

# Predicting the impact of fire on a vulnerable multi-species community using a dynamic vegetation model



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## ABSTRACT

Conservation management under human-induced changes to disturbance requires tools that can balance the needs of multiple species with different life histories and habitat requirements. Despite this urgent conservation need, landscape management typically focuses on single species and rarely includes the influence of disturbance-dependent vegetation transitions on multiple target species. In this paper, we describe a simulation model that achieves these goals, ranking possible fire management strategies from the viewpoint of protecting endangered coastal Southern Californian wildlife. The model involves the direct and indirect effects of fire on four animal species of conservation concern (coastal cactus wren, California gnatcatcher, Stephens' kangaroo rat, and Pacific pocket mouse) and five vegetation types (grass, coastal sage scrub, obligate seeding and resprouting chaparral, resprouting-only chaparral, and woodlands). Using historical fire records for the region, we predicted spatially-explicit fire frequencies and ignition probabilities. For these predictions, we simulated the location and extent of fires. Combining fire history and vegetation transition data from 1933 to 2003, we specified vegetation change probabilities under simulated fire regimes. Fire occurrence in a location altered habitat suitability, directly for each of the animal species and indirectly by changing the vegetative community. For some open-habitat species, such as the Stephens' kangaroo rat and Pacific pocket mouse, fairly frequent fire is required to reduce the density of invasive grasses and herbs. For other species, such as the coastal cactus wren and California gnatcatcher, frequent fire destroys the mature coastal sage scrub on which these species depend. The model includes a management component, allowing us to rank fire management actions. Over a 50-year time horizon, we find that populations of California gnatcatchers and Pacific pocket mouse are highly variable, and the pocket mouse is particularly prone to decline, despite prescribed burns designed to boost population viability. California gnatcatchers were also likely to be extirpated in the model, with relatively small extirpation risks for the cactus wren and Stephens' kangaroo rat. Despite conflicting requirements with respect to fire and differing life history traits among the four animals, we identified a beneficial strategy for our four target species, namely, controlling fire in coastal sage scrub.

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## 1. Introduction

Conservation management requires integrated approaches to address conservation objectives for multiple species experiencing myriad threats that span landscapes (Franklin, 1993). Though conservation objectives at the landscape scale usually need to

encompass multiple species, formal quantitative decision support models are still largely focused on single species or biodiversity surrogates (e.g. umbrella/flagship species) (Roberge and Angelstam, 2004; Simberloff, 1998). The success of specific management strategies is contingent upon understanding trade-offs among multiple species and threats. Different species have different habitat requirements, respond to threats in different ways and possess different life history traits. These species differences can lead to conflicts when managing for the conservation of multiple species as available habitat decreases and other threats increase. Successful multi-species management will depend on a clear understanding of the trade-offs imposed when species have very different resource needs and responses to conservation actions.

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In the conservation literature, “trade-offs” are often discussed in the context of compromises between biodiversity goals and economic well-being (McShane et al., 2011; Hirsch et al., 2011), or conflicts among potential services provided by natural landscapes (Faith, 2012). Few studies look at trade-offs between species in a particular landscape context. Such analyses require considerable information, often unavailable, about individual species' responses to potential landscape threats. We address the issue of trade-offs from the viewpoint of conserving multiple species on a particular landscape.

Conservation within the California Floristic Province, a global biodiversity hotspot and one of five Mediterranean-type ecosystems, illustrates the trade-offs involved in multi-species management. In California, only 10% of the coastal sage scrub habitat remains (Rubinoff, 2001) and this study focuses on one of the few extensive areas that still exists. Coastal sage scrub is a terrestrial plant community consisting of a short somewhat open canopy of mostly soft-leaved, sometimes dry-season deciduous shrubs (Kirkpatrick and Hutchinson, 1977). Increased fire frequency is threatening coastal sage scrub ecosystems, where fire frequency above the historical rate of once every 30–40 years (Keeley and Fotheringham, 2001a,b) can shift the competitive advantage towards invasive plants (Keeley et al., 2011; Fleming et al., 2009; Talluto and Suding, 2008). Short-lived invasive annuals grow quickly, leaving behind large quantities of dry, combustible biomass for most of the year (Link et al., 2006; Lambert et al., 2010), thus further increasing fire frequency (Brooks and Chambers, 2011) and invasive plant spread. This positive feedback between fire and invasive plant spread can result in vegetation type conversion from coastal sage scrub to exotic grass (Fleming et al., 2009; Talluto and Suding, 2008). Chaparral vegetation, a shrubland that is denser, taller and more evergreen than sage scrub, is even more sensitive to repeated, frequent fires than coastal sage scrub, and is also at risk of converting to exotic grassland (Jacobsen et al., 2004; Syphard et al., 2006; Keeley and Brennan, 2012).

While the native vegetation of the California Floristic Province has important global conservation value in itself, it also serves as key habitat to a host of threatened and endangered species. Here, we focus on the federally listed (under the United States Endangered Species Act) California gnatcatcher (*Poliophtila californica*), Stephens' kangaroo rat (*Dipodomys stephensii*), and Pacific pocket mouse (*Perognathus longimembris pacificus*), as well as the coastal cactus wren, a California Bird of Special Concern (*Campylorhynchus brunneicapillus*). The two bird species prefer mature coastal sage vegetation that has not recently experienced a fire (Preston and Kamada, 2012, 2009; Beyers and Wirtz, 1995), whereas the rodents prefer coastal sage scrub or grasslands that have recently burned and thus lack a dense understory of invasive grasses (O'Farrell and Uptain, 1987; Price et al., 1993, 1995; Spencer, 2005). Maintaining adequate habitat for multiple species of conservation concern with contrasting habitat requirements and life history traits is a significant challenge for land managers.

Multi-species management must account for complex processes, different habitat needs, and a range of threats, life histories, and trade-offs. Thus, integrated modeling frameworks have been promoted that coalesce available physical and ecological data into meaningful decision support tools. Examples are the landscape succession models LANDIS and LANDIS-II (Mladenoff, 2004; Scheller et al., 2007; Sturtevant et al., 2009) and MEDFIRE (De Caceres et al., 2013) that simulate vegetation succession under fire disturbance. These dynamic vegetation models can then be coupled with population models to address the joint impact of environmental stochasticity and fire on the viability of at-risk species.

Multiple species models that incorporate fire and habitat requirements for target animal species typically focus on correlating landscape features with species presence or absence. For

example, vegetation type, climate change, and fire disturbance can be used in a standard species distribution model that describes habitat suitability for multiple focal taxa (White et al., 2011; De Caceres et al., 2013). Models that include the effects of disturbances, such as fire and succession, go beyond traditional species distribution models that estimate habitat suitability based on topographic and climatic conditions (Beltrán et al., 2014; Pompe et al., 2008; Thuiller et al., 2006). However, neither of these types of models typically include dynamic, disturbance-dependent vegetation transitions that affect species occurrence and resulting conservation management decisions.

Because of the difficulties in obtaining adequate data for parameterization, models rarely consider multiple species, habitat types, threats, and management options together in one framework. An exception is the Across Trophic Level System Simulation (ATLSS) model for the Florida everglades (DeAngelis et al., 1998). This model uses topographic, vegetation, and hydrology inputs to model energy flow through three trophic levels. The model was designed to allow managers to make hydrological decisions while managing multiple focal species. Adopting this strategy for fire management in Southern California, we developed a dynamic vegetation and occupancy model with the functionality to accommodate multiple species interacting with a landscape under threat from frequent fire. We use data on the frequency of fire-induced changes in vegetation type (Fleming et al., 2009; Callaway and Davis, 1993) to model vegetation transitions among grasslands, coastal sage scrub, chaparral, and woodlands (open tree canopies dominated by live oaks) under different fire regimes. Our model addresses ecosystem threats common to Mediterranean ecosystems and allows for conservation decision-making where trade-offs between habitat requirements and altered natural disturbance regimes can stymie a clear course of action.

Although wildfire is a natural process in Southern California and other Mediterranean-climate regions, altered fire regimes may threaten wildlife directly or indirectly through vegetation transitions. We model these direct and indirect threats for the vegetation types and for the four species that rely on them. Our aim is to use available data on the locations and extent of different vegetation types, transitions between vegetation types, fire size and frequency, and species locations to create a model that simulates the dynamic tradeoffs in habitat requirements for four threatened species. We will then use the model to identify the best plausible fire management scenarios for four threatened species separately and in combination. In this way, our results highlight the fire scenarios that are most detrimental to these species and the range of fire management strategies that are most likely to support them and their habitats.

