted for viability (Keeley 1987); predation (Davey 1982; Zammit and Zedler 1993); and seed size (S&S Seed pers. comm.). The use of space-for-time substitution to estimate seed production was necessary for such a long-lived species, where it is infeasible to track the demography of the population over the lifespan of the plant. Average seedbank input $f_s(x)$ per adult plant was calculated as

$$f_s(x) = 848 + 10.1x - (0.137(x-38)^2) \text{ for } 4 \le x \le 92$$

where x is the age of the plant in years. The standard deviation (0.56) was based on the coefficient of variation (CV) of seed production from five stands (Zammit and Zedler 1993). The seedbank input was drawn from a lognormal distribution using these calculated means and standard deviations. The mean annual vegetative reproduction (0.00245) was based on field studies (Zedler *et al.* 1995) (Appendix E). Expert opinion indicates that vegetative reproduction begins at 45 years, and the offspring is the physiological equivalent of an 8-year-old plant.

There is a high degree of uncertainty about the longevity of seedbanks within the *Ceanothus* genus (Zammit and Zedler 1988), but it is has been shown that seed can persist in the soil profile long after the last adult plant dies (Tyler and D'Antonio 1995; Cummins 2003). Recent work linking age at death of isolated dead individuals with seedbank counts has documented seedbank persistence of 44 years (Appendix E). Since all dead isolated plants examined in field studies had live seed, we used 50 years as the minimum seedbank persistence and back-calculated annual viability of seeds from this assumed longevity by means of a decay function.

Because of a paucity of data on germination rates of *Ceanothus* congeners, we used the post-fire germination rate (0.032) from another obligate-seeding shrub of the maritime chaparral, *Arctostaphylos morroensis* (Odion and Tyler 2002). Incidental germination of obligate-seeding shrubs in the absence of fire is an extremely rare event and was parameterized at a rate of 1 in 100,000 based on *C. verrucosus* studies (Zedler 1995). Because we also lacked data on variability in the germination rate, variability in fire-caused seed mortality was used as a surrogate. Seed mortality from fire is both spatially and temporally highly variable, and a CV of 200% was derived from fire-related seed mortality data for multiple species (Odion and Davis 2000).

Population carrying capacity was modeled as a ceiling threshold, reflecting total available suitable habitat for each age class (Bekessy *et al.* 2004). Least-squares minimization was applied to maximum observed densities, or average plant sizes when available (Schleschinger and Gill 1978; Zammit and Zedler 1993), to estimate carrying capacity as an exponential function that declined with stand age. The model uses the ratio of the number of plants in an age class to the largest plants (in the oldest age class), which was calculated as $K(x) = 60.62\exp(-x/6.12) + 0.50$ where x is the stand age. When the population exceeded carrying capacity, vital rates were reduced by the following amounts until the population was less than or equal to carrying capacity: 50% (0–3 years), 40% (4–9 years), 30% (10–15 years), and 5% (>16 years). The adjustments to vital rates vary by age to reflect decreasing susceptibility to mortality as plants become established (Morris *et al.* 2008). This effectively introduces a delayed response to carrying capacity where younger populations above the carrying capacity respond more quickly than older populations.

First-year survival rates were recorded for two *C. verrucosus* stands resulting from fires in October 2007 (mean = 0.533; standard deviation = 0.194) (Appendix E). Survival rates for ages 2–16 were estimated from data for six obligate-seeding *Ceanothus* species (Schlesinger and Gill 1978; Kummerow *et al.* 1985; Frazer and Davis 1988; Thomas and Davis 1989; Moreno and Oechel 1992; Tyler and D'Antonio 1995; Odion and Davis 2000; Keeley 2006) (Appendix E). Using these data, the mean survival rate for 2-year-old plants was estimated as 0.763 (standard deviation of 0.158), and survival rates for stands aged 3–16 years were parameterized as

$$f_{ss}(x) = 0.779 + 0.0148x$$

where x is the stand age. Because *C. verrucosus* forms predominantly even-aged stands, and dead stems can persist for 100 years or more (Keeley 1992), we parameterized long-term survival of individuals older than 15 years through ring counts of dead individuals in a 95-year-old stand (Appendix E). Survival for stand ages greater than 15 years was very high and declined only slightly over time: years 16–41 (mean = 0.9976, standard deviation = 0.004171), and years 42–92+ (mean = 0.9902, standard deviation = 0.01348). Survival rates were selected from a lognormal distribution with the means and standard deviations reported above.

An exponential function decreasing with distance was used to estimate dispersal rates:

$$M_{ij} = \exp(-D_{ij}/b) \text{ when } D_{ij} \leq d_{max}$$

where M_{ij} is the rate of dispersal between the ith and j^{th} patch, D_{ij} is the distance between the patches, b is the average dispersal distance, and d_{max} is the maximum dispersal distance for a single time step. Average ballistic dispersal distance (1 m) (Quinn unpublished data) in the genus *Ceanothus* is likely to be much less than secondary dispersal by animals (Parker pers. comm.). Because so few data exist for seed dispersal (Higgins and Richardson 1999; Cain *et al.* 2000) we used the average dispersal distance (8 m) and standard deviation (3 m) for a similarly sized seed cached by chipmunks (Vander Wall 1994). We used sensitivity analysis to determine the effect of the maximum dispersal distance on the model output, testing maximum distances of 100 and 1000 m.

Probability of Fire

We incorporated stochastic fire events into our demographic model by means of a hazard function based on the Weibull function (Moritz 2003). The probability of a fire as a function of time since the last fire was modeled as

$$f(\mathrm{t}) = (ct^{c-1}/b^{c})\exp(-(t/b)^{c})$$

where t is the time since last fire, b is a scale parameter related to the average fire return interval, and c is the shape parameter, which reflects the degree to which fire hazard changes with time since last fire. To represent the current fire regime, we used parameters developed by Polakow *et al.* (1999) for mixed chaparral along the southern California coast using data from the Santa Monica Mountains (c = 1.42; b = 40.26). These parameters give a roughly 35-year average fire return interval. We tested fire intervals from 20 to 120 years by changing the value of the scale parameter, b, to represent the current fire regime (Polakow 1999), increasing and decreasing fire frequency (Moritz 2003; Syphard *et al.* 2007b), and conditions relevant to conservation management (Cabrillo National Monument 2005). When a fire occurs across a patch that has not burned for more than 4 years, all standing plants are killed, germination is triggered, and the time since last fire is set back to zero in the fire hazard function. Within 4 years of a fire occurring, fuel load is patchy and insufficient to carry fire uniformly across the site (Sampson 1944; Hedrick 1951; Zedler *et al.* 1983). Consequently, if a fire occurs within 4 years of the previous fire, background survival rates (in the absence of fire) are reduced by half.

Current and Future Spatial Distribution

The currently occupied habitat patches were used as the current spatial distribution of the species. Unoccupied patches that were predicted suitable within the existing range of the species were included in the model with an initial population of zero. We performed a sensitivity analysis that included unoccupied patches with suitable habitat and determined that, due to poor dispersal and fragmentation, dispersal to these patches was negligible. We accordingly excluded them from the analysis. To evaluate the potential effects of projected future climate change, we first modeled habitat suitability under the current climate; then we used that model as the basis for predicting the distribution of suitable habitat under alternative future climate projections using Maxent (Phillips and Dudik 2008). The habitat suitability model (HSM) for the current distribution was a presence-only model based on a total of 88 data points; 75% were randomly selected for training, and 25% were used for testing the model. The data points were generated by randomly selecting points within existing patches averaging one per 5 ha with a minimum of one point per patch. Populations in close proximity to each other derived from the fragmentation of larger natural populations were grouped so that highly fragmented populations were not overrepresented in the model. To represent extirpated stands (in the HSMs), we included documented historic locations more than 100 m from extant populations (Taylor 2004). Our explanatory variables represent resource gradients and environmental regimes embodying limiting factors shown to be important predictors of species distributions in southern California (Franklin 1998): summer and winter topographically distributed potential solar insolation, slope, January average minimum temperature, July average maximum temperature, average annual precipitation, soils, available water holding capacity, and topographic moisture index (see Table 2 in the body of this report) (Syphard and Franklin 2010). The topographic moisture index is based on the summed area of upslope pixels that drain into a given cell in a digital elevation model scaled by the slope of the pixel (Beven and Kirkby 1979). We retained variables with correlation coefficients less than 0.4 (Wintle *et al.* 2005); elevation was excluded due to its correlation with January minimum temperature. We used a logistic threshold of 0.221 to maximize the sum of model sensitivity (true positives) and specificity (true negatives) estimated from the training data (Allouche *et. al.* 2006) to distinguish suitable from unsuitable habitat from the Maxent output as the basis for habitat patch structure.

We used two future climate scenarios, based on the IPCC Fourth Assessment medium-high emissions scenario, produced by two different global climate models and shown to realistically simulate California's climate (Cayan *et al.* 2008). Each exhibited differing sensitivity to greenhouse gas forcing. The projections run through 2099. For our study area, the National Center for Atmospheric Research (NCAR) and the Department of Energy's (DOE's) Parallel Climate Model (PCM) projects a slightly wetter and hotter climate (2.5^{o}C increase in temperature and 8% increase in precipitation), while the National Oceanic and Atmospheric Administration (NOAA) Geophysical Fluid Dynamics Laboratory CM2.1 model (GFDL) predicts a much hotter and drier climate (4.4^{o}C increase in temperature and 26% decrease in precipitation).

Using the downscaled (1 km grid) GFDL data provided by the Sustainability Solutions Institute (http://ssi.ucsd.edu/), we averaged the predictions for 2070–2099 to reach an estimate of the projected future climate at the end of the twenty-first century. Intermediate projections were not used because the increase in temperature for both models was linear (Cayan *et al.* 2008). To represent the PCM model projections, we modified the GFDL predictions based on the model

comparisons in Cayan *et al.* (2008) for summer and winter averages; we lowered the projections in each grid cell by 2.5^{o} C for July maximum temperature and increased the projections in each grid cell by 2.1^{o} C for the January minimum temperature. The habitat suitability model developed using the existing climate variables was then applied to the climate variables averaged from the 2070–2099 PCM and GFDL projections.

We modeled a continuous change in habitat resulting from climate change using similar approaches to both Anderson *et al.* (2009) and Keith *et al.* (2008), who linked stochastic population models with a series of interpolated HSMs reflecting changes in suitability due to climate change. This approach has the effect of altering the carrying capacity of subpopulations gradually through time. In this case, carrying capacity declined in each time step based on the linearly interpolated habitat suitability projections for each habitat patch. Because *C. verrucosus* is embedded within an urban landscape and abuts the coast, its habitat contracted in response to climate change in part because habitat shifts are limited by the coast and development. We started with the current distribution and ended with the distribution modeled using the 2070–2099 average climate projections and ran our simulations for 100 years. We calculated the percentage habitat area lost per patch based on sequential HSM predictions, then reduced carrying capacity in each time step in the model by a constant amount per time step to achieve the projected decline. This produced a time series of HSMs that defined the spatial component for the population model in each time step.

Habitat Loss and Fragmentation from Development

To estimate future habitat loss and fragmentation due to anthropogenic changes in land use, we used the San Diego Association of Government's assessment of developable land (http://www.sandag.org/resources/maps_and_gis/gis_downloads/land.asp). All land identified as developable (approximately 33% of the occupied habitat) was excised from the habitat maps;the resulting map was used as the basis for simulations under the threat of development. This is a worst-case scenario, as all the habitat is removed at the onset of the simulation.

Simulations

We used RAMAS GIS® (Akçakaya 2005) to link the spatial arrangement of patches, the stochastic age-based matrix population model, and the stochastic fire functions. Initial population sizes of patches were estimated using average densities from field surveys. Stand age is equal to time since last fire; because *C. verrucosus* primarily forms even-aged cohorts, the age class of the initial population reflected the last recorded fire. Initial seedbank abundance was estimated by multiplying the average number of seeds per individual for each age class by the population size.

A sensitivity analysis was performed on model parameters or groups of parameters generated by the same function by perturbing their values (Table A-1). The model was deemed sensitive to a parameter if the relative difference in model output was greater than the initial extent of perturbation. Stochasticity was incorporated through Monte Carlo simulations for 1,500 replications over a 100-year time period to account for natural variation in the fire events and the demographic rates of the population. Expected minimum abundances (EMAs) across the 1,500 replications and average population trajectories were used to compare across treatments (McCarthy and Thompson 2001). Seed numbers were excluded from simulated population totals.

Table A-1. *Ceanothus verrucosus* sensitivity analysis results.

Model*	% change in parameter	EMA	% Change from Basic Model
Basic Model**		2800	
Stage 1 (seedbank longevity) +10% yrs	1.1%	2946	5.2%
Stage 1 (seedbank longevity) +20% yrs	2.0%	3177	13.5%
Stage 1 (seedbank longevity) +30% yrs	2.8%	3446	23.1%
Stage 2	10%	3482	24.4%
Stage 2	-10%	2137	-23.7%
Stage 3	10%	3429	22.5%
Stage 3	-10%	2300	-17.9%
Stage 4	10%	3254	16.2%
Stage 4	-10%	2451	-12.5%
Stage 5	10%	3249	16.0%
Stage 5	-10%	2370	-15.4%
Stage 6 **	10%	3051	9.0%
Stage 6	-10%	2227	-20.5%
Stage 7	10%	3257	16.3%
Stage 7	-10%	2365	-15.5%
Stage 8	10%	3096	10.6%
Stage 8	-10%	2212	-21.0%
Stage 9	10%	2883	3.0%
Stage 9	-10%	2232	-20.3%
Stage 10 ***	-10%	2422	-13.5%
Stage 11	-10%	2437	-13.0%
Stage 12	-10%	2430	-13.2%
Stage 13	-10%	2574	-8.1%
Stage 14	-10%	2427	-13.3%
Stage 15	-10%	2556	-8.7%
Stage 16	-10%	2500	-10.7%
Stage 17	-10%	2308	-17.6%
Stage 18	-10%	2332	-16.7%
Stage 19	-10%	2513	-10.3%
Stage 20	-10%	2634	-5.9%
Stage 21	-10%	2431	-13.2%
Stage 22	-10%	2514	-10.2%
Stage 23	-10%	2279	-18.6%
Stage 24	-10%	2609	-6.8%
Stage 25	-10%	2594	-7.4%
Stage 26	-10%	2393	-14.5%
Stage 27	-10%	2460	-12.1%

Model*	% change in parameter	EMA	% Change from Basic Model
Stage 28	-10%	2555	-8.8%
Stage 29	-10%	2591	-7.5%
Stage 30	-10%	2644	-5.6%
Stage 31	-10%	2578	-7.9%
Stage 32	-10%	2598	-7.2%
Stage 33	-10%	2651	-5.3%
Stage 34	-10%	2832	1.1%
Stage 35	-10%	2779	-0.8%
Stage 47	-10%	2788	-0.4%
Fecundities Stage 10	10%	2826	0.9%
Fecundities Stage 10	-10%	2773	-1.0%
Fecundities Stage 30	10%	2763	-1.3%
Fecundities Stage 30	-10%	2782	-0.6%
Fecundities Stage 47	10%	2875	2.7%
Fecundities Stage 47	-10%	2824	0.9%
Germination (post fire)	10%	3353	19.8%
Germination (post fire)	-10%	2231	-20.3%
Germination (post fire)	20%	3620	29.3%
Germination (post fire)	-20%	1747	-37.6%
Germination (post fire)	30%	4284	53.0%
Germination (post fire)	-30%	1304	-53.4%
longevity yrs +10%	2.9%	2824	0.9%
longevity yrs -10%	-6.4%	2705	-3.4%
longevity +20% yrs	4.5%	2944	5.1%
longevity -30% yrs	5.6%	3013	7.6%
remove vegetative reproduction	100%	2608	-6.9%
Double carrying capacity	100%	2803	0.1%
Halve carrying capacity	-50%	2719	-2.9%
Double germinant carrying capacity	100%	2739	-2.2%
halve germinant carrying capacity	-50%	2794	-0.2%
* each model run included 1500 replications.			
** grayed stages are not sensitive to parameter changes.			
*** from stage 10 to 47 the modeled survival is 0.998 or higher so only a decrease was evaluated			

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Appendix B—*Chorizanthe orcuttiana* Life History and Population Demographic Model

Methods

Distribution and Life History

Chorizanthe orcuttiana Parry occurs in the coastal chaparral of southern California and northern Baja California (Hickman 1993). Globally, it is ranked as G1, a critically imperiled species (CNPS 2009), and is listed as endangered under the ESA. It is a winter annual that occurs in sandy gaps in the maritime chaparral and Diegan coastal sage scrub. It experiences periodic recruitment failures due to drought (Bauder 2005) and appears to have a persistent seedbank, based on reports of populations appearing after the removal of long-established ice-plant cover (Bauder 2005).

