Effects of Climate Change and Urban Development on the Distribution and

Conservation of Vegetation in a Mediterranean Type Ecosystem

by

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ABSTRACT

Climate and land use change are projected to threaten biodiversity over the coming century. However, the combined effects of these threats on biodiversity and the capacity of current conservation networks to protect species' habitat are not well understood. The goals of this study were to evaluate the effect of climate change and urban development on vegetation distribution in a Mediterranean-type ecosystem; to identify the primary source of uncertainty in suitable habitat predictions; and to evaluate how well conservation areas protect future habitat in the Southwest ecoregion of the California Floristic Province. I used a consensusbased modeling approach combining three different species distribution models to predict current and future suitable habitat for 19 plant species representing different plant functional types (PFT) defined by fire-response (obligate seeders, resprouting shrubs), and life forms (herbs, subshurbs). I also examined the response of species grouped by range sizes (large, small). I used two climate models, two emission scenarios, two thresholds, and high-resolution (90m resolution) environmental data to create a range of potential scenarios. I evaluated the effectiveness of an existing conservation network to protect suitable habitat for rare species in light of climate and land use change. The results indicate that the area of suitable habitat for each species varied depending on the climate model, emission scenario, and threshold combination. The suitable habitat for up to four species could disappear from the ecoregion, while suitable habitat for up to 15 other species could decrease under climate change conditions.

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The centroid of the species' suitable environmental conditions could shift up to 440 km. Large net gains in suitable habitat were predicted for a few species. The suitable habitat area for herbs has a small response to climate change, while obligate seeders could be the most affected PFT. The results indicate that the other two PFTs gain a considerable amount of suitable habitat area. Several rare species could lose suitable habitat area inside designated conservation areas while gaining suitable habitat area outside. Climate change is predicted to be more important than urban development as a driver of habitat loss for vegetation in this region in the coming century. These results indicate that regional analyses of this type are useful and necessary to understand the dynamics of drivers of change at the regional scale and to inform decision making at this scale.

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INTRODUCTION

Changes in land use and climate are the two main drivers expected to greatly and negatively impact species' ranges and distributions in all terrestrial ecosystems (Sala et al., 2000). Globally, wildlands and semi-natural areas have decreased from 95% of Earth's ice-free land in 1700, to 45% in 2000 due to anthropogenic transformation (Ellis et al., 2010) causing considerable loss of biodiversity as measured by the number and relative abundance of species that occur naturally in a biome (Foley et al., 2005). During the same period land use for agriculture and urban settlements increased from 5% to 39% of total ice-free land (Ellis et al., 2010), a trend that is not implausible to continue into the future (Alcamo et al., 2006). Climate change during the past century has resulted in changes in phenology, species ranges, and community composition, among others (Walther, 2010). Considering the magnitude of land use and climate change impacts, it is imperative to understand their combined effect for biodiversity conservation at the regional scale, as studies that include only one of these factors are likely to inadequately assess the impacts of both on biodiversity change (de Chazal and Rounsevell, 2009).

The main goal of conservation areas is to protect biodiversity from current and future threats. However, the effectiveness of conservation areas in the future may be affected as the distribution of suitable habitat for the species currently present in them shift under climate change. A number of studies predict loss of suitable habitat from conservation areas due to climate change, ranging from 6 to 48%

(Araújo et al., 2004; Hannah et al., 2005; Lemieux and Scott, 2005). Therefore, the effectiveness of conservation areas needs to be assessed not only in light of climate change but also land use change to inform long-term conservation plans.

Mediterranean Type Ecosystems (MTEs) are biodiversity hotspots (Myers et al., 2000) with some of the highest plant species richness and endemism on the planet and include many species with restricted ranges (Cowling et al., 1996). MTEs are also among the most threatened biomes, as the biodiversity in them is sensitive to all the main drivers of change expected to affect species ranges and distributions in terrestrial ecosystems by the end of the century (Sala et al., 2000). The range of some species in MTEs species is expected to decrease (Benito Garzón et al., 2008) even in areas where the Mediterranean climate extent is expected to increase (Klausmeyer and Shaw, 2009). Also, the generally small size of conservation areas in MTEs makes the climate residence time in them one of the shortest of all biomes (Loarie et al., 2009). Furthermore, urban area and agriculture increased by 13% and 1%, respectively, from 1990 to 2000 in MTEs (Underwood et al., 2009). The ecological importance of MTEs makes it critical to develop more refined predictions than the ones we currently have to understand the effects of land use and climate change, and the role of conservation areas for protecting MTE biodiversity in the future.