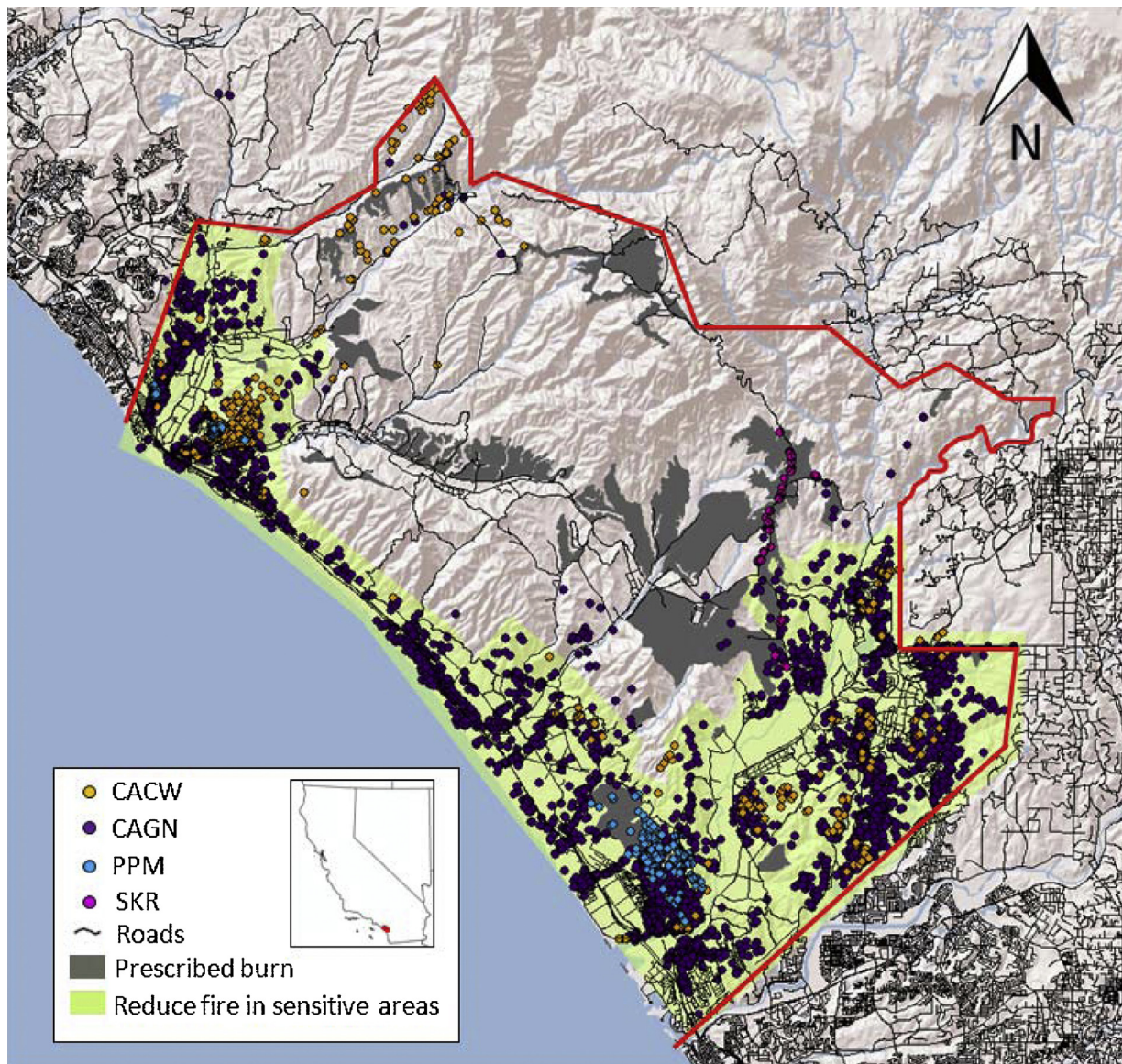
## 2. Methods

### 2.1. Overview

We developed our model for Marine Corps Base Camp Pendleton, hereafter Pendleton, a military base in northwestern San Diego County, California, USA. A little over 500 km<sup>2</sup>, the base has a high frequency of wildfire that is primarily human-caused, either intentionally or unintentionally. Land managers at Pendleton are required to maintain populations of threatened and endangered species while also meeting the base's mission to support military training exercises. These potentially conflicting conservation and land management objectives provided context for developing a model addressing multiple species and fire regimes.

Pendleton is one of the few remaining locations of critically endangered coastal sage habitat. With the exception of a part of its northern border, Pendleton is surrounded on all sides by urban



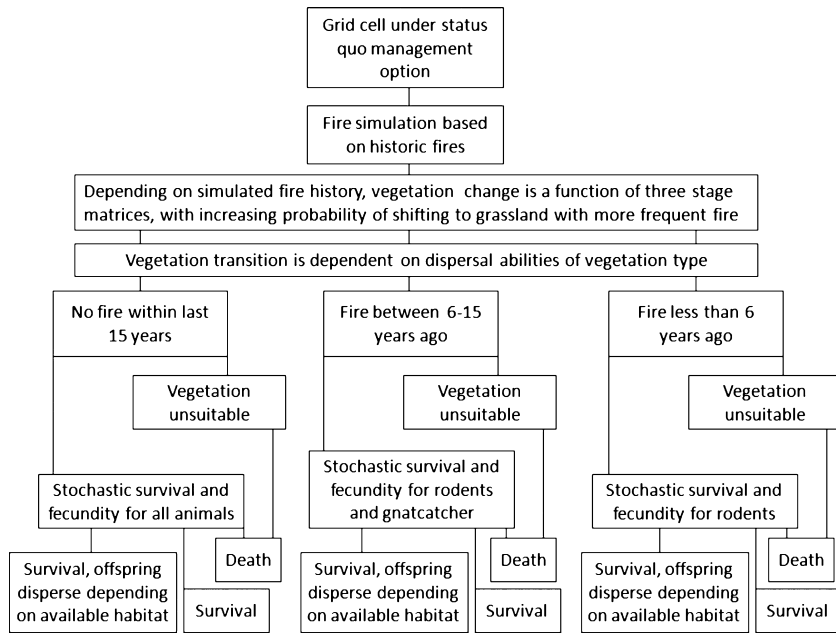


**Fig. 1.** Map of the study area. Points are observed locations for each of the four target species. The green area is the area that is protected against fire under the “Reducing fire in sensitive areas” management option. The gray areas are the prescribed burn areas.

development or the Pacific Ocean (Fig. 1). For more vagile species, such as the cactus wren, there appears to be genetic isolation of the Camp Pendleton population from the nearest population 20 km northwest in the Nature Reserve of Orange County (Barr et al., 2012). Thus, for the at-risk species occurring within Pendleton, the site constitutes the only available habitat in the area, and does not function as part of a meta-population with habitat bordering Camp Pendleton.

In our dynamic vegetation and multi-species model, the landscape was represented by a uniform grid. The resolution of the grid cells was designed to represent the territory size of a breeding pair of birds or an individual rodent, namely, one-hectare (Atwood et al., 1998a) and 0.033-ha grid cells (McClenaghan and Taylor, 1993), respectively. Each cell was potentially inhabited by one or more of the four target species under study (the coastal cactus wren, the California gnatcatcher, the Pacific pocket mouse, and the Stephens' kangaroo rat), dependent on species' associations with vegetation type. For the two bird species, presence was negatively associated with fire (they prefer late-successional habitat) and sensitive to precipitation (cactus wrens) and temperature (gnatcatchers). For

the two rodent species, presence was positively associated with fire (they prefer early-successional habitat) and sandy soils. For each annual time step, the presence or absence of all species was recorded in each cell. As described below, the presence or absence was in turn modeled dynamically and stochastically as a function of the cell's vegetation type, habitat quality, weather, fire history, and occupancy in the previous time step (Fig. 2). Because we chose grid cell sizes that were approximately the size of the target species home range, the number of occupied grid cells is a good proxy for the species' abundance. Regardless, the only data collected and used at Pendleton for wildlife monitoring is presence-absence data, making presence-absence simulation the sensible approach here and in other management contexts where presence-absence data are the only data available. For each 50-year model simulation, summary statistics on vegetation type, habitat quality, presence-absence counts, and fire history were recorded. For each species, the fraction of grid cells occupied was simulated for different management options. Averages over 500 replicated simulations were used as summary statistics. The model was developed using MATLAB® R2012a.