C. orcuttiana's restricted range likely reflects biotic and ecophysiological limitations. As for many narrow-niche endemics, limiting factors are not well known; even though the species' range is small, limiting factors may vary in different circumstances (Kluse and Doak 1999). *C. orcuttiana* occurs on sandy soils in openings in the maritime chaparral within 5 km of the coast and less than 100 m in elevation. The soil's water holding capacity is very low (average sand fraction 90.2%). Shade intolerance and poor seed dispersal may contribute to the species' lmited range (Kunin and Gaston 1993; Kluse and Doak 1999; Fox *et al.* 2006).

C. orcuttiana experiences highly variable climatic conditions. The coefficient of variation of January and February precipitation within its range was 67% over the last century. This variability is similar to that of coastal habitats of other *Chorizanthe* species (Fox *et al.* 2006), as well as southwestern deserts, which are known for their high environmental variability (Clauss and Venable 2000). Long-lived seeds create a storage effect, buffering the population from environmental variation and allowing the species to persist under unpredictable conditions (Fox *et al.* 2006).

How and when the sandy openings that comprise its habitat form, and how long they persist, are important questions because *C. orcuttiana* does not grow under shrub canopies. Consequently, changes in the spatial extent of these openings are important to population persistence. Recently at Pt. Loma, the size of one subpopulation expanded after nonnative *Acacia* shrubs were removed (Bryan Munson pers. comm.). The expansion, on the order of meters, may have resulted from either dispersal or a dormant seedbank. *C. orcuttiana* does not require fire for any part of its life cycle; because the openings where it occurs are sparsely vegetated (Bauder 2005), fire likely skips over them, or they are subject to low-intensity patchy fire (Davis *et al.* 1989). It is possible, however, that fire could have indirect effects on this species by influencing gap formation. Fires could increase suitable habitat adjacent to existing populations, or it could remove canopy cover that had been suppressing undetected populations present as seed only. It is likely that some seed remains viable after fire (Davis *et al.* 1989).

Two nonnative species, ice-plant (*Mesembryanthemum* spp.) and *Acacia* spp., threaten *C. orcuttiana* through encroachment into the canopy gaps where it occurs (Kimberly O'Connor pers. comm.). In addition, exotic annual grasses may pose a risk (CBI 2000). In southern California, *Chorizanthe* species tend to occur in sandy openings with few nonnative grasses (Bauder 2005, CBI 2000). However, in coastal scrub habitats in northern California, *Vulpia myuros,* an exotic annual grass, has been shown to compete heavily with other *Chorizanthe* species (Zador 1993 in Kluse and Doak 1999). While ice-plant and acacia effectively close canopy gaps and exclude *C. orcuttiana*, annual grasses coexist as competitors (Kluse and Doak 1999).

Unlike many narrow-niche endemics in MTEs, *C. orcuttiana* is not currently threatened by high levels of development because its current distribution (there are only six known subpopulations) occurs entirely within park or military lands not at risk of land use conversion. It is likely that there are few if any undetected populations, as thorough efforts have been recently made to survey additional suitable habitat (Bauder 2005). However, if unknown populations exist, they may be threatened by development.

Our study includes all known populations (Figure 2 main report), which extend approximately 40 km from Point Loma, near downtown San Diego, north to Encinitas. Known populations occur within 3 km of the coast and comprise six subpopulations separated by more than 175 meters. The populations range from around 10 m^2 to 1,000 m^2 in area and total 0.25 hectare. We used detailed population maps with population counts (Bauder 2005; Department of the Navy unpublished data) as a complete inventory of the known U.S. population.

Demographic Model Structure

Demographic Model Structure and Parameterization

The model is a spatially explicit stage-based matrix model structured with a 1-year time step. Seed dispersal is assumed not to occur between subpopulations. The relevant life history characteristics for this annual plant are germination, survival to seed production, seed production, seed viability, seed predation, annual germination from the seed bank, and annual seed bank mortality. Our model is limited to two stages: a seedbank and an adult stage. Transitions (Figure B-1) are functions of: 1) the proportion of seeds germinating (S_g) and mortality in the seed bank (S_m); 2) seed germination (S_g) and germinant survival to seed production (G_s); and 3) seed production (F_a), seed viability (S_v), and seed predation (S_p). We parameterized the model with available field data for this species: 8 years of population counts, seed counts from a single year, and one set of germination trials (Bauder 2005). Table B-1 includes vital rates and variation. Vital rates were drawn from a lognormal distribution using the specified means and standard deviations.

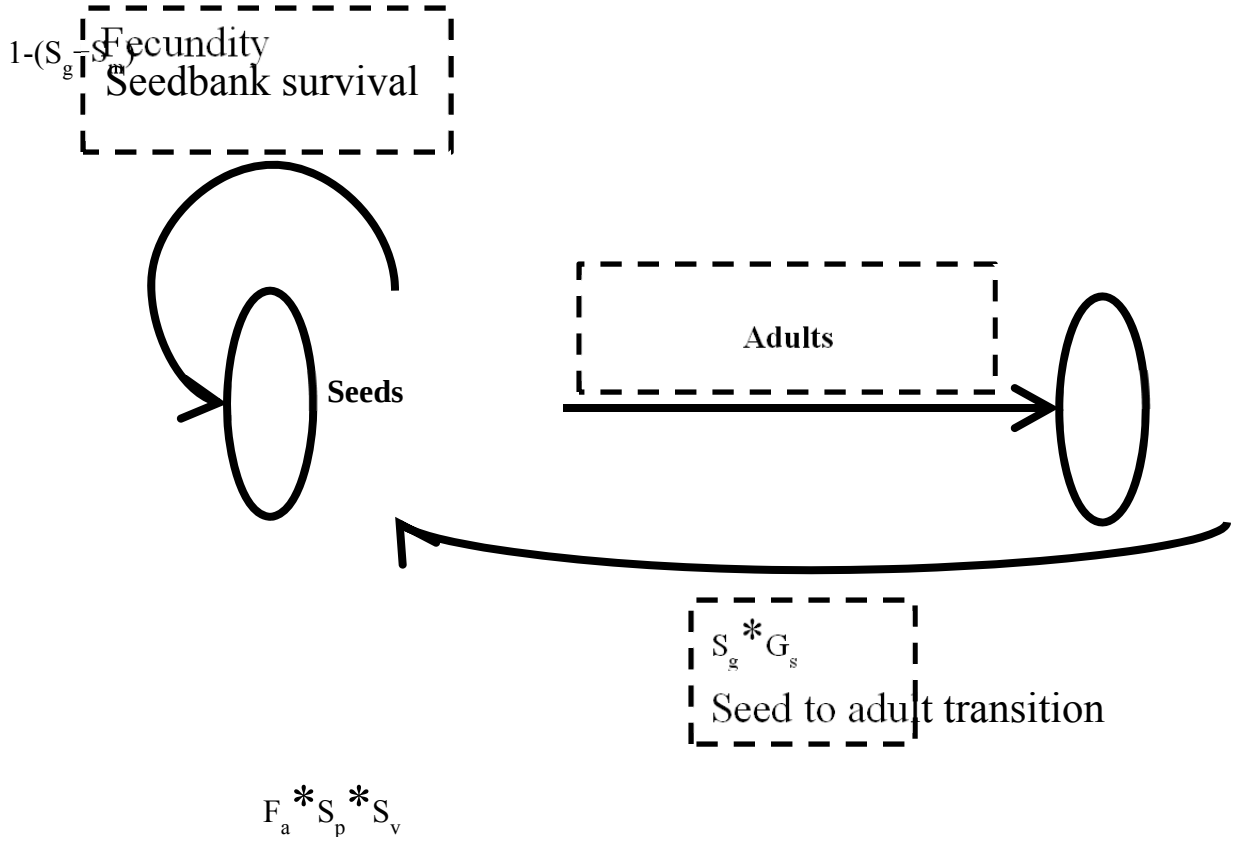

Figure B-1. Life history diagram with transition equations.

The model has very high uncertainty due to lack of data on seedbank longevity and germination rates and scarce data on fecundity. Survival rates were estimated from an eight-year series of population counts (from 1998 to 2005), fecundity from a single year (Bauder 2005) and germination from a congener (Fox *et al.* 2006). We used collateral data from *Lobularia maritima* a Mediterranean perennial herb from which also occupies openings in coastal scrub habitats, to estimate seed predation (Retana *et al.* 2004). We assumed an arbitrary seedbank size to calculate the seed to adult transition as only annual population count data and a rough estimate of seedbank longevity were available.

Seedbank

We parameterized seed survival (S_{sb}) in the seedbank (Table B-1) as

$$S_{sb} = 1 - (S_g + S_m) \qquad \text{Eq. 1}$$

where S_g is the proportion of seed germinating (0.087) (Fox *et al.* 2006) and S_m is the mortality of seeds that do not germinate (0.14), which we calculated using an exponential decay function with an assumed seedbank longevity of 20 years. The 20-year seedbank longevity is based on the appearance of a population of *C. orcuttiana* after ice-plant removal; evaluation of air photos indicated the seedbank was likely covered for more than two decades (K. O'Connor unpublished data). This resulted in a seed survival rate of 0.77. Because the estimate of seedbank longevity is highly uncertain, we used sensitivity analysis to evaluate 10- and 30-year seedbank longevity as

well, which gave seed survival estimates of 0.65 and 0.82, respectively. To represent variation, we assumed a coefficient of variation (CV) of 0.10 for S_m and used the CV (0.17) for S_g (Fox *et al.* 2006) to calculate an overall CV of 0.22. Our standard deviation was thus 0.17 for the baseline case of a seedbank longevity of 20 years.

Table B1. Mean vital rates ± 1 standard deviation includes survival in the seedbank, transition from seeds to adults, and adult fecundity. Because this is an annual plant the survival of adults is zero.

	Seeds	Adults
Seeds	0.77±0.17	24.19±19.97
Adults	0.083±0.071	0±0

Fecundity

We used 64.5 seeds per plant (based on 27 plants harvested in a dry year) for seed production (F_a) and 0.625 for seed viability (S_v) from a study of *C. orcuttiana* (Bauder 2005). For seed predation (S_p), we used an estimate of ant predation of 0.6 for a short-lived perennial (*Lobularia maritima*) of near-coastal areas of the Mediterranean region (Retana *et al.* 2004). Thus, we parameterized seed production as 24.19 viable seed per plant, including predation. While these data are for *C. orcuttiana*, with the exception of predation, they are from a single year. The variability between plants within a single year is unlikely to represent the full extent of the environmental variability from year to year (Levine *et al.* 2008). Therefore we used the CV of seed production (0.83) for a congeneric (*Chorizanthe pungens*) from two sites in a 6-year study to estimate annual variation in seed production (Fox *et al.* 2006), yielding a standard deviation of 19.97. Fox *et al.* 2006 found infrequent effects of plant density on seed set; their data showed a strong correlation (0.78) between germinant survival and fecundity for *C. pungens*. Accordingly, we assumed positive correlation between fecundities and the seed-to-adult transition.

Seed-to-Adult Transition

Because only data on population counts at flowering (Figure B-2) were available, we parameterized the seed-to-adult transition rate to include both germination and germinant survival to fruiting adult, using projected population size as a function of climate and an assumed seedbank size. We used linear regression with population counts (Bauder 2005) and independent variables (correlation coefficients < 0.28) derived from current climate data (1977–2006) to predict the population size. Monthly precipitation and temperature data were available from Lindberg Field within the study area (Figures B-3 and B-4) (Western Regional Climate Center 2009a, 2009b). We used total precipitation and average maximum temperature values over different periods to define six precipitation and temperature variables corresponding to winter (January–February), spring (March–May), and the growing season (January–May) to evaluate the best predictors of annual population counts. Spring precipitation and winter temperature had a correlation coefficient of greater than 0.28 and so was not included in our evaluations.

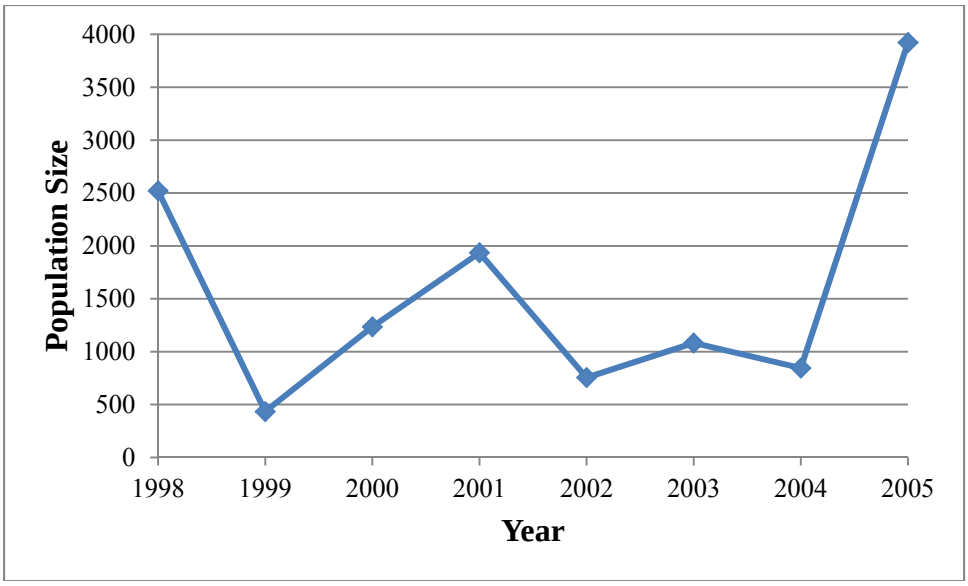

Figure B-2. Total *Chorizanthe orcuttiana* population size from all subpopulations at Pt. Loma by year.