Species Distribution Models (SDMs) extrapolate species distribution data in space and time, usually based on a statistical model. Models calibrated for current climate conditions can be used to create potential species distributions

(suitable environmental conditions maps) at different times to predict the effect of climate change on species and ecosystems (Franklin, 2010a). SDMs have been considered one of the only tools for assessing the potential impacts of climate change on species distributions (Huntley, et al., 2004), and the most plausible means by which we can translate climate change scenarios into ecological outcomes (Dobrowski et al., 2011a). Furthermore, SDMs have been widely used to analyze the impact of climate change on biodiversity (e.g., Huntley, et al., 2004, Peterson et al., 2002; Thomas et al., 2004; Thuiller et al., 2011) and are useful as information for biodiversity conservation and management plans (see Kremen, 2008).

The high floristic diversity and conservation importance of MTE have made them the subject of multiple studies analyzing the potential impacts of environmental change on species distribution. However, the combined effects of land use and climate change on biodiversity protection have seldom been addressed at the regional level in MTEs (e.g. Bomhard et al., 2005), particularly using high resolution environmental and land use data. The most comprehensive study using SDMs to analyze the impacts of climate change on the California Floristic Province concluded that up to 66% of endemic plant species would experience a habitat reduction of up to 80% by the end of the $21st$ century (Loarie et al., 2008). However this study did not analyze the effect of land use change, nor the role of conservation areas in protecting these species under climate change, and it used low-resolution environmental data, which can considerably

overestimate the suitable habitat area predicted by SDMs (Seo et al., 2009). Additionally, low-resolution climate data do not take into account topoclimate (Thornthwaite, 1954), and ground conditions, especially soil-moisture availability (Major, 1951), which control local differences in ecological regions and landscapes (Bailey, 1996). Topoclimate, which is captured better with high resolution data like the one used in this study, along with edaphic drivers, defines the physical template that organisms experience, and thus constrains habitat suitable for the growth, survival, and reproduction of organisms (Dobrowski, 2010) . In the California Floristic Province the Southwest ecoregion (Fig. 1) is a region of interest because (i) urban development is extensive and projected to expand (Syphard et al., 2011a), (ii) high resolution environmental data applied to a range or climate change scenarios exist for this region and (iii) there is a well developed conservation planning network (Natural Community Conservation Planning areas, NCCP) whose effectiveness can be evaluated in light of urban development and climate change. The NCCP program goal is to promote conservation of broad-based natural communities and species diversity by involving different stakeholders and key interests for addressing cumulative impact concerns, while continuing to allow appropriate development and growth in the region (California Fish and Game, 2003). Studying the status of and threats (urban growth and climate change) to species covered by the NCCP network allows me to contribute to fill the gaps I have identified in the literature.

While I only considered 19 species in this study, these were selected to span a

range of life forms, fire responses, and range sizes, and are representative Plant Functional Types (PFT) found in Mediterranean (Cowling and Campbell, 1980; Hobbs et al., 1997) and fire-prone ecosystems (Keeley, 1986). This allowed me to search for patterns of predicted responses that varied with species attributes that would allow these results to be generalized to other species found across MTEs globally that share the same general characteristics with the species in this study. The specific questions I addressed in this study are:

- 1. What is the projected effect of climate change on the distribution of the plant species studied, measured both by suitable habitat area change, and range centroid shift? How does the effect vary by
	- a. Species
	- b. Plant Functional Type
	- c. Range size (i.e. small range (rare) vs. large range (common) species?

Based on previous studies that projected decreases I expected plant species to lose suitable habitat under the different climate change scenarios as temperature and moisture conditions change (Thuiller et al., 2005; Kueppers et al., 2005), and species range centroids to shift as species track conditions similar to their current ones (Loarie et al., 2008). For PFTs I expected resprouters (those species that resprout in response to fire) to be most affected by a drier future climate (Esther et al., 2010), as establishment of resprouter seedlings depends on wet summer conditions

the year after a fire (Enright and Lamont, 1992; Enright et al., 1998). Last, I expected rare species to lose more suitable habitat under climate change scenarios than common species, because rare species tend to occur in localized climatic conditions that have been predicted to shrink more than areas with dominant climate types (Ohlemüller et al., 2008).