**Fig. 2.** Schematic flow diagram of events within an annual time step for a grid cell with a given vegetation type and species' presence under the status quo option. The cell will undergo a vegetation change, or no change, according to given transition probabilities, where the probabilities, arrayed in matrices, depend on the length of time elapsed since the cell's last fire. Vegetation changes make a cell more or less suitable for a target species, thus influencing the species' survival, reproduction, and dispersal.

## 2.2. Simulating fire occurrence

Historical fire data (1973–2008) were obtained from the California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (CALFIRE FRAP) and from Pendleton. Within that time period, the number of hectares burned in a year in the study area was well represented by a lognormal distribution with mean of 3.51 (corresponding to 3240 ha burned) and standard deviation of 0.31. At the beginning of each year in the model, the number of hectares burned was drawn from this distribution, simulating inter-annual variability in area burned. Because the study site is a military base, relatively large tracts of the landscape burn every year, regardless of weather (where the predominant weather effect on fire in Mediterranean Southern California is Santa Ana winds).

The total fire area was then divided into multiple fires of various sizes. The distribution of fire sizes for the period 1973–2008 was well represented by a Weibull hazard function with scale parameter 22.6 and shape parameter 0.4. For each year, we drew from the Weibull distribution repeatedly, until the sum of the draws equaled the total area that had been randomly selected from the lognormal distribution for hectares burned. The result was an annual list of fires and their sizes. This list typically included many small fires and few very large fires.

For each fire (with its size) on the list, we randomly selected an ignition location and then simulated the cell-by-cell spread of the fire around that location up to the fire's given total size. The ignition locations were drawn from a probabilistic map developed using the MaxEnt model (Phillips et al., 2006; Bar Massada et al., 2013) with historical ignition locations as the dependent variable and the following explanatory variables: mean annual maximum temperature, mean annual minimum temperature, mean annual precipitation, elevation, slope aspect (scaled using a cosine transform to give highest values for xeric southwest-facing slopes), slope gradient, vegetation type, presence of structures, road density, and a variety of military artillery variables. An additional probabilistic map representing fire occurrence frequency was developed using a negative binomial regression model that was appropriate for a count dependent variable. The dependent variable was the number of times that individual cells burned during the years 1973–2008.

The data used for modeling were drawn from a random sample of 500 cells spaced at least 457 m (1500 ft) apart. Significant predictors included mean annual maximum temperature, mean annual minimum temperature, slope, distance to roads, vegetation type, and proximity to military training exercises.

In each year for each fire in that year, the ignition site was chosen with a probability proportional to the fire ignition map discussed above. Fire spread was then modeled diffusively such that locations with high predicted fire frequency were more likely to attract a growing fire. The formula for fire spread was

$$P_{xy} = \frac{\sum_{i=x-1}^{x+1} \sum_{j=y-1}^{y+1} p_{ij} \times c_{ij}}{\sum_Y \sum_X \left( \sum_{i=x-1}^{x+1} \sum_{j=y-1}^{y+1} p_{ij} \times c_{ij} \right)}$$

where  $P_{xy}$  is the probability that a cell with coordinates (x,y) will itself start to burn given that an adjacent cell burns. The sets X and Y contain the x and y coordinates of the eight adjacent cells (four sides and four corners) to the burning cell. The coefficient  $c_{ij}$  was either 0.1 or 1 depending on whether the  $ij$ th cell was burning (1 if the cell was burning). The  $p_{ij}$  are predicted fire frequencies in the  $ij$ th cell obtained from the negative binomial fire frequency regression model.

Prescribed burns are administered every six years at specified locations at Pendleton consistently over time (Fig. 1). Locations were chosen to benefit the two endangered rodents, to serve as fire breaks around sensitive habitat, and to decrease combustible vegetation in portions of Pendleton where pyrotechnic training exercises were common. For a location and year where a prescribed burn occurred in the model, we assumed that the probability of fire spread to that location was 20% of the probability of spread in a non-prescribed-burn year. We also assumed that a wildfire that comes into contact with a prescribed burn has a 5% chance of stopping completely. Thus, we assumed that prescribed burns, on average, provided small decreases in the total area burned. There are few data on which to base these estimates of the effectiveness



of prescribed burns for limiting fire spread. However, the majority of area burned in Southern California shrublands occurs during severe wind events during which prescribed fires are not effective at reducing fire extent (Keeley and Zedler, 2009). Even when accounting for all weather conditions, prescribed fire across the landscape historically has not limited subsequent fire (Price et al., 2012). Finally, the estimated effectiveness of prescribed burns was guided by experts knowledgeable about fire at the study site.

### 2.3. Vegetation transitions

Vegetation types at Pendleton were recorded in the Weislander Vegetation Type Maps, applicable to 1933 and published in Wieslander (1935), and in a comprehensive vegetation map constructed by AMEC Earth and Environmental, Inc. in 2003 (map provided by Pendleton). We assigned each vegetated grid cell in Pendleton to one of five vegetation types: grass, coastal sage

evidence of habitat preferences that might lead to a more clustered spatial distribution of obligate seedling chaparral (Meentemeyer et al., 2001), we allocated the two chaparral types at random because, lacking specific information about their distributions, our primary objective was to include two types of chaparral with very different vulnerabilities to fire (Jacobsen et al., 2004; Zedler et al., 1983; Haidinger and Keeley, 1993; Keeley et al., 2012).

At the beginning of a simulation, the AMEC (2003) vegetation map of Pendleton, modified to include the two chaparral categories, was used as the initial vegetation distribution (Fig. 3a). After that, each grid cell in each year either stayed in its current vegetation category or transitioned to a different vegetation category. These random events were governed by three constant transition probability matrices (Eqs. (1)). For a given grid cell at a given time step, the cell's recent fire history determined which of the three matrices was applied. If the cell had experienced no fire in the last 15 years,  $T_{low}$  was used. If the cell had experienced a fire within the last six to last 14 years,  $T_{med}$  was used. If the cell had experienced a fire within the last 5 years,  $T_{high}$  was used.

$$(1)$$

$$T_{low} = \begin{matrix} & \begin{matrix} \text{Grass} \\ \text{Coastal Sage Scrub} \\ \text{O.S. Chaparral} \\ \text{Resprouting Chaparral} \\ \text{Woodlands} \end{matrix} & \begin{bmatrix} \text{Grass} & \text{Coastal Sage} & \text{O.S. Chaparral} & \text{Resprout. Chaparral} & \text{Woods} \\ 0.983 & 0.002 & 0.001 & 0.001 & 0.002 \\ 0.015 & 0.994 & 0.010 & 0.009 & 0.007 \\ 0 & 0 & 0.986 & 0.009 & 0.003 \\ 0 & 0.001 & 0.002 & 0.980 & 0.004 \\ 0.002 & 0.003 & 0.001 & 0.001 & 0.984 \end{bmatrix} \end{matrix}$$

$$T_{med} = \begin{matrix} & \begin{matrix} \text{Grass} \\ \text{Coastal Sage Scrub} \\ \text{O.S. Chaparral} \\ \text{Resprouting Chaparral} \\ \text{Woodlands} \end{matrix} & \begin{bmatrix} \text{Grass} & \text{Coastal Sage} & \text{O.S. Chaparral} & \text{Resprout. Chaparral} & \text{Woods} \\ 0.996 & 0.002 & 0.005 & 0.001 & 0 \\ 0.001 & 0.995 & 0.020 & 0.023 & 0.011 \\ 0 & 0.001 & 0.965 & 0 & 0 \\ 0.001 & 0.001 & 0.008 & 0.971 & 0.002 \\ 0.002 & 0.001 & 0.002 & 0.005 & 0.987 \end{bmatrix} \end{matrix} \quad \text{Eq. 1}$$