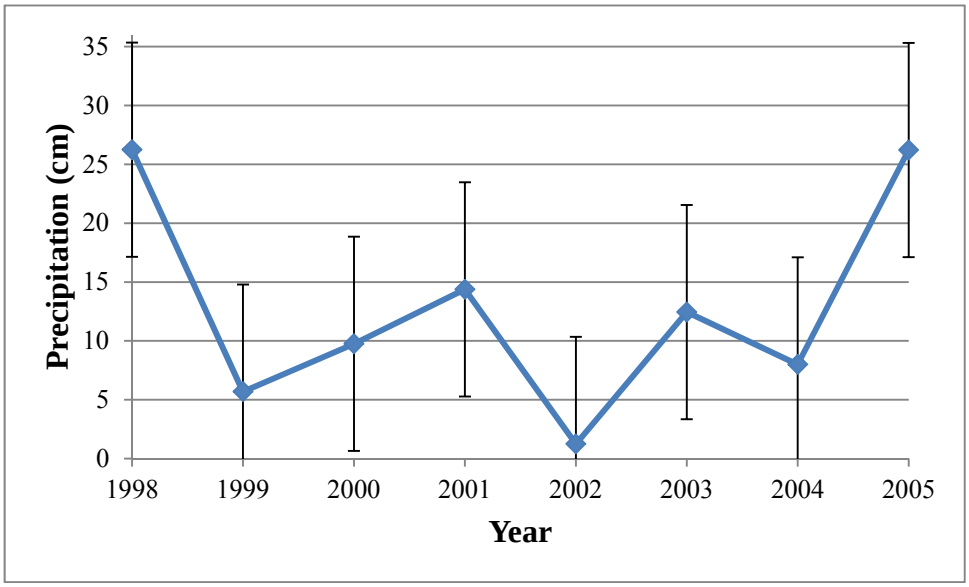

Figure B-3. Total January and February precipitation and long-term mean and stdev from Lindberg Field (Western Regional Climate Center 2009a). Error bars display 1 standard deviation.

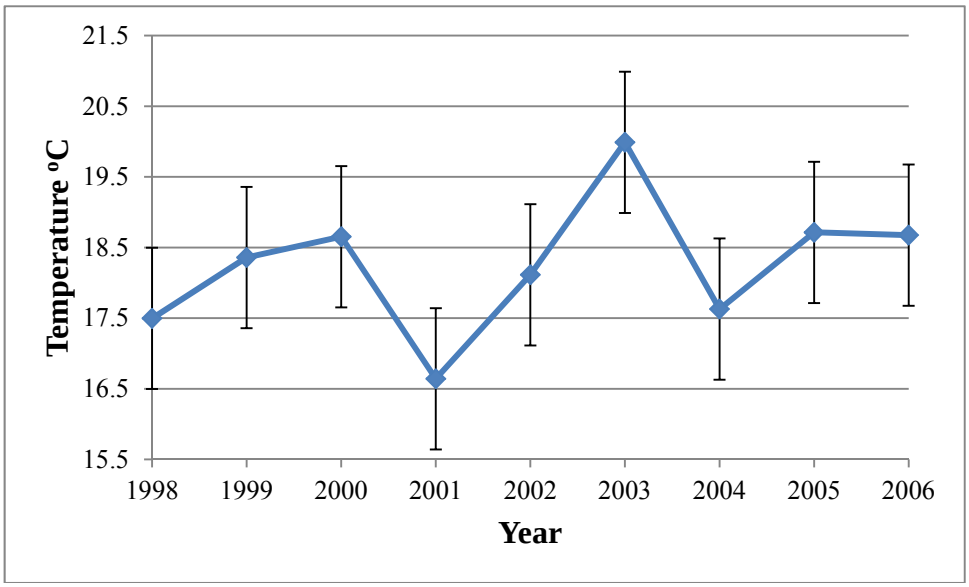

Figure B-4. Average January and February maximum temperature from Lindberg Field (Western Regional Climate Center 2009b). Error bars display 1 standard deviation.

Winter precipitation was the best single predictor ($r^2 = 0.83$) of population size; the temperature variables by themselves were very poor predictors ($r^2 < 0.06$). The best model, based on model fit (r^2) (Eq. 2) used winter precipitation and winter average maximum temperature and an interaction term ($r^2 = 0.94$, $p < 0.0073$), but winter precipitation with spring average maximum temperature ($r^2 = 0.93$) or growing season average maximum temperature ($r^2=0.93$) were almost as good. Annual adult population size at flowering (n) was calculated as

$$n = 2681.2 + 121.97 * (ppt) - 144.311(t) + 88.12.(ppt - 13) * (t - 18.2) \quad \text{Eq. 2}$$

where ppt = total January and February precipitation in cm, and t = average maximum January and February temperature in °C. The time period when the population counts (Figure B-2) were collected included both extremes and intermediate values in precipitation (including precipitation that was more than two standard deviations from the mean) (Figure B-3) and temperature (Figure B-4) and thus provided a strong basis for predicting adult population size as a function of temperature and precipitation.

To estimate the seed-to-adult transition probability we created distributions of January and February total precipitation and temperature (correlation coefficient = -0.12 for the period 1977–2006). We used bootstrapping to represent observed variability in these variables and then inserted them in equation 2 to calculate a distribution of population sizes. We used climate data from a 30-year period, the conventional timeframe over which to characterize climatic parameters (Guttman 1989), to reflect the variability in the climate that is not likely to be fully encompassed in the 8-year time series during which *C. orcuttiana* population size data were collected.

We parameterized a drought catastrophe with a probability of 0.16 of occurrence, for temperature and precipitation combinations that lie above the curve in Figure B-5. Droughts are

periods of deficiencies in water supply and encompass a wide range of definitions (Wilhite *et al.* 2007). Indices have been developed to synthesize factors influencing water availability into a single number (Hayes *et al.* 1999). We used a taxon-specific definition of drought based on equation 2 rather than a standard drought index, because while climatic variables are strongly correlated with *C. orcuttiana* population size, the standard indices are not (unpublished data). This lack of correlation is likely a reflection of the fact that definitions of droughts and the indices developed to characterize them are functions of both the climatic regime and the social or environmental impact of concern (Wilhite *et al.* 2007). We set equation 2 equal to zero and calculated the temperature for the range of precipitation values that occurred from 1977 to 2006 at Lindberg Field to develop the curve in Figure B-5. Figure B5 shows that as precipitation increases, the temperature associated with a predicted zero population size increases. Our definition of drought includes the zero population curve and the area above it in Figure B-5. This relationship reflects the interaction between precipitation and evapotranspiration (highly influenced by temperature) in drought stress (Hanson 1991). We calculated the mean (0.083) and standard deviation (0.071) of the seed-to-adult transitions using the positive population estimates divided by the proportion of seed that germinate (S_g) or die (S_m), multiplied by an arbitrary seed bank size of 100,000 as an estimate of G_s. In the time step in which the drought catastrophe occurs, survival in the seedbank (S_{sb}) remains constant but the seed-to-adult transition (S_g*G_s) is set to zero.

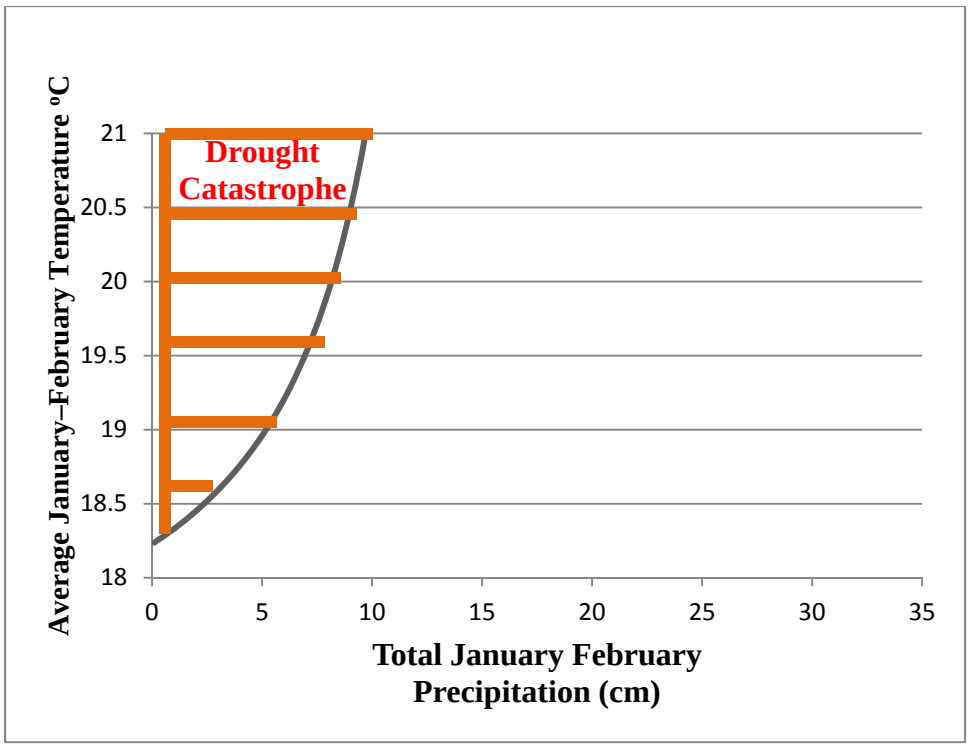

Figure B-5. Curve showing zero projected population size as a function of temperature and precipitation. A drought catastrophe occurs when the combination of temperature and precipitation lies on or above the curve. Drought catastrophes do not occur when precipitation exceeds 9.5 cm. The range of average January February temperature from 1977 to 2006 was 16.6–21.0°C. The range of total January February precipitation from 1977 to 2006 was 1.2–35.1 cm.

Carrying Capacity

Density dependence was modeled as a ceiling threshold on carrying capacity of adults. If a population exceeds the carrying capacity it is reduced to the carrying capacity in the next time step. We set carrying capacity based on an estimated maximum plant size of 64 cm^2 per plant or 156 plants per m^2, and we assumed plants filled the available space (with no overlap) at carrying capacity.

Probability of Fire

We incorporated stochastic fire events into our demographic model by means of a hazard function based on the Weibull function (Moritz 2003). The probability of a fire as a function of time since the last fire was modeled as

$$f(\mathrm{t}) = (ct^{c-1}/b^{c})\exp(-(t/b)^{c})$$

where t is the time since last fire, b is a scale parameter related to the average fire return interval, and c is the shape parameter that reflects the degree to which fire hazard changes with time since last fire. To represent the current fire regime we used parameters developed by Polakow *et al.* (1999) for mixed chaparral along the southern California coast using data from the Santa Monica Mountains (c = 1.42; b = 40.26). These parameters give a roughly 35-year average fire return interval. We tested fire intervals from 20 to 120 years by changing the value of the scale parameter, b, to represent the current fire regime (Polakow 1999), increasing and decreasing fire frequency (Moritz 2003; Syphard *et al.* 2007b), and conditions relevant to conservation management (Cabrillo National Monument 2005).

Simulations

We used RAMAS GIS® (Akçakaya 2005) to link the spatial arrangement of patches, the stochastic age-based matrix population model, and the stochastic fire functions. Initial population sizes of adults were estimated at 8.5 plants per m^2 based on observed average densities in extant populations. The number of seeds was estimated using the relative final stage abundances after a 50-year initialization period (seedbank = 0.989; adults = 0.011).

We ran two alternative sets of simulations to evaluate 1) the effects of post-fire shrub canopy closure GCGS1, and 2) exotic annual grass invasion GCGS2. To model the effects of canopy closure we gradually reduced carrying capacity to zero over an 80-year period. Fire is modeled as a catastrophe according to a Weibull hazard function (Moritz 2003). When a fire occurs, the woody canopy is removed and germination of seeds from the seedbank can occur. In the model, the carrying capacity is reset to its maximum amount to reflect habitat for GCGS1 (open sandy sites) increasing immediately after fire and then decreasing over time as the canopy closes. We selected 80 years because, based on the absence of dead stems within the openings occupied by *Chorizanthe orcuttiana* on Pt. Loma, it is likely that the openings can persist for this length of time. Fire last burned on Pt. Loma in approximately 1912 (Zedler 1995). The canopy likely closed 10–20 years later (Hanes 1971). If the canopy openings were a result of shrub ramet or genet mortality, we would expect to see the dead remnants (Keeley 1992). Indeed, we sampled stems of *Ceanothus verrucosus* at Pt. Loma that, based on ring counts, persisted for more than 70 years after death. Consequently, the lack of dead woody stems in the openings occupied by *Chorizanthe orcuttiana* means that they likely date to sometime around the last fire.

To model the effects of annual grass invasion, the initial carrying capacity of GCGS2 was set to 10% of modeled carrying capacity to reflect a population where annual grasses are already established. Like the canopy closure scenario above, fire is modeled as a catastrophe. Annual grasses are typically reduced by fire for 1–2 years, but the effects largely disappear 2–3 years after a burn (Klinger *et al.* 2006). In the time step after fire occurs, carrying capacity is restored to 100%. It is subsequently reduced in the model over a 2-year period to 10% to reflect the temporary nature of exotic annual grass control by fire. We used 90% reduction in carrying capacity, as Brooks and Berry (2006) found that annual grasses can account for up to 91% of the biomass of an annual community in an arid environment.

A sensitivity analysis was performed on model parameters by perturbing their values by ±10% with the exception of seedbank longevity, which was changed to represent a change in longevity of ±10 years (Table B-2). The model was deemed sensitive to a parameter if the relative difference in model output was greater than the initial extent of perturbation. The model included both demographic and environmental stochasticity, which were incorporated through Monte Carlo simulations for 1,500 replications over a 100-year time period. This accounted for natural variation in the fire events and the demographic rates of the population. EMAs across the 1,500 replications and average population trajectories were used to compare across treatments (McCarthy and Thompson 2001). Seed numbers were included in simulated population totals.

Table B-2. Sensitivity analysis results.

Model*	% change in parameter	Expected Minimum Abundance	% Change from Basic Model
Stage Matrix			
Basic (drought but no fire catastrophes)**		525574.6	0.0%
Fecundity Adults +10%	10%	562355.6	7.0%
Fecundity Adults -10%	-10%	475081.9	-9.6%
Seedbank longevity =10 years; seed to seed transition= 0.6541	10%	225045.8	-57.2%
Seedbank longevity =30 years; seed to seed transition= 0.8180	-10%	615734.3	17.2%
Seed to adult +10%	10%	540877.9	2.9%
Seed to adult-10%	-10%	482210.1	-8.3%
Alternate Catastrophe Scenarios			
GCGS1 FRI=35 (reduce K to 0 over 80 years post fire catastrophe)		149842.2	-71.5%
GCGS2 FRI=35 (set K to 10%, increase to 100% after fire, decline to 10% within 2 years post fire catastrophe)		430973.2	-18.0%
* each model run included 1500 replications.			
** grayed stages are not sensitive to parameter changes.			

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Appendix C—*Quercus dumosa* Life History and Population Demographic Model

Distribution and Life History

Quercus dumosa Nutt., a very long-lived shrub, occurs in the coastal chaparral of southern California and northern Baja California (Hickman 1993; Keeley 1993). Globally, it is ranked as a critically imperiled to imperiled species, intermediate between G1 and G2 (CNPS 2009). Like many narrow-niche endemics in MTE, it is threatened by high levels of development. Our study focuses on the U.S. portion of the range, which extends approximately 85 km north of the U.S. border with Mexico and 20 km inland from the coast and comprises 188 subpopulations (greater than 0.01 ha and separated by more than 44 meters) totaling 671 ha. We used detailed population maps with population counts for most of the U.S. range (Roberts unpublished data) supplemented by location-specific survey reports for some conservation lands and military installations (Dossey and Associates 2006; TDI 2007, CNLM unpublished data). We updated these maps using aerial photography and field surveys, and we estimated population sizes through direct counts or density estimates where sizes were not included in survey results and added several unrecorded populations, resulting in a complete inventory of the known U.S. population.