2. What is the extent of suitable habitat for the study species supported by the current network of conservation areas, individually and together, and how is that projected to change under climate change scenarios and urban growth?

I expected that current conservation areas might be insufficient to protect a significant fraction of species ranges as the climate in many of these areas could shift in such a way that there is no habitat overlap between the coolest parts of the conservation area in the future and the warmest fraction today (Ackerly et al., 2010), and urban growth might take place in areas of future suitable habitat. However, I also expected that suitable habitat might shift from one conservation area to another, therefore useful information could be gained by analyzing the predicted species habitat suitability in individual conservation areas.

- 3. What are the major sources of uncertainty for these projections? How much does the use of different
	- a. Thresholds applied to predicted probabilities of species occurrence to define suitable habitat
- b. Climate models
- c. Emission scenarios

influence the predicted suitable habitat of the species?

I hypothesized that the use of different threshold criteria (Freeman and Moisen, 2008) and climate models (Buisson et al., 2010) would contribute most to the variation observed in the results.

METHODS

Study Area, Species, and Environmental Data

I analyzed the effects of climate change on plant species distribution for a slightly modified (Syphard et al., 2011b) Southwest ecoregion (Davis et al., 1995) of the California Floristic Province that includes the entire Transverse Ranges, and the southern ranger districts of the Los Padres National Forest extending into northern Santa Barbara and San Luis Obispo counties (Fig. 1). The combined effects of urban growth and climate change were analyzed in a subregion (southern portion) of the Southwest ecoregion. This subregion included parts of western San Diego, western Riverside, and Orange Counties (Fig. 1). The total area of this subregion is approximately 1.6 million ha. It is in this subregion that the NCCP program areas are located and therefore where predictions of urban growth were developed. The total area under the NCCP program in this subregion is approximately 1.1 million ha.

I used spatially explicit data on occurrences for 19 plant species (Table 1) that was compiled from the Calflora database (http://www.calflora.org), and the California Department of Fish and Game's Natural Diversity Database (http://www.dfg.ca.gov/ whdab/html/cnddb.html). These species were chosen because they represent groups of plants found in most Mediterranean and fireprone ecosystems. Plant functional types were defined by life form (herbs, and subshrubs) (Cowling and Campbell, 1980; Hobbs et al., 1997) and fire response (obligate seeders, and resprouters) (Keeley, 1981; Keeley et al., 2006; Keeley and

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Davis, 2007). Additionally these species span small to large range sizes (Syphard and Franklin, 2010). Small-range (rare) species were designated using the Calflora threatened index, and a maximum estimated range size of $10,000 \text{ km}^2$ (based on the total area of sub-ecoregions within which occurrences have been recorded).

I used the same combination of six climate, two terrain, and three soil variables as predictors to project both present and future suitable habitats. These variables were selected based on their hypothesized relationship to the distribution of plant species in Southern California (e.g. Davis & Goetz 1990; Franklin 1998, 2002; Franklin et al., 2000). Bioclimatic predictors describing the current climate were derived from monthly climate averages for 1970-1999. The six bioclimatic variables were selected from 10 initial candidate variables using a principal component analysis, which determined that the six selected variables were largely uncorrelated. The variables selected were: maximum temperature of warmest period, growing days above 5° C, mean annual precipitation, temperature seasonality, precipitation in the warmest quarter, and an aridity index. The aridity index was defined as the quotient between annual precipitation and potential evapotranspiration.

Climate data (precipitation, and temperature) were downscaled to 90 m following a procedure described by Flint and Flint (2012). The method of constructed analogs was used to statistically downscale climate data from global climate models to 12 km. This approach is a deterministic linear simplification of

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the relationship between the current weather or climate pattern (dependent variable) and selected historical patterns (independent variables) that describe the evolution of weather or climate for a future period (Hidalgo et al., 2008). Spatial downscaling was used to downscale the climate data from 12 km to 4 km for bias correction using a model that interpolates very sparsely located climate data over regional domains and combines a spatial Gradient and Inverse Distance Squared weighting to monthly point data with multiple regressions (Nalder and Wein, 1998) modified with a nugget effect specified as the length of the coarse resolution grid (Flint and Flint, 2012). Bias correction was performed using a historically measured dataset, PRISM (Daly et al., 2008), with the same spatial resolution as the spatially downscaled parameter set. Further spatial downscaling was used to develop the final 90m dataset for model application.