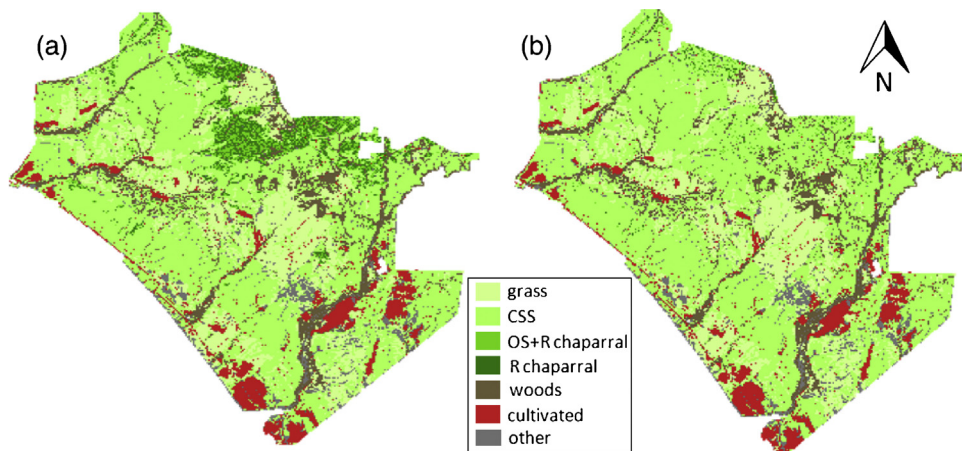
$$T_{high} = \begin{matrix} & \begin{matrix} \text{Grass} \\ \text{Coastal Sage Scrub} \\ \text{O.S. Chaparral} \\ \text{Resprouting Chaparral} \\ \text{Woodlands} \end{matrix} & \begin{bmatrix} \text{Grass} & \text{Coastal Sage} & \text{O.S. Chaparral} & \text{Resprout. Chaparral} & \text{Woods} \\ 0.994 & 0.008 & 0.003 & 0.006 & 0.008 \\ 0.005 & 0.989 & 0.010 & 0.016 & 0.006 \\ 0 & 0 & 0.969 & 0 & 0 \\ 0 & 0.001 & 0.010 & 0.970 & 0.001 \\ 0.001 & 0.002 & 0.008 & 0.008 & 0.985 \end{bmatrix} \end{matrix}$$

scrub, two chaparral functional types, and woodlands. Each particular cell's vegetation type made it more or less habitable for each of the four target species, and, in the simulation model, each cell's vegetation type may change over time due to fire and environmental stochasticity.

The two types of chaparral were "chaparral composed of obligate seeding and resprouting species" and "chaparral with resprouting species only". Our Weislander and AMEC data did not distinguish the two types of chaparral, but we enforced the distinction to create a simulation model that included more and less fire-sensitive chaparral (as on Fig. 3a), thus laying a foundation for studying the roles of obligate seeding versus resprouting species in vegetation dynamics across heterogeneous landscapes. We assigned each chaparral cell in Pendleton to one of the two types at random. By definition, obligate seeding (O.S.) species are cued to germinate only after a fire, whereas resprouting species have individuals that often survive a fire and resprout from well-protected stems or root crowns. These constitute the two major fire-response strategies of chaparral shrubs, and the distribution of species characterized by these traits varies across the landscape, often within heterogeneous mosaics (Keeley and Davis, 2007). While there is

For each matrix, the five columns correspond to current year vegetation type, and the five rows correspond to next year vegetation type. Thus, the  $(i,j)$ th element of a given matrix is the probability that, if the cell is in vegetation type  $j$  this year, it will be in vegetation type  $i$  the next year. Therefore, each column of each matrix must sum to one. In all matrices, the ordering of vegetation types is grass, coastal sage scrub, obligate-or-resprouting chaparral ("O.S. Chaparral"), resprouting-only chaparral ("Resprout. Chaparral"), and woodlands (as shown). The large diagonal elements of the matrices reflect the fact that vegetation transitions are infrequent (as also illustrated by Fig. 3).

The transition probability values in  $T_{low}$ ,  $T_{med}$ , and  $T_{high}$  are based on the observed vegetation changes between the 1933 Weislander maps and the 2003 AMEC maps, and on the fire frequencies for those years. For each grid cell on the landscape we noted its original vegetation type in 1933 and then its final vegetation type in 2003. We then recorded the average fire frequency in the grid cell. If there was fire, on average, less than five years ago, we recorded the fraction of grid cells that remained as a particular vegetation type versus transitioned to another type for all grid cells with this fire frequency. These fractional changes resulted in  $T_{high}$ . We followed the same procedure for all original vegetation types and fire



**Fig. 3.** Map of (a) initial vegetation and (b) modal (most likely) vegetation outcome by the end of the time horizon for simulations run at one hectare resolution. CSS = coastal sage scrub. Map (b) shows increases in grass and decline in chaparral as compared to (a).

frequencies of 6–15 years ( $T_{med}$ ) and 15 or more years ( $T_{low}$ ). In this way, we used the empirical data to populate the transition matrices, with minor modifications to incorporate the two types of chaparral. Transition rates for the two types of chaparral were guided by various studies suggesting that obligate seeding species are more sensitive to repeated fires than resprouting species (Jacobsen et al., 2004; Zedler et al., 1983; Haidinger and Keeley, 1993; Keeley et al., 2012). Additionally, the literature suggests that frequent fire often causes invasion by non-native grasses (Talluto and Suding, 2008; Minnich and Dezzani, 1998; Lippitt et al., 2013; Keeley and Brennan, 2012). Further, we found good agreement between our vegetation transitions and those studied in Callaway and Davis (1993) for coastal Central California, as site-specific vegetation transition data were lacking.

A vegetation type change for a particular cell required that another cell containing the new vegetation type be close enough to allow dispersal. In simulations, the required proximity for dispersal was less than 400 m for a type change to coastal sage scrub, less than 100 m for a type change to obligate-or-resprouting chaparral, less than 100 m for a type change to resprouting-only chaparral, and less than 500 m for a type change to woodlands. Coastal sage scrub species tend to have longer dispersal distances than chaparral (Keeley and Davis, 2007). Grass was assumed to have unlimited dispersal ability, as the species and seedbank required for invasions are likely present in all cells. However, grass can be prevented from dominating the landscape by priority effects (e.g. the persistence of woody vegetation).

#### 2.4. Species inputs

Initial presence-absence maps (Fig. 1) for the four wildlife species were based on biological surveys performed from 1989 to 2010. Vegetation type and fire frequency were used to model dynamic habitat suitability maps for the species. Species could expand to occupy additional habitat or contract to abandon previously occupied habitat.

##### 2.4.1. Coastal cactus wren

To model the impact of fire on cactus wren occupancy, we assumed that the wrens occur only on mature coastal sage scrub that has not burned in the last 15 years. This criterion assured time for regrowth of the *Opuntia* or *Cylindropuntia* cactus species on which the wrens nest (Preston and Kamada, 2009). In each year for each cell in which the wrens were present, they might disappear, survive in the current location, or survive and also spread to nearby locations. Survival and growth parameters were assumed to

depend on weather according to the following relationship (K. Preston, unpublished data), which describes the number of fledglings per mating pair of cactus wrens as a function of annual precipitation (“Precip”):

$$\text{fledglings} = 0.1329 \times \text{Precip} + 0.9714 \quad (2)$$

In the simulations, we select “Precip” every year by drawing randomly from a lognormal distribution with mean 1.008 and standard deviation 0.200 and raised to the power 10 (to convert to units of inches). The choice of a lognormal distribution was based on data from the Western Regional Climate Center (2011) for the two nearest stations, Oceanside and Vista, California.