The species' restricted range likely reflects both biotic and ecophysiological limitations. Climate, based on its effect on seedling establishment, has been identified as differentially limiting the distribution of three Mediterranean oaks and is also likely to influence the range of *Q. dumosa*. Drought length, summer precipitation and temperature have been identified as influential climatic variables (Sharp and Sprague 1967; Purves *et al.* 2007). In addition, dispersal dynamics are thought to be an important influence in the size of oak range, which is correlated with acorn size (Aizen and Patterson 1990; Purves *et al.* 2007). Indeed, like its range, *Q. dumosa's* acorns are small (http://efloras.org).

Q. dumosa occupies the persistence niche with a strong resprouting response to disturbance (Bellingham and Sparrow 2000; Keeley *et al.* 2006). Because the persistence niche is associated with low post-disturbance mortality and low reliance on seedling establishment, species in this niche are more influenced by processes that affect adult survival than recruitment (Bond and Midgley 2001). In keeping with ecological theory that suggests that strong resprouters should perform best under high severity disturbances with intermediate to high frequency (Bellingham and Sparrow 2000), *Q. dumosa* has been shown to be resilient to high severity fires under a wide range of fire intervals (Keeley 1992).

For long-lived species such as *Q. dumosa*, resprouting sustains population sizes during long periods of poor or no recruitment (Bond and Midgley 2001; Abrahamson and Layne 2003). As would be expected for such species, mortality rates are high for juveniles but decline to very low levels in adults. Mature *Q. dumosa* resprout vigorously after fire and experience very low fire-related mortality. Individual stems turn over regularly, typically living less than 100 years (Keeley 1985). Due to resprouting, this individual *Q. dumosa* have lifespans on the order of centuries (Keeley 1993) and may live much longer (May *et al.* 2009).

Seedling establishment in oaks is highly episodic both spatially and temporally and reflects predation of both fruits and seedlings, as well as the frequency of sequential weather conditions that result in successful flowering, acorn production, germination, and survival of seedlings through the first two summers (Lawson 1993; Koenig and Knops 1996; Pulido and Diaz 2005; MacDougall *et al.* 2010; Rodriguez-Calcerrada *et al.* 2010). Over the life of a population it appears that recruitment of new individuals only occurs infrequently and in very old stands

(> 50–60 years). This does not necessarily mean that acorns never germinate, but seedlings of obligate resprouters do not typically survive in younger stands, presumably because of xeric conditions (Patric and Hanes 1964; Keeley 1992; Pratt *et al.* 2008; Pratt *et al.* 2010). Seedling presence is correlated with litter depth and litter biomass (Keeley 1992), and the lack of seedlings in younger stands may be because seedlings are physiologically less resistant to the high-stress post-fire environment than non-sprouters or facultative sprouters (Jacobsen *et al.* 2007; Pratt *et al.* 2008 Pratt *et al.* 2010). In addition, low light conditions appear to be required for successful scrub oak seedling establishment (Pratt *et al.* 2008). While all the factors required for successful seedling establishment are not fully understood, it has been shown that understory conditions, potentially important to seedling establishment, continue to develop in southern California scrub oak stands up to 80 years after plant establishment (Black 1987; Johnson-Maynard *et al.* 2004).

When seedlings do establish, as has been shown for other oak species (Lawson *et al.* 1997), they tend to form a long-lived persistent seedling bank (Keeley 1992). Seedling establishment is most likely to occur under canopies in very old stands, but recruitment of saplings to the canopy requires the opening of a canopy gap through the mortality of individual stems or entire plants. Consequently, seedlings can persist for decades suppressed by the canopy until they die or a canopy gap forms (Keeley 1992; Lawson *et al.* 1997). Even though stand-replacing fires typical of chaparral can kill mature individuals (Keeley 2006), fire intensity varies significantly over relatively short distances (3–5 m) and mortality is correlated with soil heating (Odion and Davis 2000). The variation in fire intensity combined with the presence of well-developed basal burls allows survival and resprouting after fire. Because of this ability to survive fire, and the need for post–seedling establishment gap formation to allow recruitment to the canopy, it has been hypothesized that scrub oak species may require fires to recruit saplings to the canopy (Keeley 2000).

The acorns of *Q. dumosa* mature in a single season (Plumb *et al.* 1983), a characteristic that is typical of (Abrahamson *et al.* 2002a) but not exclusive to white oaks (Koenig *et al.* 1996). Acorn crops vary dramatically in size across oak species. Cyclical production of large seed crops is often referred to as masting, but the definitions of masting and mast years vary and are not clear cut (Silverton 1980; Kelly 1994; Herrera *et al.* 1998; Koenig and Knopps 2000; LaMontagne and Boutin 2009). Most published accounts of masting trees belong to the "putative" masting group, which includes species with high variation (CV > 1 to 1.2) but without definitive attributes of masting (Kelly 1994).

Despite the lack of specificity in the definition of masting, one relevant aspect with respect to model development is whether interannual distributions of acorn production reflect seed availability for germination. One of the hypothesized evolutionary strategies of masting—*predator satiation*—would result in the actual year-to-year distribution of seed available for germination to be different from the year-to-year distribution of seed production, because a disproportionate number of seeds escape predation in mast years. Predator satiation appears to occur in some oak species (Espalta *et al.* 2008) but not in others (Abrahamson and Layne 2003). In a study of scrub oaks in Florida, the authors concluded that predator avoidance is not likely to be occurring due to the relatively low temporal variability of crop sizes (CV < 1), and they suggested that this may be due to the small size of shrub ramets and consequent low number of acorns produced (Abrahamson and Layne 2003). Because *Q. dumosa* shares with the Florida species a number of factors that drive acorn production (discussed in more detail in *Fecundity*

below), we assume similar variability in production and do not include spikes in seed availability for germination that would result from predators being unable to track seed production.

Background—Use of Data from Congener Tree Species to Represent a Shrub

Quercus is a diverse genus comprising 23 species in California (CALFLORA) and is divided into three subgenera. Data from nine oak species (four from California, three from the Mediterranean, and two from Florida) and one obligate seeding shrub (*Malosma laurina*) were used to parameterize this model. The historical literature does not distinguish *Q. dumosa* from several other California scrub oaks: *Q. turbinella, Q. john-tuckeri, Q. cornelius-mulleri, Q. berberidifolia*, and *Q. pacifica* (http://www.efloras.org). As a result of this lack of distinction and *Q. dumosa's* very small range, there are virtually no vital rate data published for the currently recognized taxon. Most of the data reported from the literature as *Q. dumosa* are likely to be from the taxon currently recognized as *Q. berberdifolia*.

We prioritized the data from the white oak subgenus, scrub oaks, and oaks from MTEs for use in our model. However, with the exception of fecundity and adult mortality, all the data we used were from tree oak species. To gain some compatibility between the tree oak data and *Q. dumosa* for our transitions between subadult stages, we utilized portions of datasets that best represent closed canopy shrublands, which burn in high-intensity stand-replacing fires (Keeley *et al.* 2008).

Our survival data for the germinant, small seedling, seedling, and sapling size classes came from a study of the effects of fire on *Q. engelmannii* and *Q. agrifolia* (Lawson 1993). In those woodlands, seedling and sapling recruitment occurs both under and outside the canopy, with significantly higher growth rates and lower mortality outside the canopy (Lawson *et al.* 1997). To represent the low light environment of the chaparral understory in the absence of fire (Davis and Mooney 1986; Pratt *et al.* 2008), we used data from unburned individuals in control plots and unburned individuals in burn plots that occurred under the canopies of mature oaks.

To represent survival of these stages after high-intensity stand-replacing fires we used only data from severely burned individuals (Table C1, damage class 1) to represent post-fire transitions. Overall fire intensity is less for fires in oak woodlands than in chaparral (Lawson 1993; Keeley 2000). The fire temperature in oak woodlands (average 118–213°C, maximum 302°C) (Lawson 1993, unpublished data) only reached the lower end of the range (250–500°C) typical for chaparral fires (Keeley 2000), and chaparral fires can be much hotter (775–925°C) (Odion and Davis 2000). However, because fire effects on individuals depend on the severity of the damage (Moreno and Oechel 1989; Lawson 1993), selecting the subset of individuals with a level of fire damage similar to that caused by a chaparral fire is a reasonable method of representing this functional type. Lawson (1993) recorded two measures of fire severity: diameter of smallest twig remaining (Moreno and Oechel 1989) and percent ground surface burned within 0.5 meter of the plant, along with a class rating of fire damage (Table C-1). Keeley *et al.* (2008) reported minimum stem diameter of remaining plants to be zero (entire plant consumed) to 4.9 cm for five large chaparral fires. The individuals in damage class 1 were a reasonable surrogate for estimating post-fire survival in scrub oak because they had: 1) a high average surface area burned around the plant, 2) an average minimum stem diameter of 0.19 cm, 3) a range of 0–4.1 cm for minimum stem diameter remaining, 4) no photosynthetically active tissue remaining, and 5) almost 20% of individuals completely consumed by fire.

Table C-1. Fire severity indicators by damage class including average surface area burned within 0.5 m of the plant, average minimum diameter of remaining stems (calculated without zeros), presence of post-fire photosynthetically active tissue, and the percent of individuals where above ground tissue was completely consumed by fire. Only individuals in damage class 1 were used in this model to estimate survival following the high-intensity stand-replacing fires typical of scrub oak. All data are from Lawson (unpublished data).

Damage class	N	Average Surface Area Burned Mean (stdev)		Average Minimum Stem Diameter (cm) Mean (stdev)		Range Stem Diameter	Photosynthetically Active Tissue	% Completely Consumed by Fire
1	580	78%	(22%)	0.19	(0.21)	0–4.1	N	18%
2	261	58%	(27%)	0.11	(0.07)	0.05–1.0	N	N/A
3	1168	54%	(31%)	0.10	(0.07)	0.05–1.0	Y	N/A
4	366	13%	(24%)	0.10	(0.03)	0.05–0.2	Y	N/A

Unlike tree oak species, seedlings of scrub oak are rarely reported from stands less than 50–60 years old (Keeley 1992) and optimal conditions for seedling establishment my take up to 80 years after fire to develop (Black 1987; Johnson-Maynard *et al.* 2004). There is evidence that seedlings do germinate (Keeley 1981; Keeley *et al.* 2006) and it is likely that the occasional seedling survives, but the mortality of seedlings of obligate seeders after fire is very high (Thomas and Davis 1988). We represented this by reducing seedling survival for 80 years after fire (see *Post-Fire Germinant Establishment* below).

Therefore, in summary, while our model relies heavily on data from a study of tree oaks (Lawson 1993) it is an approximation of the obligate resprouting shrub *Q. dumosa* because we implemented the procedures listed below.

1. Calculated transitions in the absence of fire between small seedling, seedling, and sapling stages using only individuals growing under the canopy to represent the low light environment typical of closed canopy scrub oak chaparral communities (Keeley 1992; Bond and Midgley 2001; Pratt *et al.* 2008).
2. Calculated post-fire transitions between small seedling, seedling, and sapling stages using only severely burned individuals (Table C-1) to represent high intensity stand replacing fires typical of scrub oak communities (Keeley *et al.* 2008).
3. Parameterized very low germinant survival for 80 years after fire to represent a phenomenon reported in a number of studies for *Q. dumosa* (likely *Q. berberdifolia*)—i.e., that seedlings only occur in very old stands (Patric and Hanes 1964; Frazer and Davis 1988; Thomas and Davis 1989; Keeley 1992).

Demographic Model Structure and Parameterization

The model is a spatially explicit stage-based matrix model structured with a 2-year time step and incorporating dispersal. The first two stages are age-based and the remaining four are size-based. The model includes acorns, germinants (year of germination plus the next year), small seedlings (<15 cm height), seedlings (15–49.99 cm height), saplings (>49.99 cm height), and adults (>149.99 cm height). This structure reflects the high and variable mortality in acorns and

germinants, which declines and becomes more stable in older individuals where fecundity and mortality are related more to size than to age (Silvertown and Charlesworth 2001). Fire is incorporated in the model as a catastrophe: an extreme environmental fluctuation independent of the variability modeled in the standard deviation matrix, which occurs with a specified probability. Vital rates were drawn from a lognormal distribution with the specified means and standard deviations (Table C-2).

Table C-2. Transition rates between stages per 2-year time step ± 1 standard deviation. The values in the top row are fecundities, and the remainder represent the proportion of individuals that transition from one stage (column) to the next (row). The diagonal represents individuals that remain in the same stage. Numbers below the diagonal represent individuals that move to a larger size class. Numbers above the diagonal represent individuals that move to a smaller size class.

Mean Vital Rates Matrix						
	Acorns	Germinant	Small seedling	Seedling	Sapling	Adult
Acorns	0 ± 0	0 ± 0	0 ± 0	0 ± 0	11.6 ± 6.3	147.2 ± 87.3
Germinant	0.04 ± 0.0156	0.3158 ± 0.7063	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Small seedling	0 ± 0	0.0782 ± 0.1748	0.4190 ± 0.0958	0.0665 ± 0.0318	0.0034 ± 0.0003	0 ± 0
Seedling	0 ± 0	0.0147 ± 0.0015	0.2027 ± 0.0883	0.6081 ± 0.1076	0.0290 ± 0.0109	0 ± 0
Sapling	0 ± 0	0 ± 0	0.0012 ± 0.0001	0.1093 ± 0.0579	0.8208 ± 0.1055	0.000001 ± 0.000001
Adult	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.01024 ± 0.001	0.9802 ± 0.0050

Fecundity

We used the data from a 27-year time series for two white oak species that, like *Q. dumosa*, produced acorns that matured in a single year (Abrahamson and Layne 2003). Unfortunately, no studies of acorn production for scrub oak were available from MTEs. We evaluated acorn production cycles and factors influencing crop size variance to determine whether these species were acceptable surrogates for *Q. dumosa*. Both Florida species had 2- to 3-year cycles in annual crop sizes, just as those reported by Koenig *et al.* 1996 for tree oaks in California's Mediterranean-type climate. In addition, spring temperatures during flowering have been shown to drive acorn production in white oaks (Sharp and Sprague 1967; Sork *et al.* 1993; Koenig *et al.* 1996), and the CVs for average spring month (March–May) temperatures was similar for central Florida (2–4%) (http://www.sercc.com/cgi-bin/sercc/cliMAIN.pl?fl0369) and coastal southern California (3%) (Western Regional Climate Center 2009). On the other hand, Abrahamson and Layne (2003) found that precipitation was a significant driver of acorn crop size in three of six species-by-site combinations, and that precipitation during the wettest month is much more variable in coastal southern California (CV = 104%) than in central Florida (CV = 51%). Finally, small stature is thought to reduce variability of fecundity in scrub oaks compared to trees as the upper bound on crop size is constrained (Abrahamson and Layne 2003). We concluded that due to the similarity in length of crop cycles, variance in spring temperatures, and plant stature, these species were reasonable surrogates for *Q. dumosa*.

All size classes were used to parameterize acorn production from adults because adult plants have ramets of all size classes; the two smallest classes were used to parameterize sapling acorn production. We used data on the number of ramets per genet from a study of *Q. agrifolia* and *Q.*

engelmannii to represent the number of stems per sapling (Lawson unpublished data). While these data are from tree species that typically have fewer stems than shrubs (Hickman 1993), they come from a high fire environment, which produces multi-stemmed growth forms in typically single-stemmed species (Lawson 1993). Seed production and seed size is generally inversely correlated within phylogenetic groups of plants (Silvertown and Charlesworth 2001; Abrahamson and Layne 2003). Since seed size is similar between the two species and *Q. dumosa* (*Q. geminata* 15–20 mm x 9-12 mm, *Q. chapmanii* 15–20 mm x 9-13 mm, and *Q. dumosa* 10–20 mm x 5–10 mm) (http://efloras.org), no adjustment was made for it. Because acorns do not survive more than a single year, acorn survival was parameterized as zero.