Bioclimatic predictors describing the end of century climate were derived from monthly climate averages using downscaled simulated future climate data for the period 2070-2099 from the Geophysical Fluid Dynamics Laboratory (GFDL) model, and the Parallel Climate Model (PCM). These two particular climate models were used because they realistically simulate the distribution of monthly temperatures and the strong seasonal cycle of precipitation that exists in California's recent historical climate (Cayan et al., 2008). Additionally, I used two contrasting emissions scenarios A2 (medium-high) and B1 (low) developed by the Intergovernmental Panel on Climate Change based on demographic and socio-economic development, and technological change (Nakićenović et al.,

2000). The A2 scenario describes a very heterogeneous world based on selfreliance and local identities, continuously increasing global population, and regionally oriented and per capita oriented economic growth, resulting in an increase of over 20 Gt CO₂/yr from 1990 levels to reach 30 Gt CO₂/yr by 2100. The B1 scenario describes a convergent world with emphasis on global solutions to economic, social, and environmental issues, with a population that peaks in mid-century and declines thereafter, rapid economic changes toward a service and information economy with reductions in material intensity, and the introduction of clean and resource-efficient technologies resulting in an increase in $CO₂$ emissions that peak around mid-century and decline thereafter to levels below 1990 by 2100. The GFDL model has a relatively high sensitivity of global and regional temperature to greenhouse forcing while the PCM has relative low sensitivity compared to other global climate models (Cayan et al., 2008). Both climate models project higher temperatures in Southern California (the region of study for this project) but their different sensitivity to greenhouse forcing results in the GFDL model projecting higher temperatures than the PCM. Precipitation projections vary substantially between the two models with the GFDL predicting 22% and 26% decrease (depending on which emission scenario is used) in annual precipitation by the end of the century. On the other hand PCM predicts a 7% and 8% annual precipitation increase (Cayan et al., 2008). These scenarios give a range of climate scenarios to compare, and are well established in the literature (Lenihan et al., 2008; Shaw et al., 2009; Sork et al., 2010).

I used slope angle, and potential summer solstice solar insolation (Rich et al., 1995), both derived from the U.S. Geological Survey 30m resolution digital elevation model, as the terrain variables. The soil variables I used were soil depth, soil available water capacity, and soil pH and were created using the California State Soil Geographic Database (STATSGO). All climate, terrain, and soil variables were resampled to 100m.

Current (2000) and Future (2050) Urban Extent

I used urban development as representative of land use change, as it is the most significant source of land use change in southern California. Current urban extent was created using a national data set for the continental U.S in which housing density was mapped every decade from 1940 to 2000 (Hammer et al., 2004). Syphard et al. (2011b) converted these data into a binary urban extent (i.e., urban or undeveloped) for the Southwest ecoregion selecting a threshold where any pixel containing a density equal to or higher than 128 units/ km^2 was considered urban. For future urban extent (2050), the current urban extent was used as the baseline layer, and urban development was simulated using SLEUTH, a cellular automaton model (Clarke, 2008). SLEUTH requires six input layers (Slope, Land use, Exclusion (areas restricted from development), Urban extent, Transportation, and Hillshade) which it uses in gridded map form. A successive application of rules that govern state changes over time, to the set of states associated with cells covering an urban area yields states beyond the initial

conditions. Five parameters control SLEUTH's behavior entirely. These parameters control the random likelihood of any pixel turning urban (dispersion), the likelihood of cells starting their own independent growth trajectory (breed), the regular outward expansion of existing urban areas and infill (spread), the degree of resistance of urbanization to growing up steep slopes (slope) and the attraction of new development toward roads (road gravity). Furthermore, these parameters are interrelated. For this project federal and conservation lands were excluded from development, but NCCP lands were allowed to develop.

The urban growth and climate change simulations are asynchronous. However using urban development for 2050 is reasonable for analyzing the combined effects of climate change and urban growth by the end of the century because the high probability development rate slowed over time and plateaus by 2050 (for details see Syphard et al., 2011b). Additionally, even if the urban growth effect is doubled between 2050 and 2080, the qualitative effect of urban growth vs climate change does not change (see results).