The number of fledglings calculated in Eq. (2) was substituted into a matrix population model with the same form as in Akçakaya and Atwood (1997), who model California gnatcatcher survival and growth in a context very similar to ours. Their population transition matrix, adapted for Coastal cactus wren here, is:

$$R_{CACW} = \begin{bmatrix} \text{fledglings} \times 0.5 \times 0.32 & \text{fledglings} \times 0.5 \times 0.64 \\ 0.32 & 0.64 \end{bmatrix} \quad (3)$$

The juvenile and adult survival rates (0.32 and 0.64, respectively) are from Atwood et al. (1998b). The 0.5 values in the top row were required because Eq. (3) describes the number of fledglings per pair, not per individual. For each annual time step, the value of “fledglings” (Eq. (2)) was substituted into the matrix  $R_{CACW}$  (Eq. (3)), thus incorporating environmental stochasticity in (lognormally-distributed) growth rates through variability in the number of fledglings. Demographic stochasticity was incorporated through individually random survival and number of offspring: each individual was randomly chosen to survive or die based on a binomial draw from the corresponding mean survivals for juveniles and adults in the second row of Eq. (3). Each surviving individual would then be assigned a number of offspring selected from a Poisson distribution with mean (fledglings  $\times$  0.5).

Our dispersal assumptions are tailored to empirical observations in Atwood et al. (1998b, Fig. 19, pp. 32). The probabilities that nearby cells receive an immigrant fledgling from its birth cell are assumed to decline with their distances from the birth cell: 65% of fledglings disperse between 0–1 km, 10% disperse between 1 and 2 km, and so on (see Atwood et al., 1998b). For each new offspring, if there are  $x$  cells within 0 to 1 km of the target cell, each of the  $x$  cells had a probability of  $0.65/x$  of receiving a particular immigrant fledgling; if there are  $y$  cells within 1 to 2 km of the target cell, their probability of receiving a particular immigrant fledgling is  $0.10/y$ .

The sum of the dispersal probabilities for a particular immigrant over all cells within an assumed maximum dispersal of 10 km is 1.

#### 2.4.2. California gnatcatcher

The assumptions for the California gnatcatcher are similar to those for the cactus wren. We assumed that the gnatcatcher occurs only on coastal sage scrub that has not burned in the last 8 years. The non-burn restriction assures time for regrowth of the gnatcatcher's coastal sage (*Artemisia californica*) habitat (Beyers and Wirtz, 1995, p.86). For the gnatcatcher, unlike the wren, growth and survival depend on temperature (Atwood et al., 1998b; K. Preston, personal communication). Cold, wet winters decrease survival.

To investigate the temperature effect, adult survival observations from Atwood et al. (1998b) were regressed on deviation in minimum January temperature ( $=[\text{mean of January daily minimum temperature for a given year}] - [\text{mean of January daily minimum temperature averaged over the available years of climate data}]$ ). The regression supported the hypothesis that gnatcatcher survival declines in cold winters. In addition, Atwood et al. (1998b) provided data for survival from two sites, allowing a second test. The absolute differences in temperature between the two sites tended to be greater than the absolute differences among years for either site separately.

Based on these considerations, we assumed that gnatcatcher populations are locally adapted to the mean temperature of their location, suggesting that the *deviation* around this temperature is the critical variable to consider. In specifying an average temperature over the period for which data were available, the unadjusted average was adjusted to remove the impact of climate warming, resulting in a histogram of deviations about a constant mean. The intercept of the regression described in the preceding paragraph was altered to reflect the average survival that Atwood observed at his sites (Atwood observed a mean survival of 0.55, whereas the y-intercept of a plot of adult survival against temperature deviation was 0.42). The resulting equation for gnatcatcher survival was:

$$\text{survival} = 0.15 \times \text{TempDev} + 0.55. \quad (4)$$

The variable “TempDev” was simulated as a random draw from a normal distribution with mean 0 and standard deviation 2.58. This distribution is based on a histogram of the climate-warming-corrected temperature deviation data from the Western Regional Climate Center (2011) for Oceanside, CA, the closest weather station to the study site.

Simulated adult survival from Eq. (4) was substituted into a vital rates matrix based on empirically derived fecundity and juvenile survival from Atwood et al. (1998b). Thus a population matrix similar to Eq. (3) for wrens was formed:

$$R_{\text{CAGN}} = \begin{bmatrix} 2.83 \times 0.5 \times 0.34 & 2.83 \times 0.5 \times 0.55 \\ 0.34 & \text{survival} \end{bmatrix}. \quad (5)$$

The entries in the first row are the expected numbers of offspring per individual for juveniles and adults respectively. They compensate for gnatcatcher deaths and, if large enough, lead to population growth from one year to the next. The 2.83 in the two elements of the first row is the average number of offspring per pair; it is multiplied by 0.5 to give the average number of offspring per individual bird rather than per pair. The upper left element is further multiplied by the survival rate 0.34 for juveniles. The upper right element is multiplied by the average adult survival rate 0.55 from Eq. (4). The entries in the second row of the population matrix are the survival rates of juveniles and adults (from Eq. (4)). The annual time step increase is assumed to occur after nestlings have fledged. Just as for cactus wrens, individual survival and reproduction is randomly selected based on a binomial draw from the means in Eq.

(5), where gnatcatcher dispersal follows Figure 20 (p. 32) in Atwood et al. (1998b).

#### 2.4.3. Stephens' kangaroo rat

Rodents were modeled differently from the two bird species. First, we found no relationship between climate variables and the population growth and survival rates of the Stephens' kangaroo rat in the study area, and no climate–population relationships were found in the literature. Second, the Stephens' kangaroo rat is a soil specialist that lives on friable, well-drained sandy loam or loamy sand soils. To represent this habitat preference, we created a soil map to exclude the kangaroo rat from all sites that were not labeled sandy loam or loamy sand.

Studies have shown that frequent fires help to create the open vegetation Stephens' kangaroo rats prefer (Price and Waser, 1984; Price et al., 1993, 1995; Shier, 2011). However, none of these studies monitored actual populations through time. To obtain population growth rates, Kelt et al. (2005, 2008) sampled Stephens' kangaroo rat populations bimonthly from November 1996 through October 2000, where plots received no treatment or were mowed or grazed. For the purposes here, we treated mowing and grazing as similar to burning. However this is likely an underestimate of the benefit of burning, given that twice as many translocated individuals (added post-treatment) were found on burned plots compared to mowed and grazed (Shier, 2011). The average growth rate in rat population was 0.93 on control plots and 1.08 on vegetation removed plots in their study. Standard deviations across plots were not reported in Kelt et al. (2005), but a standard deviation of 0.26 was reported by S. Pearson-Springs (personal communication) for a somewhat similar situation.

We simulated the population growth rate of each cell in each year as a random draw from a normal distribution with mean  $r_{\text{skr}}$  and standard deviation  $\sigma_{\text{skr}}$ , where

$$r_{\text{skr}} = \max[1.09 - 0.016 \times (\text{time since last fire}), 0.93],$$

$$\sigma_{\text{skr}} = 0.26. \quad (6)$$

The coefficient 0.016 assumes that in ten years a burned site with an average  $r = 1.09$  becomes an unburned site with  $r = 0.93$ . In this way, a simulated population growth rate was generated for each occupied grid cell in each year in our overall simulation model. The high standard deviation in growth rate ( $\sigma_{\text{skr}} = 0.26$ ) is in line with data for other *Dipodomys* species (Heske et al., 1994; Brown and Heske, 1990).

Shier and Swaisgood (2012) report that dispersing kangaroo rats can move 100–200 m in search of new territory. Thus, individuals were only allowed to disperse up to 200 m (or roughly 10 grid cells away, where grid cells are roughly 18 m on a side).

#### 2.4.4. Pacific pocket mouse

There were no growth and survival rates available for the Pacific pocket mouse. Thus, we used data from *P. longimembris* residing north of Las Vegas to parameterize growth rates (French et al., 1967, 1974). As with the kangaroo rat, we tried correlating the available pocket mouse data with climate variables, but no relationship was found. The mean and standard deviation of the growth rate for the pocket mouse was specified as

$$r_{\text{ppm}} = \max[1.10 - 0.016 \times (\text{time since last fire}), 0.94],$$

$$\sigma_{\text{ppm}} = 0.31, \quad (7)$$

which is analogous to Eq. (6) for the kangaroo rat. The lead coefficient 1.09 in Eq. (6) was increased to 1.10 in Eq. (7) and the standard deviation was increased from 0.26 to 0.31. These changes are based on the French et al. (1974) study of *P. longimembris* in Arizona. The



**Table 1**

Simulation-based measures of the average effects of management options (rows of the table) on vegetation types (columns of the table). For each management option, 500 simulations of 50 years each were run. For a given simulation, the number of grid cells (one hectare resolution) for each of the five vegetation types was recorded at the beginning and end of the 50 years. For a given vegetation type, the ratio of the ending number to the beginning number is a summary measure of management effectiveness for that vegetation type. A ratio greater than one indicates a positive management effect, and a ratio less than one indicates a negative management effect, with absolutely larger ratios indicating stronger effects. (A summary ratio of one would mean that positive and negative changes had canceled each other in the averaging.) For each cell, the first number is the summary ratio; and the second number (entered in  $\pm$  form), is the standard deviation of the summary ratio across the 500 simulations for that cell.