Post-Fire Fecundity

In the year of the fire, no acorns were produced; in the first year after fire, fewer than 2% of ramets produced acorns. Averaged over the size classes of both species, these ramets produced 65% the number of pre-fire acorns. By the fifth year after fire, both *Q. geminata* and *Q. chapmanii* had equaled or exceeded the percentage of acorn-bearing ramets and the number of acorns per ramet compared to pre-burn levels (Abrahamson and Layne 2002b). However, it is likely that the total number of acorns produced per genet continues to increase with canopy volume. Accordingly, we parameterized post-fire acorn production at from 1.3% of mean values (Table C-2) in the first time step after fire and increased this to the mean values over a 14-year period to represent the time to canopy closure (Hanes 1971).

Germination

Because of the lack of data on germination rates for scrub oaks, we used germination rates from *Q. ilex*, a Mediterranean tree species (Pulido and Diaz 2005). Acorn predation is subsumed in these rates. The average germination based on the number of viable acorns and including acorn predation and germination is 0.02. The value for the 2-year time step thus became 0.04 (Table C-2). We used a CV of 0.39 (Rodriguez-Calcerada et al. 2010) from the survival of naturally established seedlings to calculate the standard deviation (0.0156) (Table C-2).

Post-Fire Germinant Survival

In general, limited data are available for post-fire survival of germinants of obligate seeding shrubs because they do not generally establish after fire (Pratt *et al.* 2008). We used 0.0001 based on data from another obligate seeding chaparral shrub (*Malosma laurina*) for the probability of germinant survival in the first time step after fire (Thomas and Davis 1989) and increased this by a constant amount per time step over 80 years (Black 1987; Keeley 1992; Johnson-Maynard *et al.* 2004) to reflect very low seedling establishment after fire. We modeled this factor as increasing over time because the presence of seedlings in mature stands is correlated with litter depth, which increases as canopy volume increases (Black 1987; Keeley 1992; Johnson-Maynard *et al.* 2004). Because this parameter is highly uncertain, we conducted a sensitivity analysis with no trend in germinant survival and a increase in germinant survival from 0 to the full parameter value over 50 years, as that is the time frame when seedlings begin to be reported from stands of *Q. dumosa*.

Survival

Survival and transition rates and their standard deviations (Table C-2) for the germinant, small seedling, seedling, and sapling stages in the absence of fire were taken from a study of *Q. engelmannii* and *Q. agrifolia* (Lawson 1993 and Lawson unpublished data) and included only those individuals growing under the canopy of mature trees to represent a closed canopy system.

For transitions represented by a very small sample size (< 5 individuals), the standard deviation was set to 10% of the mean, and a sensitivity analysis was conducted on the parameter. This involved three uncommon transitions with very low mean rates among the following stages (Table C-2): germinant to seedling, small seedling to sapling, and sapling to small seedling. The observed 2-year survival rate of 0.1029 for germinant survival was split into the germinant to germinant (S_{gg}) survival and the germinant to small seedling transition ($T_{g\text{-ss}}$), such that it satisfied the following equation:

$$0.1029 = S_{gg} + \left(S_{gg} \times T_{g-ss}\right) \qquad \text{Eq 1}$$

Regrowth of adults after fire is rapid. While we do not have specific data, it is likely that most adults recover to the adult size class within the first time step (Hanes 1971; Keeley and Keeley 1981; Pausas 1997). We parameterized the adult-to-sapling transition after fire as 2%. The longevity of *Q. dumosa* is uncertain, although it is on the order of centuries. One study found many stands with no dead individuals and one 120-year-old stand where only 20% of the plants were dead (Keeley 1993). To parameterize adult survival, we used an exponential decay function to back-calculate survival based on an adult longevity of 300 years. Because this is highly uncertain, we performed a sensitivity analysis to evaluate a range of life spans from 250 to 400 years.

Post-Fire Survival

Post-fire survival and transition rates for the germinant, small seedling, seedling, and sapling stages in the absence of fire were taken from a study of *Q. engelmannii* and *Q. agrifolia* (Lawson 1993 and Lawson unpublished data) and included only individuals that were severely burned (Table C-1) to represent stand-replacing crown fire systems. These rates were used to calculate multipliers (Table C-3) that were applied to the stage matrix (Table C-2) when a fire occurs.

Mature scrub oak are rarely killed by fire, regenerating through vegetative resprouts (Hedrick 1951; Keeley 2000). We used data from the literature (Keeley 2006) to parameterize 98% survival after fire. Burned individuals remain in the adult size class as resprouts and typically exceed 1.5 m within 2 years after fire (Hanes 1971). Because this parameter comes from a study of six sites burned in a single year, and adult mortality is anticipated to be a primary driver of population dynamics in *Q. dumosa* (Bond and Midgley 2001), we performed a sensitivity analysis on it.

Table C-3. The catastrophe matrix consists of multipliers that are applied to the vital rates in Table C2 to reflect the effect of the catastrophe.

Catastrophe Matrix (multipliers)						
	Acorn	Germinant	Small seedling	Seedling	Sapling	Adult
Acorn	0	0	0	0	1	1
Germinant	0	1	0	0	0	0
Small seedling	0	1	0.6359	3.8150	1	0
Seedling	0	1	0.0295	0.1227	17.235	0
Sapling	0	0	0	0	0.3046	20000
Adult	0	0	0	0	0	0.99

Dispersal

An exponential function decreasing with distance was used to estimate dispersal rates:

$$M_{ij} = a \times e^{-D_{ij}/b} \text{ when } D_{ij} \leq d_{max} \quad \text{Eq 2}$$

where M_{ij} is the rate of dispersal between the ith and j^{th} patch, a is the maximum dispersal rate between very close patches, D_{ij} is the distance between the patches, b is the average dispersal distance, and d_{max} is the maximum dispersal distance for a single time step. Only acorns are allowed to disperse. We parameterized a as 0.1 to reflect the availability of multiple patches to disperse to avoid, as much as possible, all propagules dispersing to each available patch, potentially resulting in unrealistically high dispersal rates out of each patch. The choice of 0.1 was arbitrary, and we used sensitivity analysis to evaluate the effect of the maximum dispersal rate on model results. Acorns are primarily dispersed by small mammals and birds (den Ouden 2004). We used data from *Q. robur* and *Q. petraea* to parameterize small mammal dispersal of acorns (den Ouden 2004) and from *Q. ilex* to parameterize jay dispersal of acorns (Gomez 2003). Average dispersal distance was 321 m for jays and 28 m for mice. The maximum dispersal distance was set at 2,000 m (den Ouden 2004). We created two separate patch-to-patch dispersal rate matrices based on these parameters, multiplied each by the respective proportion of the acorn crop they dispersed, and summed them to create the final dispersal matrix. We used the average (47%) of three widely varying estimates of the proportion taken from the canopy (Gurnell 1993; Tanton 1965 in den Ouden 2004) to represent jay dispersal and the remainder (53%) to represent small mammal dispersal. Because dispersal of acorns by vertebrates is thought to be directed to suitable habitat (Gomez 2003; Purves *et al.* 2007), it was not necessary to parameterize additional loss to represent caching in unsuitable habitat.

Carrying Capacity and Density Dependence

Population carrying capacity was modeled as a ceiling threshold reflecting total available suitable habitat for each age class (Lawson *et al.* 2010). Maximum carrying capacity was estimated set to 2,420 adults/ha, the maximum reported density in the literature (Keeley 1992). Initial abundance of adults was estimated at 19.18/ha based on survey data (CNLM unpublished data; Roberts unpublished data; Dossey and Associates 2006 TDI 2007). The ratio of seedlings and saplings per adult was set to 2.05 times the number of adults (Keeley 1985, 1989). The total initial population of all stages thus was 58.50/ha. Estimated relative sizes of the stages (acorns were excluded from density dependence) were used to establish the ratio of the number of plants in an age class to the largest plants (Table C-4, average weights); small seedlings were estimated to be two times larger than germinants, seedlings were estimated to be two times larger than small seedlings, saplings were estimated to be five times larger than seedlings, and adults were estimated to be six times larger than saplings. When the population exceeded carrying capacity, the vital rates (Table C-2) were gradually reduced until the population was less than or equal to the carrying capacity. This was achieved by multiplying survival and transition rates by "density dependence factors" once the population exceeded carrying capacity. These factors are applied to survival rates for plants remaining in the same stage (elements on the diagonal in the matrix) and forward transitions—i.e., the proportion of survivors moving to the next age class (elements on the lower subdiagonal in the matrix). The adjustments to vital rates vary by stage to reflect decreasing susceptibility to density-dependent mortality as plants become established (Morris *et al.* 2008). Once the population decreased to or below carrying capacity, these factors ceased to be applied.

Table C-4. The average weights are the ratio of the number of plants in a given age class to the largest plants (in this case "adults"). The average weights allow the populations of each stage to be converted into adult equivalents to determine when carrying capacity has been exceeded. When carrying capacity has been exceeded the density dependence factors are used to reduce vital rates.

Stage	Average weight	Density dependence factors
Germinant	0.008	0.50
Small seedling	0.017	0.40
Seedling	0.033	0.25
Sapling	0.167	0.10
Adult	1.000	0.05

Probability of Fire

We incorporated stochastic fire events into our demographic model by means of a hazard function based on the Weibull function (Moritz 2003). The probability of a fire as a function of time since the last fire was modeled as:

$$f(\mathrm{t}) = (ct^{c-1}/b^{c}) \exp(-(t/b)^{c})$$

where t is the time since last fire, b is a scale parameter related to the average fire return interval, and c is the shape parameter, which reflects the degree to which fire hazard changes with time since last fire. To represent the current fire regime, we used parameters developed by Polakow et al. (1999) for mixed chaparral along the southern California coast using data from the Santa Monica Mountains (c = 1.42; b = 40.26). These parameters give a roughly 35-year average fire return interval. We tested fire intervals from 20 to 120 years by changing the value of the scale parameter, b, to represent the current fire regime (Polakow 1999), increasing and decreasing fire frequency (Moritz 2003; Syphard et al. 2007b), and conditions relevant to conservation management (Cabrillo National Monument 2005).

Simulations

We used RAMAS GIS® (Akçakaya 2005) to link the spatial arrangement of patches, the stochastic stage-based matrix population model, and the stochastic fire functions. Initial population sizes of patches were estimated using average densities from field surveys to represent adults, and the number of juveniles per adult from the literature to represent the other stages.

A sensitivity analysis was performed on model parameters by perturbing mean vital rate values and three standard deviations (germinant to seedling, small seedling to sapling, and sapling to small seedling) by $\pm$10% (Table C-5). The model was deemed sensitive to a parameter if the relative difference in model output was greater than the initial extent of perturbation. In addition, sensitivity analyses were performed on 1) the maximum dispersal rate evaluating values of 0.05 and 0.15, 2) post-fire adult survival evaluating values of $\pm$0.5% (this corresponds to catastrophe matrix multipliers for adult survival of 0.9951 and 0.9850) and plant lifespan, which (adult to adult survival) was evaluated at 250 years (2-year survival of 0.9763) and 400 years (2-year survival of 0.9851). Stochasticity was incorporated through Monte Carlo simulations for 1,500

replications over a 100-year time period to account for natural variation in the fire events and the demographic rates of the population. Expected minimum abundances (EMAs) across the 1,500 replications and average population trajectories were used to compare across treatments (McCarthy and Thompson 2001). Acorn numbers were excluded from simulated population totals.

Table C-5. Sensitivity analysis results.

Model*	% Change in Parameter	Expected Minimum Abundance	% Change from Basic Model
Stage Matrix			
Basic**		59.1	0.0%
Transitions			
Fecundity saplings +10%	10%	58.0	-1.9%
Fecundity saplings -10%	-10%	58.4	-1.2%
Fecundity adults +10%	10%	60.5	2.4%
Fecundity adults -10%	-10%	56.8	-3.9%
Acorns to germinants +10%	10%	60.1	1.7%
Acorns to germinants -10%	-10%	57.5	-2.7%
Germinants to germinants +10%	10%	59.6	0.8%
Germinants to germinants -10%	-10%	58.8	-0.5%
Germinants to small seedlings +10%	10%	59.5	0.7%
Germinants to small seedlings -10%	-10%	58.2	-1.5%
Germinants to seedlings +10%	10%	60.3	2.0%
Germinants to seedlings -10%	-10%	59.8	1.2%
Small seedlings to seedlings +10%	10%	59.4	0.8%
Small seedlings to seedlings -10%	-10%	58.9	1.2%
Small seedlings to saplings +10%	10%	59.6	0.8%
Small seedlings to saplings -10%	-10%	61.0	3.2%
Small seedlings to small seedlings +10%	10%	60.2	1.9%
Small seedlings to small seedlings -10%	-10%	58.4	-1.2%
Seedlings to small seedlings +10%	10%	59.2	0.2%
Seedlings to small seedlings -10%	-10%	58.5	-1.0%
Seedlings to seedlings +10%	10%	61.1	3.4%
Seedlings to seedlings -10%	-10%	58.0	-1.9%
Seedlings to saplings +10%	10%	59.8	1.2%
Seedlings to saplings -10%	-10%	58.2	-1.5%
Saplings to small seedlings +10%	10%	59.3	0.3%
Saplings to small seedlings -10%	-10%	59.1	0.0%
Saplings to seedlings +10%	10%	59.9	1.4%
Saplings to seedlings -10%	-10%	58.9	-0.3%
Saplings to saplings +10%	10%	62.8	6.3%
Saplings to saplings -10%	-10%	57.5	-2.7%
Saplings to adults +10%	10%	59.9	1.4%
Saplings to adults -10	-10%	58.1	-1.7%
Adults to adults (+ 0.5% to a 400 yr lifespan)	0.50%	69.6	17.8%
Adults to adults (- 0.4% to a 250 yr lifespan)	-0.40%	52.4	-11.3%

Model*	% Change in Parameter	Expected Minimum Abundance	% Change from Basic Model
Standard deviations			
Germinants to seedlings stdev +10%	10%	59.8	1.2%
Germinants to seedlings stdev -10%	-10%	58.7	-0.7%
Small seedlings to saplings stdev +10%	10%	58.8	-0.5%
Small seedlings to saplings stdev -10%	-10%	58.7	-0.7%
Saplings to small seedlings stdev +10%	10%	59.7	1.0%
Saplings to small seedlings stdev -10%	-10%	57.8	-2.2%
Germinants to germinants stdev (stdev=mean)	-55%	58.8	-0.5%
Germainant to small seedlings (stdev=mean)	-55%	60.2	1.9%
Post-fire trend in survival			
Post-fire trend in germinant survival over 50 years	37.5%	63.7	7.8%
Catastrophe Matrix			
Post fire adult survival +0.5% (catastrophe matrix value 0.9951)	0.5%	59.6	0.8%
Post fire adult survival -0.5% (catastrophe matrix value 0.9850)	-0.5%	59.8	1.2%
* each model run included 1500 replications.			
** grayed stages are not sensitive to parameter changes.			