Species Distribution Models

I created suitability habitat models with three SDM methods for each species using present environmental conditions to calculate current habitat suitability. I then used future predicted climate data to create future habitat suitability maps. I used generalized additive models (GAMs), decision trees (Random Forests, RFs), and maximum entropy (MaxEnt) because they each fit the data differently

(Franklin, 2010a) and are among the best performing methods (Elith et al., 2006) as measured by the Area Under the Receiver Operator Curve (AUC), a threshold independent statistic. Additionally, by selecting these three model approaches I was able to avoid averaging their predictions with those of models with low accuracy (low AUC) when I created the ensemble models (see below).

GAMs are a non-parametric extension of generalized linear models in which the global regression coefficients are replaced by a scatter plot smoothing function, allowing the data to determine the shape of the species response curves rather than being limited by the shapes available in a parametric class (Yee and Mitchell, 1991). Regression tree analysis is a technique that constructs a set of decision rules on the predictor variables rather than trying to determine if there is a pre-specified relationship between the response and the predictors (Prasad et al., 2006). In RF, an ensemble decision tree method, a "forest" of many trees is constructed with a randomized subset of predictors via bootstrapping samples (resampling without replacement) (Prasad et al., 2006), and then averaged to reduce the variance component of the output. MaxEnt is a presence only data machine learning technique (Philips et al. (2004; Philips et al., 2006) that minimizes the relative entropy between the probability density from the presence data and the landscape (Elith et al., 2011).

To fit the SDMs I used 10,000 random points for background (MaxEnt) or as pseudoabsences (GAM, RF) to maximize MaxEnt performance, and to not reduce the species prevalences in GAMs and RFs more than necessary. I down-weighted

the absence data for GAM and RF so that the sum of the weighted absences was equal to the sum of the number of presences. A 1:1 ratio of presence to absence yields an optimal balance between omission and commission errors (McPherson et al., 2004). Additionally, I retained all predictors rather than using a variable selection technique, so all the models would have the same variables and to retain all temperature-related variables. I estimated GAMs using a logit link for the binary response, and smoothing splines using up to four target degrees of freedom. I estimated RFs from 500 trees using three randomly selected variables for each tree, and evaluated using averaged "out-of-bag" predictions from the RF models. I created MaxEnt models using one sample without replacement replicate 75/25% (training/testing) instead of ten replications with no sample without replacement allowed because I did not find any substantial difference between these two methods during comparison tests. I evaluated the predictive performance of individual SDMs based on 500 samples with replacement estimates of the AUC (Marmion et al., 2009). I fit the models using R (http://CRAN.R-project.org/) for GAM and RF and MaxEnt 3.3.3a software.

I developed consensus models for each species using the AUC-weighted weighted average (WA) of all models (1), which has been shown to be superior to Median(all), Median(PCA), and Median(AUC) (Marmion et al., 2009):

$$
WA_{i} = \frac{\sum_{j} (AUC_{mj_{i}} \times mj_{i})}{\sum_{j} AUC_{mj_{i}}} \tag{1}
$$

where m_i are the probability occurrence values of the ith plant species in a given grid cell for a j single species model. In consensus forecasting a measure of the central tendency is calculated for the ensemble of forecasts; in averaging several models, the 'signal' of interest emerges from the 'noise' associated with individual model errors and uncertainties (Araujo and New, 2007).

From the continuous probability maps produced by the SDMs, I created binary maps using two thresholds (cut-off of occurrence probability value) to discriminate suitable versus unsuitable habitat. This allowed me to calculate habitat gain, loss, and stable under climate change and land use scenarios, and made these results comparable to other studies (e.g., Kueppers et al., 2005; Loarie et al., 2008). I used two well-established threshold criteria based on model performance, Maximum Sensitivity + Specificity as a low threshold and Maximum Kappa (MaxKappa) as a high threshold (Freeman and Moisen, 2008). Maximum Sensitivity + Specificity minimizes probability of total false positives and negatives, while MaxKappa maximizes the proportion of correctly classified locations after accounting for the probability of chance agreement.

After creating the binary suitability maps, I overlaid these maps with current and future (2050) urban extents to analyze the independent and combined effects of climate and land use change. I assumed there is no interaction between climate and land use change. Additionally, I calculated the centroid of the current and future suitable habitat for each species and calculated the distance between the

two as an indicator of the displacement of the core suitable habitat. All these processes were completed using ArcGIS 9.3.1 (ESRI, Redlands, CA, USA).