	Grass	Coastal sage scrub	Obligate seeding and resprouting chaparral	Resprouting only chaparral	Woods
Status Quo	1.209 $\pm$ 0.030	0.974 $\pm$ 0.009	0.399 $\pm$ 0.033	0.406 $\pm$ 0.017	1.156 $\pm$ 0.018
Reduce burn area	1.145 $\pm$ 0.029	0.990 $\pm$ 0.008	0.439 $\pm$ 0.033	0.421 $\pm$ 0.017	1.184 $\pm$ 0.020
Alter burn site	1.203 $\pm$ 0.028	0.975 $\pm$ 0.008	0.398 $\pm$ 0.030	0.407 $\pm$ 0.016	1.162 $\pm$ 0.019
Protect CSS	1.185 $\pm$ 0.026	0.982 $\pm$ 0.007	0.369 $\pm$ 0.028	0.391 $\pm$ 0.016	1.178 $\pm$ 0.020
Restore	1.207 $\pm$ 0.030	0.974 $\pm$ 0.009	0.401 $\pm$ 0.031	0.403 $\pm$ 0.016	1.158 $\pm$ 0.019
No prescribed burn	1.184 $\pm$ 0.034	0.983 $\pm$ 0.010	0.388 $\pm$ 0.029	0.404 $\pm$ 0.017	1.166 $\pm$ 0.021

dispersal assumption for the pocket mouse was similar to the kangaroo rat but modified by the requirement that the mouse live within 4 km of the coast. These population growth assumptions lead to high variability in the modeled pocket mouse populations, which is in line with other data for *Perognathus* species in the [Global Population Dynamics Database \(2010\)](#).

### 2.5. Management options

While we focused on four target species in coastal Southern California, the modeling framework is fully applicable to other species across a range of fire responses and habitat preferences. Six management options were chosen to represent a realistic and varied set of alternatives for the study site that are also broadly relevant to conservation of fire-sensitive species in Mediterranean and other fire prone ecosystems worldwide. These were: (i) the status quo, (ii) reducing the total area burned, (iii) reducing the probability of fire where it might have the greatest negative impact on the focal bird species, (iv) preventing certain vegetation types from burning, (v) restoring habitat to allow for earlier re-colonization after a fire, and (vi) not using prescribed burns. The preceding subsections describe the status quo scenario. Under the reduced burn scenario, we reduced the average of total area burned by 25% (from an average of 3240 ha burned to 2450 ha), changing the mean of the lognormal distribution describing the number of hectares burned in a year from 3.51 to 3.39. For option (iii), we altered the fire spread map such that areas where the cactus wren and gnatcatcher were present had a 75% lower probability of burning as compared to the status quo option ([Fig. 3](#)). For option (iv), we reduced the probability of fire spread to coastal sage scrub (the habitat of our two fire sensitive birds) by 90%. For option (v) we simulated habitat restoration by reducing the number of years that must pass before cactus wren (from 15 to 8 years) and gnatcatchers (from 8 to 4 years) can re-colonize burned areas. For the rodents, we decreased the rate at which rodent growth rate decreased with time since last fire (from 0.016 to 0.008 in Eqs. (6) and (7)). For option (vi), we removed all prescribed burns from simulations.

**Table 2**

Effects of management options on the presences of the four wildlife species. For each management option, 500 simulations of 50 years each were run. For a given simulation, the number of grid cells (one-hectare resolution for birds and 0.033-ha resolution for rodents) for each of the four target animals was recorded at the beginning and end of the 50 years. For a given animal, the ratio of the ending number to the beginning number is a summary measure of management effectiveness for that animal. For each cell, the first number is the summary ratio; and the second number (entered in  $\pm$  form), is the standard deviation of the summary ratio across the 500 simulations for that cell. The number in parentheses is the fraction of simulations that resulted in extirpation over the 50 year time horizon.

	Cactus wren	Gnatcatcher	Stephens kangaroo rat	Pacific pocket mouse
Status Quo	0.191 $\pm$ 0.262 (0.084)	0.074 $\pm$ 0.142 (0.144)	2.959 $\pm$ 4.756 (0.070)	0.668 $\pm$ 1.434 (0.199)
Reduce burn area	0.276 $\pm$ 0.308 (0.030)	0.139 $\pm$ 0.335 (0.096)	2.752 $\pm$ 3.939 (0.080)	0.536 $\pm$ 1.212 (0.234)
Alter Burn Site	0.197 $\pm$ 0.231 (0.074)	0.101 $\pm$ 0.204 (0.136)	3.087 $\pm$ 4.994 (0.072)	0.631 $\pm$ 1.425 (0.192)
Protect CSS	0.397 $\pm$ 0.386 (0.014)	0.185 $\pm$ 0.354 (0.084)	3.022 $\pm$ 4.658 (0.066)	0.630 $\pm$ 1.311 (0.208)
Restore	0.182 $\pm$ 0.228 (0.092)	0.061 $\pm$ 0.141 (0.198)	4.205 $\pm$ 6.135 (0.046)	1.170 $\pm$ 2.016 (0.132)
No prescribed burn	0.193 $\pm$ 0.241 (0.058)	0.102 $\pm$ 0.251 (0.156)	0.863 $\pm$ 1.981 (0.208)	0.163 $\pm$ 0.752 (0.500)