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Appendix D—*Neotoma macrotis* Life History and Population Demographic Model

Methods

Distribution and Life History

Neotoma macrotis is a widespread species occurring in woody habitats including chaparral, coastal sage scrub, oak and riparian woodlands, and coniferous forests in coastal central and southern California and in the Sierra Nevada at elevations less than 5,000 ft. (Kelly 1990; Matocq 2002; Braswell 2007). It is widespread within our study area, occurring mainly in chaparral, and is associated with *Malosma laurina* (Schwilk and Keeley 1998; G. Fleming unpublished data). Globally, it is ranked as G5, a secure species (NatureServe 2009).

Woodrats are nocturnal rodents active year-round. They are small, with an adult weight of 200–350 grams (g) (McEachern *et al.* 2007), and typically produce between one and five litters per year. Juveniles mature in 9–12 months and live for an average of 1.6 years with (Matocq 2002) and a maximum of 3–4 years (Lee and Tietje 2005). *N. macrotis* was previously considered part of *N. fuscipes* and was only recently separated (Matocq 2002). Our study area is well within the the species' range, which extends approximately 120 km inland from the coast in San Diego County, approximately 50 km south of the U.S.-Mexico border, and almost 500 km north.

They build large aboveground stick houses (Cunningham 2005) and are territorial with respect to house usage, but they exhibit spatial overlap in home ranges (McEachern *et al.* 2007). Home range size appears to be density dependent in females (Kelly 1990); for a closely related species, *N. fuscipes* (Matocq 2002), significant home range overlap (up to 25% in the non-breeding season) can occur (Cranford 1977). Matocq and Lacey (2004) in a study of individually marked females found that *N. macrotis* was not strongly philopatric, although others have found evidence of philopatry, which may be influenced by density dependence (Kelly 1989; McEachern *et al.* 2007). Dispersal is typically age dependent, involving subadults (Matocq and Lacey 2004; Cunningham 2005,).

Precipitation, through its effect on food resources, has been shown to be important to small mammal population dynamics (Meserve *et al.* 2001; Lima *et al.* 2002). Annual precipitation is thought to drive population dynamics through its influence on food availability in our study area (Dana Morin pers. comm.). Although small mammals are expected to increase in abundance in response to extreme precipitation associated with El Niño Southern Oscillation events (Jaksic 2001; Braswell 2007), woodrat populations in coastal southern California did not show a response (Braswell 2007).

Woodrats are very sensitive to fire. In fact, unburned refugia appear to be required for woodrats to survive the moderate to hot fires typical of chaparral (Wirtz *et al.* 1988; Schwilk and Keeley 1998). Wirtz *et al.* (1988), in a study of four chaparral burns, found that no marked woodrats survived experimental fires. It can take up to 2 years for woodrats to colonize new habitat after fire (Wirtz 1982; Wirtz *et al.* 1988), but this is dependent on the location of source populations and can be impeded by habitat fragmentation (McGregor *et al.* 2008).

Woodrats are highly affected by habitat fragmentation. Bolger *et al.* 1997 concluded that rodents in fragmented habitats in San Diego were incapable of colonizing fragments where populations had been extirpated. This may be because they generally do not cross roads even if traffic is light (McGregor *et al.* 2008). In a study of small mammal use of road rights of way (ROWs) and adjacent habitats, *N. fuscipes* presence was negatively correlated with ROWs (possibly due to lack of woody cover), and they were not found road-killed (Adams and Geis 1983). Rather than being killed crossing roads, they may be avoiding them, as small mammals have been shown to

avoid the road surface itself independent of the amount of traffic or noise (McGregor *et al.* 2008).

The combination of fire sensitivity and road avoidance may mean that this species, which is thought to be secure, may not be able to persist within the study area without periodic reintroduction due to high levels of fragmentation from land conversion and road development and the presence of catastrophic wildfire. In other words, the threat from habitat loss for this species is not so much the direct loss of habitat but the disruption of landscape-level processes—specifically colonization of extirpated patches after fire.

The preservation of woodrat middens in desert regions from the Pleistocene and Holocene has facilitated detailed documentation of woodrat response to climate change, including rapid climate change (Wells 1976; Smith and Betancourt 2003). Documented responses include adaptation through change in body mass as well as range shifts and extirpations. While individual species of *Neotoma* respond in different degrees to changes in summer and winter temperature, body size in this genus generally decreases as temperature increases (Smith and Betancourt 2003; Smith *et al.* 2009). As would be expected, demographic rates reflecting climatic parameters and fecundity in *N. macrotis* have been shown to be correlated with the preceding winter's low temperature (Lee and Tietje 2005).

We used known locations from museum specimens (San Diego County Mammal Atlas unpublished data; Scott Tremor pers. comm.) and modeled the species' current extent using Maxent. This approach predicted a very widespread distribution, but because the species is known primarily from woody habitats (Kelly 1990; Schwilk and Keeley 1998; Matocq 2002 Braswell 2007), we constrained its distribution to the current distribution of woody habitats.

Demographic Model Structure and Parameterization

The model is a spatially explicit age-based matrix model structured with a 1-year time step and includes dispersal. It includes four 1-year age classes with a maximum age of 4 years (Lee and Tietje 2005). The model includes only females. Demographic rates in small mammals are highly variable and are influenced by many factors, including precipitation and vegetation type (Kelly 1990; Lee and Tietje 2005; Braswell 2007). Demographic rates were taken from a mark and recapture study of *N. macrotis* (Kelly 1990). Vital rates were drawn from a lognormal distribution with the specified means and standard deviations (Table D-1).

Fecundity

Fecundity (Table D-1) was calculated from seven 3-year chronological matrilines as the number of female offspring per adult female (Kelly 1990). Matrilines start with a group of females that all breed. Consequently, to calculate fecundity estimates for all—not just successful—females, in addition to using the offspring of successful females, we estimated the number of unsuccessful females as follows.

1. For the individuals that did not reproduce, we assumed that the first year after an individual was born it had a probability of 0.44 x 0.40 (Table D-1) of being an unsuccessful mother; the second year we assumed that it had a 0.44 x 0.4 x 0.4 probability of being an unsuccessful mother.
2. We summed those probabilities to get the expected total number of unsuccessful females per year and used that in our calculation of average annual fecundity.

3. We used the average proportion of unsuccessful females in the second and third years to adjust the first-year fecundity estimate to include all females, not just successful mothers.

The standard deviation (Table D-1) represents year-to-year variation from the matrilines. We used 22% of the average annual fecundity value for ages > 1 year to represent fecundity in the first-year age class (Kelly 1990).

Table D-1. Mean vital rates. The numbers in the top row are fecundities and the numbers on the subdiagonal are transition rates from one age class to the next.

Age Classes	0–1 year	1–2 years	2–3 years	3–4 years
0–1 year	0.26 ± 0.062	1.19 ± 0.19	1.19 ± 0.19	1.19 ± 0.19
1–2 years	0.44 ± 0.037	0 ± 0	0 ± 0	0 ± 0
2–3 years	0 ± 0	.40 ± 0.033	0 ± 0	0 ± 0
3–4 years	0 ± 0	0 ± 0	.40 ± 0.033	0 ± 0

Post-Fire Fecundity

All animals are killed by fire (Wirtz *et al.* 1988); accordingly, we set fecundity and all survivals to zero in the time step after fire. Fecundity rates return to the original parameters in the next time step.

Survival

We used survival from Kelly (1989) and estimated variation from Lee and Tietje (2005): 0.44 for year 0–1, 0.40 for years 1–2, 0.40 for years 2–3, and approaching zero afterward. A CV of 0.084 for survival was calculated using annual survival over 3 years in high and low shrub density plots (Lee and Tietje 2005). We only used the data from the first 3 years of the study because of an explained decline in the population over the subsequent 3 years.

Post-Fire Survival

Post-fire survival was set to zero for one time-step (Wirtz *et al.* 1988; Schwilk and Keeley 1998).

Carrying Capacity

Density dependence was modeled as a ceiling threshold on the carrying capacity of adults, which allows exponential growth until all territories are occupied. If a population exceeds the carrying capacity, it is reduced to the carrying capacity in the next time step. We set carrying capacity to 34 adult females (it does not act on the 0–1 age class) per ha, based on home range size. We calculated average home range size (396 m^2) from Kelly (1989), excluding those territories not adjacent to other female territories and assuming a 25% overlap (Cranford 1977).

Dispersal

An exponential function decreasing with distance was used to estimate dispersal rates between two patches:

$$M_{ij} = a \times e^{-D_{ij}/b} when\ D_{ij} \leq d_{max}$$

where M_{ij} is the rate of dispersal between the ith and j^{th} patch, a is the maximum dispersal rate between very close patches, D_{ij} is the distance between the patches, b is the average dispersal distance, and d_{max} is the maximum dispersal distance for a single time step. We limited dispersal to the 0–1 age class to reflect natal dispersal (Matocq and Lacey 2004). We parameterized a as

0.1 to constrain the total proportion of individuals dispersing out of a patch to multiple nearby patches. Since the choice of 0.1 was arbitrary, we performed sensitivity analysis to evaluate the effect of the maximum dispersal rate on model results. We used 62.3 m as the average dispersal distance (Matocq and Lacey 2004) and 1,600 m as the maximum dispersal distance (Smith 1965). Because woodrats do not typically disperse across roads (Bolger *et al.* 1997; Adams and Geis 1983; McGregor *et al.* 2008) we used paved roads (http://www.sandag.org/resources/maps_and_gis/gis_downloads) to define polygons within which dispersal could occur between populations. To represent paved roads as dispersal barriers, dispersal was set to zero between populations occurring in different polygons regardless of how close they were to each other.

Probability of Fire

We incorporated stochastic fire events into our demographic model by means of a hazard function based on the Weibull function (Moritz 2003). The probability of a fire as a function of time since the last fire was modeled as:

$$f(\mathrm{t}) = (ct^{c-1}/b^{c})\exp(-(t/b)^{c})$$

where t is the time since last fire, b is a scale parameter related to the average fire return interval, and c is the shape parameter, which reflects the degree to which fire hazard changes with time since last fire. To represent the current fire regime, we used parameters developed by Polakow *et al.* (1999) for mixed chaparral along the southern California coast using data from the Santa Monica Mountains (c = 1.42; b = 40.26). These parameters give a roughly 35-year average fire return interval. We tested fire intervals from 20 to 120 years by changing the value of the scale parameter, b, to represent the current fire regime (Polakow 1999), increasing and decreasing fire frequency (Moritz 2003; Syphard *et al.* 2007b), and conditions relevant to conservation management (Cabrillo National Monument 2005).

Simulations

We used RAMAS GIS® (Akçakaya 2005) to link the spatial arrangement of patches (as determined by habitat suitability models), the stochastic age-based matrix population model, and the stochastic fire functions. We used the stable age distribution (Table D-2) to allocate initial abundances across the stages. Fire is modeled as a probabilistic catastrophe based on the Weibull function above. In the time step that the catastrophe occurs, the vital rates in Table D-1 are multiplied by zero.

Table D-2. The proportions for each age class in this table represent the stable age distribution of the model. It is based on survivals and fecundities and does not account for density dependence, stochasticity, or catastrophes (Akçakaya *et al.* 1999).

Age Class	Proportion
0–1 year	0.605
1–2 years	0.257
2–3 years	0.099
3–4 years	0.038

Initial population sizes of 19/ha were estimated based on the literature (Kelly 1990; Matocq and Lacey 2004; Lee and Tietje 2005).

A sensitivity analysis was performed on model parameters by perturbing their values by ± 10% (Table D-3). In addition, sensitivity analyses were run on the maximum dispersal rate evaluating values of $a = 0.05$ and $a = 0.15$. The model was deemed sensitive to a parameter if the relative difference in model output was greater than the initial extent of perturbation. Stochasticity was incorporated through Monte Carlo simulations for 1,500 replications over a 100-year time period to account for natural variation in the fire events and the demographic rates of the population. EMAs across the 1,500 replications and average population trajectories were used to compare model results (McCarthy and Thompson 2001).

D-3. Sensitivity analysis results.

Model	% change in parameter	Expected Minimum Abundance	% Change from Basic Model
Stage Matrix			
Basic Model		234	0.0%
Fecundity 0–1 year +10%	10%	319	36.3%
Fecundity 0–1 year -10%	-10%	178	-24.0%
Fecundity 1–2 year +10%	10%	360	53.7%
Fecundity 1–2 year -10%	-10%	88	-62.5%
Fecundity 2–3 year +10%	10%	292	25.0%
Fecundity 2–3 year -10%	-10%	175	-25.4%
Fecundity 3–4 year +10%	10%	259	10.6%
Fecundity 3–4 year -10%	-10%	206	-11.8%
Transition 0–1 to 1–2 +10%	10%	377	61.0%
Transition 0–1 to 1–2 -10%	-10%	44	-81.4%
Transition 1–2 to 2–3 +10%	10%	303	29.3%
Transition 1–2 to 2–3 -10%	-10%	151	-35.3%
Transition 2–3 to 3–4 +10%	10%	260	11.3%
Transition 2–3 to 3–4 -10%*	-10%	226	-3.4%
Transition 3–4 to 4–5 +10% (this adds a stage)*	10%	255	9.0%
* grayed stages are not sensitive to parameter changes.			

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Appendix E—*Ceanothus verrucosus* and *Quercus dumosa* Field Studies

Introduction

Our objective was to use the best available data supplemented with what could be collected in a short period of time to develop a framework for conservation decisions. Data were collected to support two of the models: *Ceanothus verrucosus* and *Quercus dumosa*. For the *C. verrucosus* model, post-fire seedling establishment data was collected for *C. verrucosus* and its congener *C. tomentosus.* In addition, because *C. verrucosus* only establishes after fire, we were able to use a novel method: relying on ring counts of dead standing individuals for determining long-term mortality. Using the ring count method to establish age at death, we were able to build on a previous study (Cummins 2003) to estimate minimum seedbank longevity. Finally, existing population spatial data for *C. verrucosus* and *Q. dumosa* were ground truthed; during this effort, new populations of *C. verrucosus* and *Q. dumosa* were mapped. The results of these field studies are reported here.

Methods

Post-Fire Recruitment—*C. tomentosus*

The original plan for this study was to sample up to five recently burned stands of *C. verrucosus* to document juvenile recruitment. However, we were able to find a only single site where *C. verrucosus* had burned in the 2003 wildfires. Because there were no other *C. verrucosus* stands that burned, we chose *C. tomentosus* as a surrogate. *C. tomentosus* has very similar qualitative life history characteristics, with the exception that *C. verrucosus* lives longer and vegetatively propagates through layering (Paul Zedler pers. comm.). We resampled six of MCAS Miramar's long-term monitoring plots that had burned in 2003. We used the methods described below, summarized from O'Leary (2003).

Each of MCAS Miramar's long-term monitoring plots was 25 by 25 m, marked at the corners with rebar. Corner locations were recorded with a sub-meter accuracy global positioning system (GPS) unit. Four 25 m transects were established within each plot from a baseline along one of the plot's four sides. They were placed randomly within each quarter of the plot with the constraint that they must be at least 2 m apart. Species richness, percent cover per species, shrub height and density, physical disturbance, land use, and percent ground cover of organic matter were sampled in each plot. On sloping surfaces, baselines were placed parallel to the contour on either the top or base of a plot depending on the approach to the plot. A modified point intercept method was used and cover sampled every 1 m starting at 0.5 m along the transects by recording all species that hit a vertically positioned rod. Density was sampled in 1 m increments along a 1 m belt placed randomly on one side of each transect. For each plant in the belt, species, height, and life stage (seedling, adult resprout, adult, and dead adult) were recorded. We relocated the transects most recently sampled and marked them at both ends with rebar to facilitate future resampling. We recorded plant height and added "dead seedling" as a life stage.