Natural Community Conservation Planning Areas

I analyzed change in suitable habitat for all small range (rare) species (Table 1) in the seven NCCP areas located within San Diego, Western Riverside, and Orange Counties because the core habitats for these rare species are located within the southern portion of the Southwest ecoregion (Fig. 1). The rare species in this study are all targeted for conservation within the NCCP. I only analyzed the part of the San Diego County Multiple Habitat Conservation Open Space Plan that lies within the California Floristic Province and Southwest ecoregion boundaries (Fig. 1). I compared projections for two of the plans, the San Diego County Multiple Species Conservation Plan and San Diego County Multiple Habitat Conservation Open Space Plan, versus all the other NCCP areas aggregated to analyze the ability of the individual and combined NCCP areas to provide suitable habitat for these rare species in the face of climate change and urban growth.

Analysis

I performed statistical tests to test if projected habitat area changes resulting from different climate models, emission scenarios, and thresholds, or by grouping the plants into PFT or range sizes (Table 1) were significantly different (α =

0.05). The suitable habitat results were non-normal, and the sample sizes and variances were different between groups. These conditions violate the assumptions for commonly used statistical tests (e.g. Kruskal-Wallis, Dunnett, or Tukey-Kramer); therefore I used a non-parametric procedure developed by Herberich, et al (2010) for comparing multiple means in unbalanced designs. This test makes no assumptions regarding the distribution, sample sizes, or variance homogeneity. This procedure was implemented using the multicomp package in R.

RESULTS

Species Distribution Models

Species distribution models resulting from AUC-weighted averaging had high accuracy when evaluated with current distribution data (bootstrapped $AUC > 0.9$) in most cases except for four large-range species (Table 1). I found that in general, precipitation and maximum temperature of the warmest period were the variables that contributed the most to fitting the models. Soil variables and potential summer solstice solar insolation were in general the least important predictors, but were important for some species (Appendix A).

Effects of climate on habitat distribution

I projected between zero and nine of the species to lose suitable habitat under the PCM, and between one and 15 of the species to lose habitat under the GFDL model (Table 2). Additionally, under climate change, I projected up to one quarter of the modeled species to lose their entire suitable habitat within the Southwest ecoregion by the end of the $21st$ century (Table 2). Of the species that were projected to maintain suitable habitat somewhere within the Southwest ecoregion under climate change, I projected up to two to lose their entire current suitable habitat (i.e., there is no overlap between predicted current and future distribution of habitat), with six additional species losing between 90 – 99% of their current habitat (Table 3). Here and in the following results, the variation in area estimates arises from the use of different climate models, emissions

scenarios, and thresholds (see *Uncertainty*), and the range of species losing or gaining habitat is bracketed between the best (combination of PCM, low emission scenario and low threshold) and the worst-case scenario (combination of GFDL, medium-high emission scenario, and high threshold).

I predicted that obligate seeders could be the PFT most affected by climate change as all PFTs except for obligate seeders gain suitable habitat (on average) using the high threshold (Fig. 2). The differences in average area change between obligate seeders and the other PFTs are all significant using the high threshold (herbs $p = 0.04$, resprouting shrubs $p < 0.01$, and subshrubs $p < 0.01$). On the other hand, when I used the low threshold, the average suitable area of all four PFTs increased, with herbs gaining the smallest area (143,000 ha). The increase in area for herbs ($p = 0.02$) and obligate seeders ($p = 0.03$) using the low threshold was significantly smaller than the increase in area for subshrubs, but not significantly different from that of resprouters (Fig. 2). I predicted herbaceous species to be resilient to climate change as they showed the smallest predicted changes, with low variability, in suitable habitat under both thresholds (Fig. 2). These results are the average from pooling the climate models and scenarios.

Just as I found for suitable habitat area under different combinations of climate change models and emission scenarios, the average predicted shift distance for all species suitable habitat centroids was greater using the low threshold than the high threshold (Fig. 3). However the average per-species suitable habitat shift with the low threshold was greater for only 11 of the 19 species, with one species showing a negligible difference between both thresholds. The largest average single suitable habitat centroid shift (average of the two climate scenarios and two emission scenarios under each threshold for each species) was 185 km, but my projections suggested that suitable habitat centroids could shift up to 440 km.