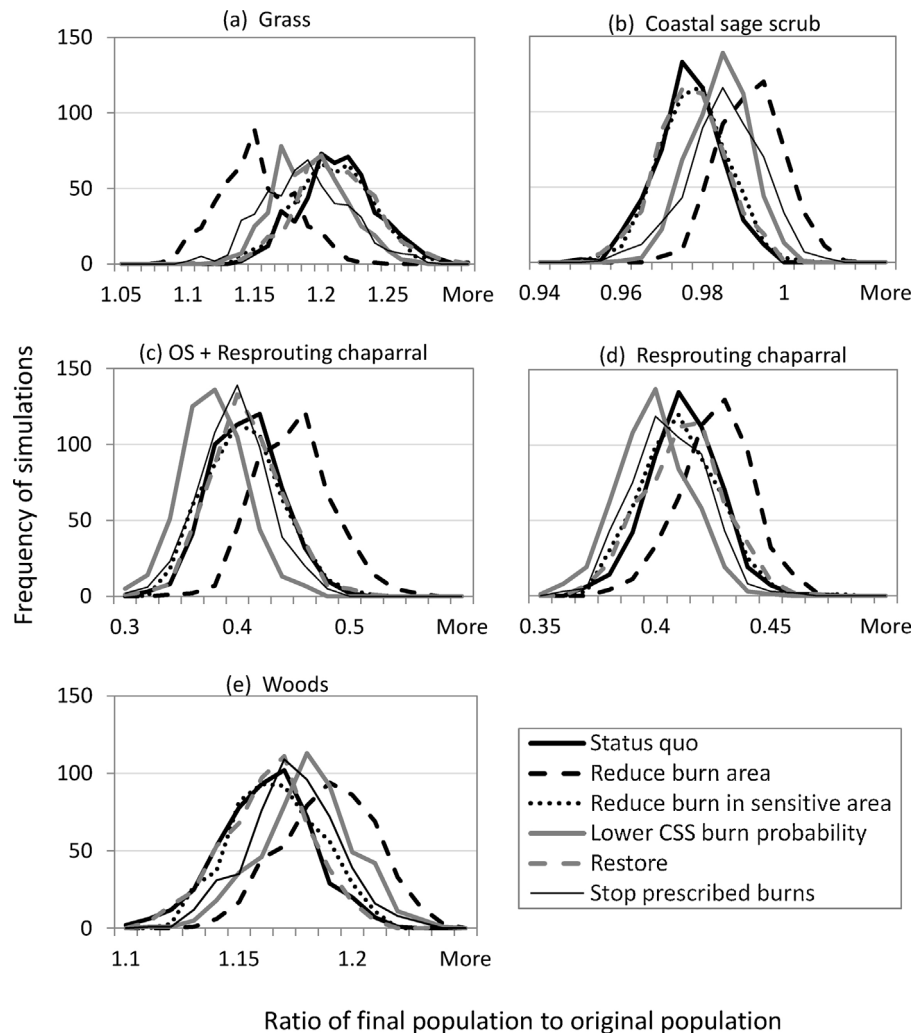
### 3. Results

The best management option varied by vegetation type and focal wildlife species ([Tables 1 and 2](#), [Figs. 4 and 5](#)). The status quo option resulted in the most fire and was thus the best option for grass ([Table 1](#); [Fig. 4](#)), and among good options for the rodents ([Table 2](#); [Fig. 5](#)). For all of the other vegetation types and for the birds, reducing the total area burned was the best or second best option. Under all management options, there was a large decline in chaparral ([Table 1](#); [Fig. 4](#)) and a high probability that the pocket mouse would be extirpated (greater than 19% chance; [Table 2](#)). Both bird species experienced a greater than 50% decline in occupancy in more than 70% of all simulations across all scenarios ([Fig. 5](#)).

The variability in outcomes for a given management option was much smaller for vegetation than for animals, with the gnatcatcher and the Pacific pocket mouse having the highest variability. For all of the rodent simulations, the standard deviation across model runs was at least 40% larger than the mean ([Table 2](#)). This high variability across model runs was not a consequence of too few simulations. For the “status quo” scenario, we ran the model 6000 times and found that, above 300 runs, the observed mean and standard deviation were stable. This indicates that scenario rankings are robust to our choice of run replication.

The habitat restoration option was not beneficial to the birds, but it was very beneficial to the rodents ([Table 2](#); [Fig. 5](#)). Across all scenarios, lowering the probability of fire in coastal sage scrub was the best option when considering both the birds and the rodents simultaneously. Under that management option, both bird species and the kangaroo rat saw increases in abundance as compared to the status quo. For the pocket mouse, while the average fraction of initially occupied habitat remaining at the end of the simulation decreased (moving from 0.668 under the status quo to 0.630), the extinction risk was nearly unchanged (moving from 0.199 under the status quo to 0.208) under the protect-coastal-sage-from-fire management option. This option, however, was not good for chaparral, as it resulted in a more precipitous decrease in abundance as compared to the status quo option.





**Fig. 4.** Histograms of the fraction of the initial number of grid cells (1 ha resolution) of each habitat type that remain in that habitat type at the end of the model time horizon for (a) grass, (b) coastal sage scrub, (c) chaparral with obligate seeding and resprouting species, (d) chaparral with only resprouting species, and (e) woods for each management option considered.

The most likely sites to support the target species across the time horizon were sites that had the preferred fire regime and were initially occupied or adjacent to initially occupied sites (Fig. 6, compare to Fig. 1). For example, birds were not initially located in areas with high predicted fire frequencies, and continued to be absent from those areas at the end of the time horizon. The rodents were most likely to occur in prescribed burn areas that had been initially occupied or were adjacent to initially occupied areas.

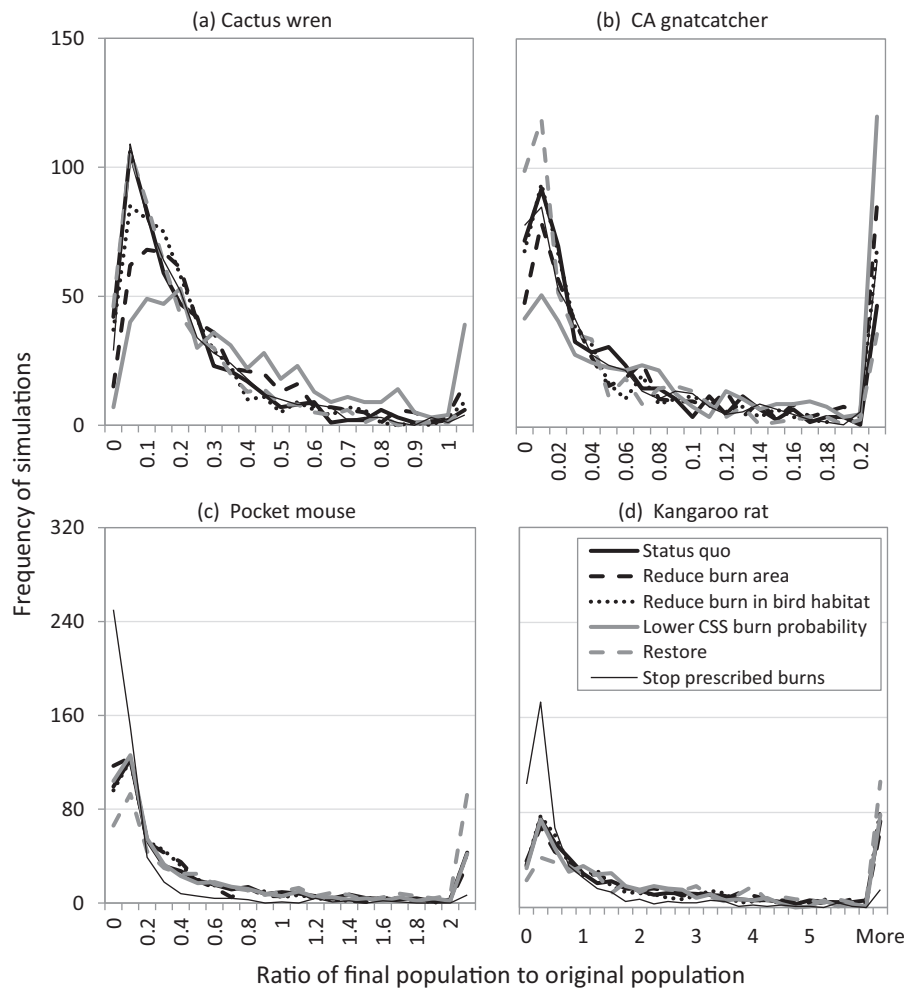
#### 4. Discussion

We demonstrate the utility of a spatially explicit simulation model of landscape dynamics for supporting decision making in a multi-species conservation context. Other studies have acknowledged the importance of modeling habitat dynamics and habitat management in a conservation context (Breininger et al., 2010; Johst et al., 2011; Mairota et al., 2014), but at most have linked dynamic landscape simulations to one animal species (e.g., Akçakaya et al., 2004, 2005). Our model, however, is unusual in the literature in that it includes the direct and indirect impacts of fire on multiple vulnerable species and vegetation types under dynamic disturbance, all as functions of multiple management interventions. Further, the model considers both plant (vegetation) and animal conservation targets simultaneously,

allowing us to consider conservation trade-offs amongst different taxa.

By including fire's impacts on at-risk species directly through fire and indirectly through vegetation transition, we have built a model that incorporates more ecological and landscape processes in conservation decision-making. The impact of fire-dependent vegetation transitions is different for birds and rodents and thus a model that incorporates this process is critical to exploring trade-offs among multiple species. The recognition that landscapes are not static has led to important advances for exploring trade-offs in economic contexts (Newburn et al., 2005; Meir et al., 2004), where land use change increases opportunity costs.

Our model, applied to one of the few remaining locations of critically endangered coastal sage habitat, included four target wildlife species (two birds and two rodents, each a species of special concern), four vegetation types, and six management options. Across all management options, there were large declines in cactus wren, California gnatcatcher, and Pacific pocket mouse populations. The declines in bird populations are not surprising given the observed post-fire declines in cactus wren and gnatcatcher abundances at a variety of sites throughout Southern California. At Camp Pendleton, gnatcatcher densities were roughly ten-fold lower in recently burned sites (Mayer and Wirtz, 1995; Wirtz et al., 1997). Cactus wren have been found to be potentially more sensitive to fire



**Fig. 5.** Histograms of the fraction of the initially occupied grid cells that remain occupied at the end of the model time horizon for (a) cactus wren, (b) California gnatcatchers, (c) Pacific pocket mice, and (d) Stephens' kangaroo rats for each management option considered. Grid cells were one hectare resolution for the birds and 0.033 ha resolution for the rodents.