Fire Intensity

To estimate the fire intensity on each burned plot, we used methods from Keeley (1998), which modified those developed by Moreno and Oechel (1989). Moreno and Oechel found a strong correlation between minimum stem diameter (chamise) remaining and maximum fire temperature. We randomly selected one of the 1 m segments along the density transect on each of the four transects within a plot to collect these data. If there was no shrub in that segment, we collected data from the closest shrub in the belt. Following Keeley's (1998) method, we

measured the smallest diameter twig remaining that was at least 1 cm long and the height of the skeleton.

Post-Fire Recruitment—*C. verrucosus*

The objective of this study was to measure post-fire *C. verrucosus* establishment and mortality. In winter 2007–2008, one hundred forty-seven 1 square meter (m^2) plots were randomly established at Bernardo Mountain and one hundred twenty-five 2 m^2 plots were established at Crosby Estates. The plots were larger at Crosby Estates because the density was low. Transects were randomly located along baselines, and plots were randomly placed along the transects (15 transects at Bernardo Mountain and 10 at Crosby Estates). The plots along the transects were separated by a minimum of 2 m, the minimum distance to avoid spatial auto correlation in this community (Schmalbach et al. 2007). Site visits were made to determine when the seedlings began to emerge, and sampling was initiated at the end of February 2008 to ensure that all seedlings were marked and recorded. This is consistent with other work that found maximum seedling densities in late spring for *C. greggii* at Sky Oaks (Kummerow 1985). Each seedling was individually marked with a toothpick or wire (Figure E-1) to ensure that all establishment was accounted for. The sites were then visited monthly during the first year to determine survival, once at the end of the second year to monitor survival, and once early in the third year to monitor flowering. First year monitoring was completed in December 2008, when it was determined that sufficient rain had fallen to stop drought-related mortality. Second year monitoring was conducted in December 2009. Sampling to determine the proportion of plants flowering was conducted in March 2010. Cumulative survival was calculated for each sampling period the first year and at the end of the second.

Figure E-1. Marked live and dead *C. verrucosus* seedlings.

Population Structure, Long-Term Mortality, and Vegetative Recruitment in Mature Stands

Since *C. verrucosus* reproduces primarily by seed in the first year after fire, it forms even-aged stands (Zedler 1995). We considered resampling transects established by others to obtain data on rates of mortality, but previous studies have not used permanently marked transects, though

some were documented using GPS units. In addition, and perhaps more importantly, that method would only yield data on rates since the last sample. Previous studies have used ring counts to age individuals at Cabrillo National Monument (Zedler 1995) and for *Ceanothus* species in general (Keeley 1993), and dead stems in chaparral have been documented to persist for up to a century (Keeley 1992). Accordingly, we collected stem cross sections from all dead individuals and made ring counts to reconstruct mortality over time.

The transects were 50 m long and 4 m wide. We recorded vegetative cover, density, size structure, and layering using Zedler's (1995) methods and collected a stem cross section from each dead individual within the belt transect. GPS coordinates were collected for each transect and the transects were permanently marked with rebar to facilitate relocation.

We used density data from Zedler (1995) in sample size calculations, using the formula n = (Z)2*(stdev)2/B, where Z is the standard normal deviate for a given confidence level and B is the precision level expressed as half the chosen confidence interval width. Because this equation underestimates the needed sample size, a corrected n based on Kupper and Hafner (1989) was taken from a table based on the calculated n (Elzinga et.al. 1998). The result was eight transects for a 90% confidence level and a precision level of $\pm$ 20%

Transects were randomly selected stratified by aspect (east facing, west facing, and flat). We did not include transects whose sampling might affect populations of *Chorizanthe orcuttiana*. We navigated to the start point using a GPS unit with sub-meter accuracy. The transect was run in a random direction. If a randomly selected transect did not have any *C. verrucosus*, we did not use it. We randomly selected select three angles for each start point to ensure sufficient transects. Only one transect was run from each point; the additional angles were used only where the first had no *C. verrucosus*. If a transect crossed a previously selected transect, we did not use it. Transects that exit *C. verrucosus* chaparral were stopped at the edge of the population and were not used if less than 15 m long. The line intercept transect included only woody and suffrutescent species. For these individuals the following was recorded: species, intercept, and live or dead. Height of the canopy was measured every 10 m.

In the belt transects we recorded the following information.

- Location (along and distance from transect).
- Developmental stage (seedling [germinated within last year], sapling [less than 8 years old], mature, dead).
- Height (for mature individuals).
- Canopy dimensions for mature individuals (longest dimension and the longest dimension perpendicular to that).
- Layering—for *C. verrucosus* only, occurrence of layering for all prostrate branches (initiating, branches, separation, non-rooted) and origin (seed or vegetative).
- Origin—the base of the trunk on all sampled *C. verrucosus* was observed and evidence of a layering origin recorded. To be recorded as vegetative origin there must be evidence of a branch at the base of the shrub pointing toward the decaying branch of another shrub. If it is questionable it was recorded as such (Zedler 1995).
- All prostrate branches were recorded as initiating, rooted branches, separated, or non-rooted using the following definitions from Zedler (1995):

    - initiating—if a branch has fine white adventitious roots
    - rooted branches—if a branch is strongly rooted
    - separated—these are strongly rooted branches where the branches beyond the new rooting node are larger than the proximal
    - non-rooted—prostrate branches with no roots.
- For each individual dead *C. verrucosus* within the crown area, the percentage of the crown area occupied was estimated.
- Stem cross sections - All dead *C. verrucosus* were cut at the base and a slab removed to age the plant at death through ring counts. The cut was be made below the lowest branch and, if necessary, below ground level.

Twenty-eight dead adult *C. verrucosus* were collected on 17 transects established on Naval Base Pt. Loma and Cabrillo National Monument (Figure E-2). Stem cross sections were sanded and the rings counted (Figure E-3). Due to the typically irregular growth pattern, multiple counts were sometimes required to determine the oldest axis. Once the oldest axis was established, three counts were made and averaged for each individual. One cross section was missing from Transect 449 meter 2.5; rather than leave this out of the analysis, it was assigned the mean longevity of those individuals that died on transect 449. This seemed less inaccurate than assuming that it the plant did not die; its year of death thus was assigned as 1962.

Figure E-2. Collection of dead *C. verrucosus* at Pt. Loma.

Figure E-3. *C. verrucosus* stem cross section processed for ring counts.

Seedbank Longevity

Cummins (2003) made seed counts from soil samples taken from 16 pairs of live and dead wart-stemmed ceanothus that were sufficiently isolated to avoid seed rain from adjacent plants. Eight of those pairs were definitively relocated, and stem cross sections were taken to determine age at death. The same methods were used as earlier in this study to develop the adult mortality curve Because *C. verrucosus* forms even-aged stands, this approach allowed the length of time from death of the plant to seedbank sample collection to be established, thereby providing information on seedbank longevity. Due to the typically irregular growth pattern, multiple counts were sometimes required to determine the oldest axis. Once the oldest axis was established, three counts were made and averaged for each individual.

Population Maps

Habitat maps from the California Natural Diversity Database were updated by adding data from other studies (Dossey and Associates 2006; TDI 2007; CNLMN unpublished data; Fred Roberts unpublished data), excising developed lands from the polygons, and conducting extensive field surveys where mapped populations were verified and unrecorded populations added.

Results

Post-Fire Recruitment—*C. tomentosus*

C. tomentosus used as a surrogate due to life history similarities. Juvenile survival estimates were made by sampling monitoring transects on Marine Corps Air Station Miramar which burned in 2003 twice, in the fall of 2006 and in the fall of 2007. The results are shown in table E1.

Table E-1. *C. tomentosus* seedling survival the fourth year after fire.

N Transects	N Seedlings	Mean Survival	Std Dev Survival
6	1323	0.858	0.142

In the single *C. verrucosus* plot we were able to establish in areas burned by the 2003 wildfires, there were 34 dead *C. verrucosus* adults in the belt transects but only 6 seedlings in 2006 and 5 in 2005. The survival rate was 83%, but the density was almost an order of magnitude less. There were 0.41 adults/m^2 prior to the fire and 0.060 seedlings/m^2 in the same area 4 years after the post-fire seedling establishment event.

Post-Fire Recruitment—*C. verrucosus*

Survival

Survival was similar after germination on the two sites until June of the first year (2008). At that point, survival dropped at Crosby Estates and remained about 25% less than at Bernardo Mountain for the remainder of 2008 (Figures E-4 and E-5). The first year survival at Bernardo Mountain (Figure E-4) was 67% (stdev 30.7%; n = 94); at Crosby Estates (Figure E-5) it was 39.5% (stdev 38.7%; n = 72). Cumulative survival through the second year at Bernardo Mountain (Figure E-6) was 58.3% (stdev 51.2%; n = 94); at Crosby Estates it was 35.9% (stdev 45.1%; n = 72) (Figure E-7).

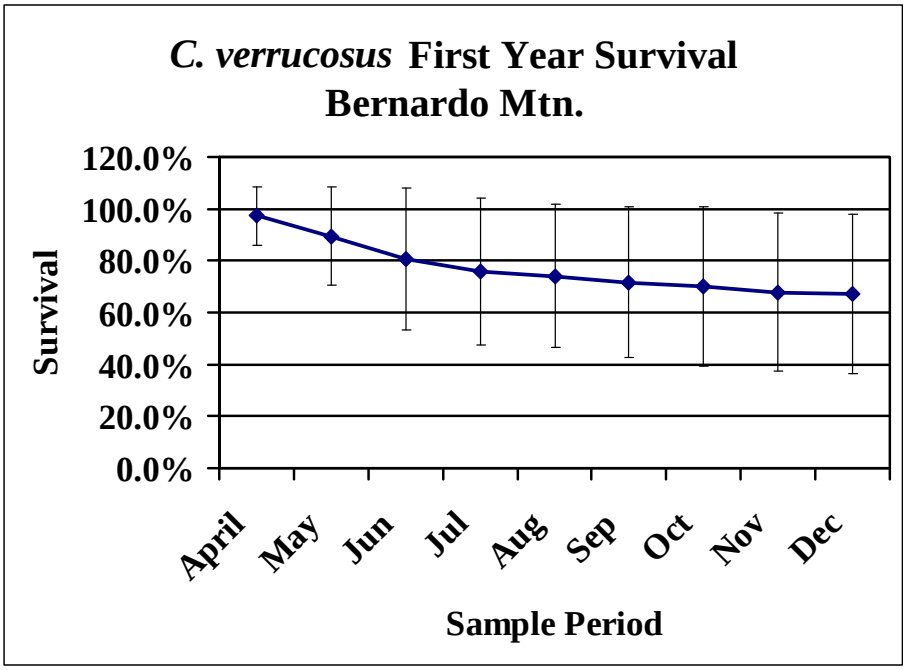

Figure E-4. Cumulative survival during the first year after fire (2008) at Bernardo Mountain.

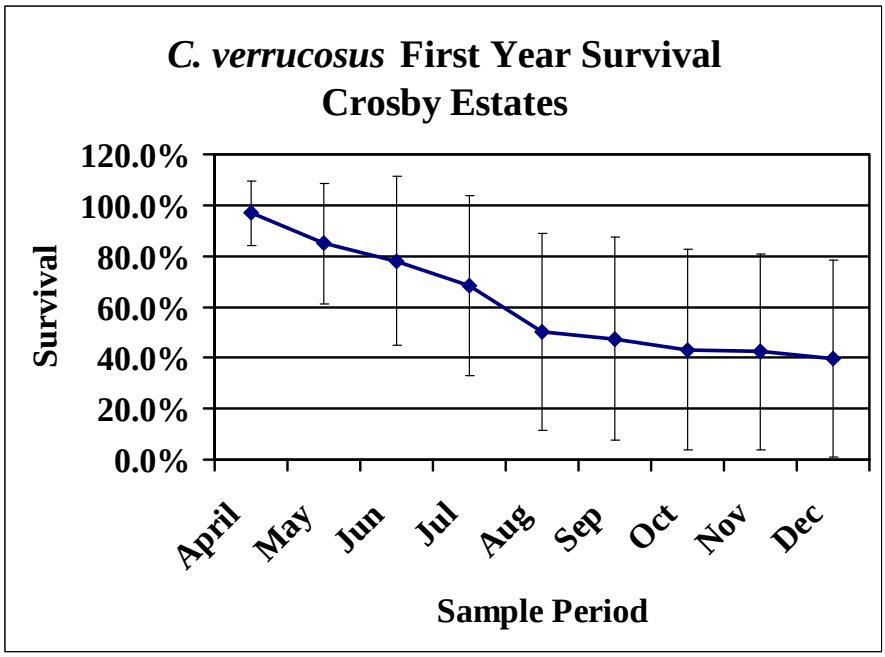

Figure E-5. Cumulative survival during the first year after fire (2008) at Crosby Estates.

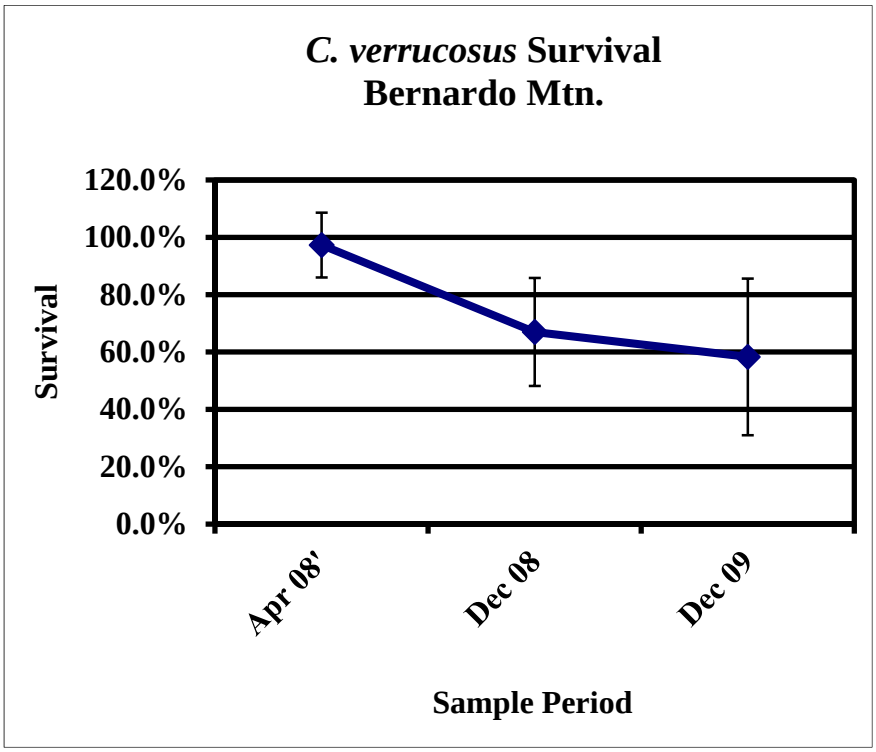

Figure E-6. Cumulative survival during the first 2 years after fire (2008–2009) at Bernardo Mountain.