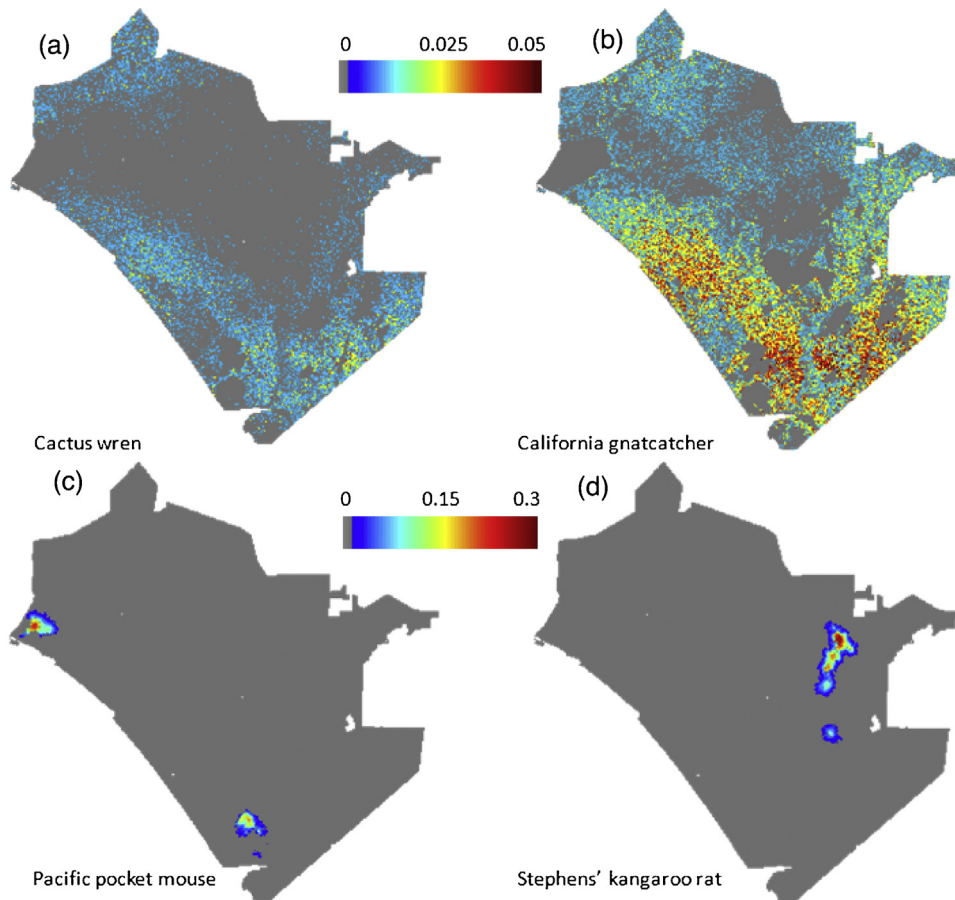
with long-lasting, post-fire population declines of 63% and 82.1% for populations in northeastern San Diego and Orange Counties (Hamilton, 2009; Leatherman, 2009). Predicted declines in Pacific pocket mouse populations are consistent with the species' critically endangered status (Spencer, 2005), where active interventions are believed necessary to prevent Pacific pocket mouse extinction. Although the predicted population trajectories are plausible in our study system, because of inherent uncertainties in any modeling exercise, the real strength of our modeling approach is that it can project the relative effects of different management options on populations of multiple focal species. Relative effects of management options, or management rankings, have been shown in the literature to be more reliable than absolute values of model output (McCarthy et al., 2003).

Although no single management option was best in all comparisons, one management option emerged as broadly the most effective—lowering the burn probability of coastal sage scrub. In particular, protecting coastal sage scrub from fire resulted in population improvements for the California cactus wren, the California gnatcatcher, and the Stephen's kangaroo rat and resulted in little harm to the Pacific pocket mouse. All four target species occur in coastal sage scrub, with the birds occurring exclusively in coastal sage scrub and the rodents occurring in both coastal sage scrub and grass. Preventing coastal sage scrub from burning benefits the birds by reducing vegetation transition to grass and by avoiding long post-burn vegetation recovery times (wrens and gnatcatchers

require 15 and 8 years, respectively, of post-burn recovery before moving back to a burn location). Lowering the probability of coastal sage scrub burning has little impact on rodents so long as there is enough burning (including prescribed burning) to prevent a dense understory of invasive grasses. The rodents live in both coastal sage scrub areas and grass areas, which are typically interspersed. When one has not burned recently enough, the rodents can move to the other.

As compared to the status quo option, protecting coastal sage scrub resulted in a more precipitous decrease in abundance of all chaparral, likely due to fire-spread from coastal sage scrub into adjacent chaparral. Thus, our results demonstrate the importance of “spill-over” from one vegetation type to another (coastal sage scrub to chaparral), which may or may not occur in real landscapes. Overall, chaparral declined considerably over the model time horizon. These declines are consistent with observed declines from the 1933 to 2003 vegetation censuses performed on Camp Pendleton and studies from other sites showing that chaparral is sensitive to increased fire frequency (Jacobsen et al., 2004; Zedler et al., 1983; Haidinger and Keeley, 1993; Keeley et al., 2012).

For birds, the habitat restoration option was designed to speed the recovery of vegetation after a fire, allowing birds to re-colonize burned areas sooner. However, wildfires were frequent enough in the simulations to overwhelm the restoration effect, leaving no benefit for the birds. In additional simulations (not shown), we found that if we further decreased the post-fire duration before



**Fig. 6.** Maps showing average occupancy over the 500 simulations for each grid cell (1 ha resolution) at the end of the time horizon for each species: (a) cactus wren (CACW), (b) California gnatcatcher (CAGN), (c) Pacific pocket mouse (PPM), and (d) Stephens' kangaroo rat (SKR). The color legend is shared for the birds ((a) and (b)) and for the rodents ((c) and (d)).

birds could re-colonize burned areas (e.g., allowing cactus wren to colonize after 4 years and gnatcatchers after 2 years), we saw only modest improvements in bird occupancy. For rodents, restoration was designed to delay the recovery of the thick vegetation understory which prevents rodent foraging, thus prolonging the duration of favorable habitat that followed a fire. The rodents did receive substantial benefit from the simulated restoration option. For rodent habitat, land managers may want to consider mowing, grazing, or additional prescribed burns in years with high invasive grass growth.

For rodents, outcomes varied from one extreme to the other across model runs. For both species, extirpation and more than doubling of occupied area were both likely outcomes. This variability in the model is consistent with reported variability in populations of similar species. [Heske et al. \(1994\)](#), [Brown and Heske \(1990\)](#), and [French et al. \(1974\)](#) have reported widely fluctuating rodent populations. From a management perspective, large swings in populations offer two lessons. First, detecting the impact of vegetation management might be obfuscated by natural population fluctuations. Second, to confirm the impacts of vegetation management, a greater investment in population monitoring may be needed (perhaps in conjunction with simulation models to highlight the most informative data).

We ran all simulations at a grid cell resolution consistent with the average range size of the different target species. However, we ran additional simulations at coarser resolutions and found that the resulting management decisions were unaltered. We found that the finer the resolution (up to the species' respective range sizes), the larger the overall predicted population size. This is not

surprising as dispersal limitations may prevent species from occupying all available habitat in a region, and fewer grid cells, due to coarser resolution, would limit local population expansion. Regardless, the grid cell resolution did change the most beneficial management options.

Our goal was to demonstrate how tradeoffs in multiple species' habitat requirements could be represented in a coherent multi-species model with the aim of exploring a range of species management objectives and habitat management interventions. The model quantified the relative benefits of six habitat management options and demonstrated that the management action that is optimal (of those tested) across species is not necessarily the best option for all species. Although our model is tailored to wildlife and vegetation in coastal Southern California, the threats faced by this region are common to the world's five Mediterranean ecosystems, all of which are biodiversity hotspots ([Myers et al., 2000](#)). Understanding the frequency of vegetation type transitions is essential to modeling post-fire succession in Mediterranean ecosystems and ultimately providing conservation management recommendations for multiple threatened species in these regions.

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