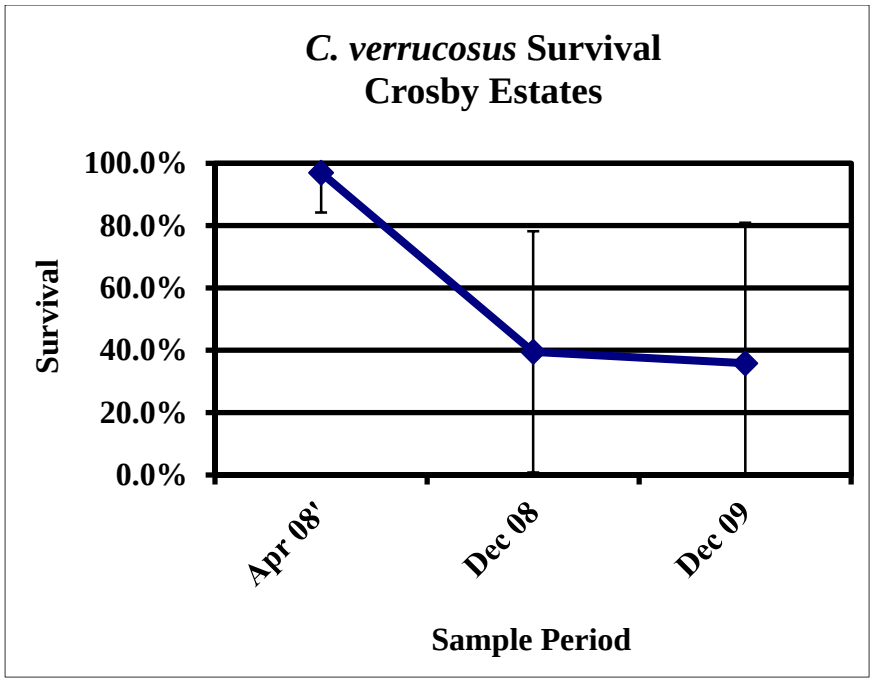

Figure E-7. Cumulative survival during the first 2 years after fire (2008–2009) at Crosby Estates.

Flowering

Seed production both at Bernardo Mountain and Crosby Estates began in the second year after fire (Figures E-8 and E-9). The number of plants flowering in each plot was recorded on March 11 and 15, 2010 (Table E-2). For the most part, flowering individuals were more than 50 centimeters (cm) tall, although flowers were found on plants as small as 25 cm. The numbers of flowers ranged from one to hundreds. The difference between the two sites was striking—the percentage flowering was almost five times more at Bernardo Mountain than at Crosby Estates. The spatial distribution, about one-third of the plots, was similar.

Table E-2. Percentage of *C. verrucosus* seedlings flowering.

Site	N plants	% Flowering	% Plots with Flowering Plants
Bernardo Mtn.	446	11.4%	31%
Crosby Estates	244	2.5%	37%

Figure E-8. Flowering and seed production at Bernardo Mountain—March 2010.

Figure E-9. Large 2-year-old *C. verrucosus* with hundreds of flowers at Bernardo Mountain—March 2010.

Bernardo Mountain appears to be better habitat for *C. verrucosus* than Crosby Estates, although the population at Crosby Estates is widespread on the site and, based on seedling densities, appears sustainable. Seedling density was not necessarily a conclusive indicator of higher suitability, because it would depend in part on pre-fire shrub density; however, survival was higher, and a much higher proportion of seedlings initiated flowering in the second year. *C. tomentosus* comingled with *C. verrucosus* (Figure E-10) at the higher elevations at Bernardo Mountain but not at Crosby Estates. A few small *C. tomentosus* were misidentified as *C. verrucosus* in some of the early sampling periods, but as all the seedlings were marked this was readily rectified as the plants grew.

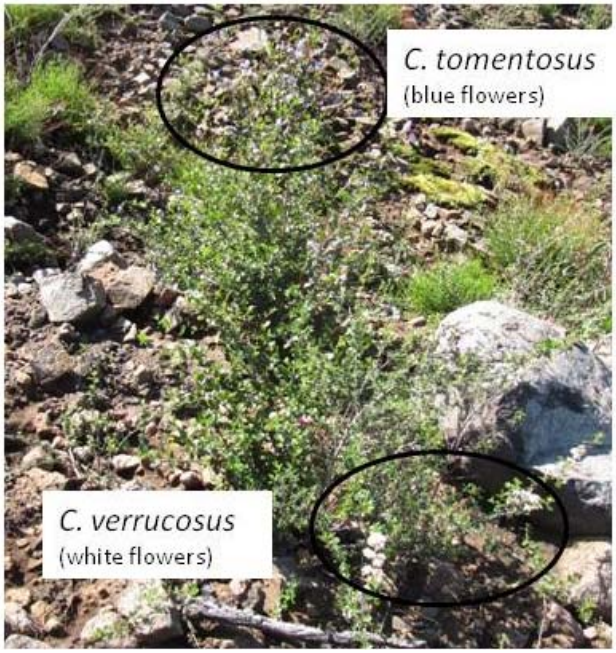

Figure E-10. *C. verrucosus* and *C. tomentosus* growing side by side at Bernardo Mountain.

Given average survival rates for obligate seeding species within the *Ceanothus* genus, these establishment rates are sufficient to establish stands within the range of variation seen in extant *C. verrucosus* populations (Lawson unpublished data). However, the distribution of *C. verrucosus* is closely tied to climate—in particular, minimum January temperatures and maximum July temperatures (Lawson et al. 2010)—which, based on weather records at Lindberg Field in coastal San Diego County, have increased significantly over the last century (Western Regional Climate Center 2009). In addition, global climate models project these variables to continue to increase in the future (Cayan et al. 2008). Coupled with projected increases in variability—which may include extreme droughts—these climate changes may threaten the persistence of *C. verrucosus*. Consequently, it is not certain that survival rates seen in the past are a good indicator of future conditions. Monitoring survival, particularly over the next 15 years as the plants are becoming established, will be important to inform management.

Population Structure, Long-Term Mortality, and Vegetative Recruitment in Mature Stands.

Seventeen transects were sampled and a total of 113 *C. verrucosus* were sampled (Table E-3). Twenty-five percent were dead and 7% were produced by vegetative reproduction.

Table E-3. Population structure for mature *C. verrucosus* stands.

N transects	17
total number in all transects	113
% dead	25%
Mean density live	0.025/m^2
Mean density dead	0.008/m^2
Max live density	0.115/m^2
Max total density	0.135/m^2
Variation in pct dead	0-86%
N live independent plants produced by vegetative reproduction	8
% independent plants produced by vegetative reproduction	7%
Average live canopy area per plant (m^2/plant)	3.6(5.5)

The remains of dead shrubs only persist over a certain size; based on condition of the stems observed and the fact that the oldest stem died at approximately 22 years of age, it was assumed that the mortality recorded began at age 20. In the sample that died at age 22, the wood was starting to decay but the rings were clearly discernable. Figure E-11 shows adult survivorship by age.

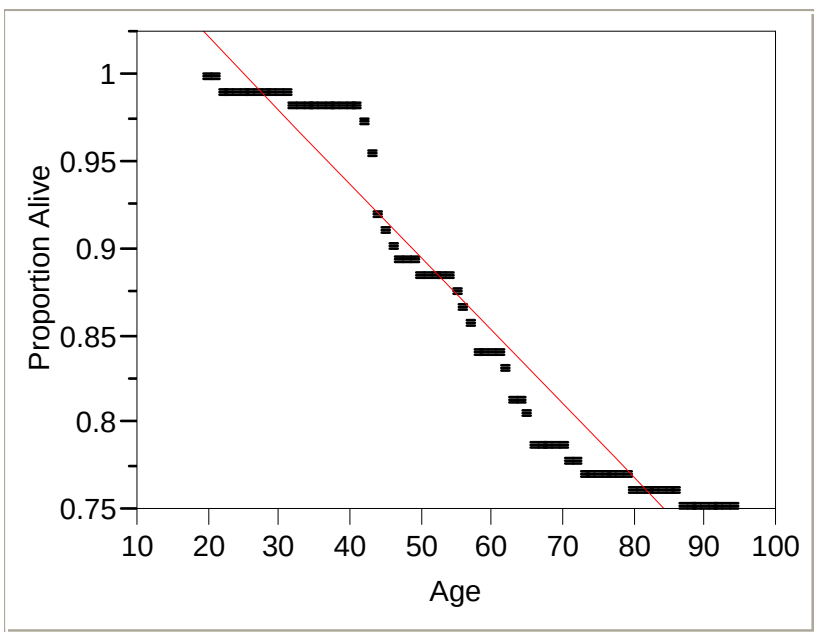

Figure E-11. *C. verrucosus* adult survivorship by age.

A linear model was fit to the data, yielding the equation Proportion alive (survivorship) = 1.107 - 0.00422*Age with an R^2 of 0.95.

Seedbank Longevity

Equal volumes of soil were collected and processed for seed. Although there were insufficient data to estimate seedbank size (Cummins 2003), all dead individuals (Table E-4) had a seedbank, even the one that had been dead the longest (44 years). Accordingly, 44 years was considered a lower bound on seedbank longevity, and a minimum 50-year seedbank longevity was assumed.

Table E-4. Seedbank associated with isolated dead *Ceanothus verrucosus* and time between death and seedbank sampling.

Sample	Age at Death	Time between death and seedbank sampling	Seed Count*
P1	66	16	2
P3	44	38	4
P4	49	33	3
P9	68	14	1
P11	46	36	9
P13	38	44	12
P14	62	20	10
* Cummins 2003			

3.5 Population Maps

Previously mapped populations were visited and polygon boundaries and population estimates were verified. In the course of this work, new populations were also mapped. Figure E-12 shows the results for *C. verrucosus*, and Figure E-13 shows the results for *Q. dumosa*.

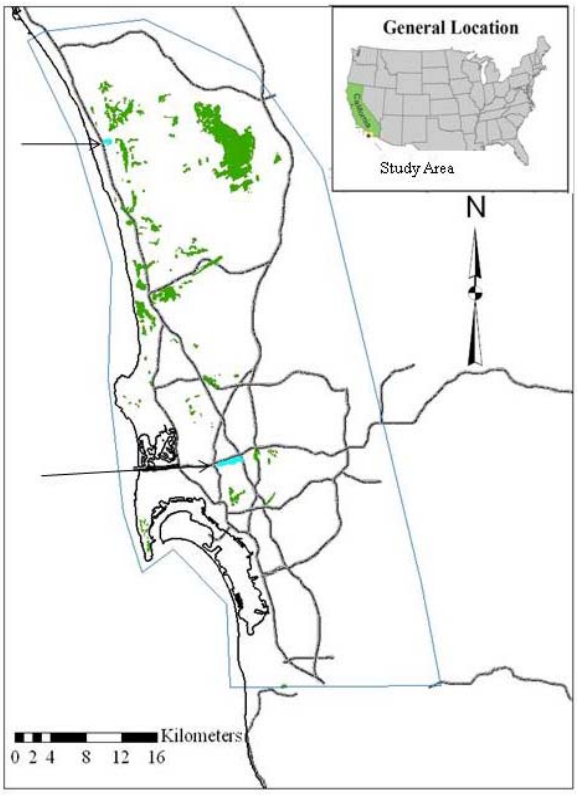

Figure E-12. Distribution of *C. verrucosus* (green) in study area. Previous mapping efforts and population estimates were verified, and two new populations were found (highlighted in blue with black arrows).

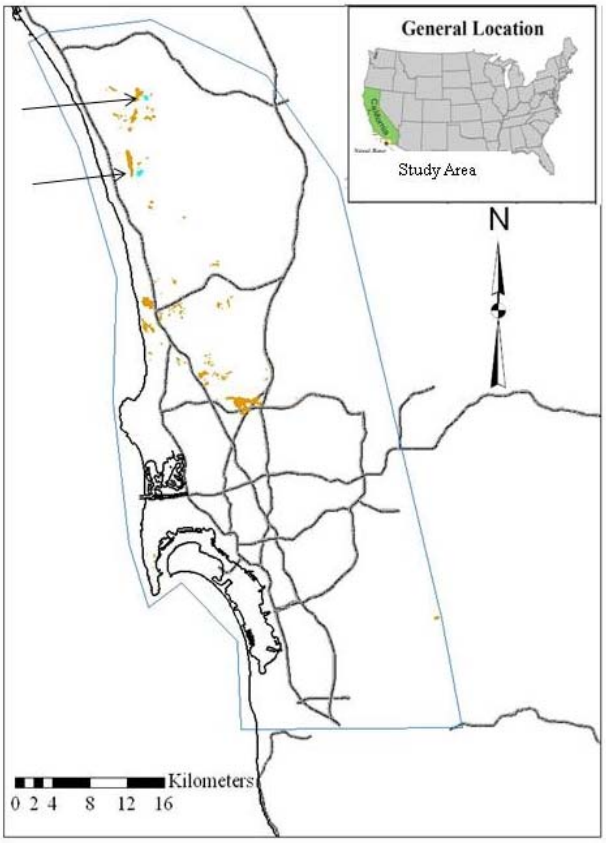

Figure E-13. Distribution of *Q. dumosa* (yellow) in study area. Previous mapping efforts and population estimates were verified, and two new populations were found (highlighted in blue with black arrows).

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Appendix F—Publications and Degrees Obtained

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List of Scientific/Technical Publications

Lawson DM (2011) Multi-species conservation in the context of global change. PhD Dissertation. University of California, Davis and San Diego State University USA.
Lawson DM (2011) *Ceanothus verrucosus* establishment and survival after the 2007 wildfires on San Dieguito River Valley Conservancy Lands, San Diego County, California

Lawson, D, Regan, H, Zedler, P, *et al.* (2010). Cumulative effects of land use, altered fire regime and climate change on persistence of Ceanothus verrucosus, a rare, fire-dependent plant species. Global change biology, 16(9), 2518-2529.

Lawson DM (2008) Monitoring Ceanothus verrucosus establishment after fire on San Dieguito River Valley Conservancy Lands. Report.

Lawson DM (2008) Examination of Habitat Fragmentation and Effects on Species Persistence in the Vicinity of Naval Base Pt. Loma and Marine Corps Air Station Miramar, San Diego, CA. 2008 Annual Report. SERDP Project Number 1473.

Lawson DM (2007) Examination of Habitat Fragmentation and Effects on Species Persistence in the Vicinity of Naval Base Pt. Loma and Marine Corps Air Station Miramar, San Diego, CA. 2007 Annual Report. SERDP Project Number 1473

Lawson DM (2006) Examination of Habitat Fragmentation and Effects on Species Persistence in the Vicinity of Naval Base Pt. Loma and Marine Corps Air Station Miramar, San Diego, CA. 2006 Annual Report. SERDP Project Number 1473.

Degrees Obtained with this Work

Dawn M. Lawson received PhD in Ecology from the Joint Doctoral Program in Ecology, University of California, Davis and San Diego State University June 2011.

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4. TITLE AND SUBTITLE
Examination of Habitat Fragmentation and Effects on Species Persistence in the Vicinity of Naval Base Pt. Loma and Marine Corps Air Station Miramar, San Diego, CA and Development of a Multi-Species Planning Framework for Fragmented Landscapes

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14. ABSTRACT
Develop methods to identify optimal management for metapopulations of sensitive species occurring in highly fragmented landscapes where subpopulations may be isolated and not functioning as true metapopulations. Use the best available data or data that can be assembled within a short period of time so that options are not foreclosed by land use conversion before decisions can be made. This project will help sustain military missions by linking habitat preservation and management on and off military installations so that species persistence can be maximized and the Department of Defense's (DoD's) proportion of the responsibility for management does not increase over time.

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