Small range species seem to have higher site fidelity than large range species (Fig. 4). This is evidenced by the smaller change and variability, in general, in area as a response to climate change. I predicted the suitable habitat for small range species to increase less (low threshold) or show little change (high threshold) compared to large range species (Fig. 4). The difference between small and large range species was significant ($p = 0.006$) using the low threshold for area prediction, but this difference is not significant using the high threshold.

Climate and Land Use Change in NCCP areas

Current suitable habitat inside the conservation areas for the study species ranges from ~2000 ha to 77,000 ha (Table 4). Future suitable habitat in the same area ranges from \sim 3 ha to 48,000 ha. I predicted climatically suitable habitat inside the conservation areas to decrease for seven species (Table 4). However, I predicted three of these species to gain habitat overall, one to lose a proportional amount of overall and protected habitat, and the three others to contract and lose most of their overall habitat. I predicted the other two species to gain suitable habitat overall and inside the protected areas.

Current urban extent in this subregion was calculated to be 266,000 ha and it was projected to increase by 48% to roughly 395,000 ha in 2050 (Syphard et al., 2011b). The projected rate of high-probability development occurs rapidly at the beginning but the rate slows down and levels off over time (Syphard et al., 2011b). These results suggest that the urban area for 2080 would be similar to 2050. The relative effects of climate and urban development differed among species. I projected all nine small range species to lose suitable habitat in response to urban development; however, four species were projected to lose a relatively small amount (Table 5). Additionally, I projected climate change to have a negative impact on seven of these species, and a positive impact on two (Table 5). Of the seven species that were negatively impacted by urban growth and climate change, climate change was the dominant driver for five. For the two species that are negatively impacted by urban growth but positively impacted by climate change, climate change is also the dominant driver (Table 5). The combined effect of climate change and urban development was different than the simple addition of both effects. For five of the species the combined effect is smaller than the sum of both effects, while for four of the species it is larger than the sum of both effects (Table 5).

I projected an increase in the suitable habitat of two species in San Diego County Multiple Species Conservation Plan area (Fig. 5a). I projected a considerable increase for two species and a slight increase for an additional one in the San Diego County Multiple Habitat Conservation Open Space Plan area (Fig.

5b). The other NCCP areas collectively, were predicted to become a refuge for two species (Fig. 5c). However, some of these species overlap, and the whole NCCP region is a refuge for only four species. All four of these species gain a substantial amount of total suitable habitat; however, two of them lose on average 30% and 78% of their protected habitat (Table 4). I obtained these results using the high threshold but I observed the same general pattern when I did the analysis using the low threshold (Appendix B).

Uncertainty

In general, I projected a slight (high threshold) to moderate (low threshold) increase in species' suitable habitat (Fig. 6). However, this gain was mainly driven by a few species that gained a large amount of suitable habitat. The difference between the average change in suitable habitat projected by the high and the low thresholds was statistically significant for all species ($p < 0.001$), with the median gain in projected habitat area near 30,000 ha for the high threshold, and 400,000 ha for the low threshold (Fig. 6). When I separated the results from the climate models by threshold (i.e., GFDL vs. PCM using high or low threshold) the difference between the projected changes in suitable area under the two models was not significant (Fig. 7a). But when I separated the emissions scenarios by threshold (i.e. A2 vs. B1 using high or low threshold) the difference between the suitable area change in each emission scenario was significant ($p =$ 0.05 for high threshold and $p = 0.05$ for low threshold), with the medium-high

emissions scenario (A2) projecting more modest suitable habitat gain (~ 2,800 ha, A2 high threshold) than the low emissions scenario (B1) (\sim 60,000 ha, B1 high threshold) (Fig. 7b).

DISCUSSION

Effects of climate change on species habitat suitability and distribution

Similar to Loarie et al. (2008), I projected most of the study species to lose a significant percentage of suitable habitat; however, the magnitude of the loss differed between the two studies. The suitable habitat areas predicted by Loarie et al. (2008) for the same 19 species considered in this study ranged from 3 to 468 times larger than ours, depending on the threshold I used. This difference cannot be attributed to differences in prevalence (species frequency in the training data) between the two studies. Neither study had a consistently higher or lower prevalence, nor was there a relationship between suitable area and prevalence. The environmental data were four orders of magnitude finer-grained than those used by Loarie et al. (2008) (100 x 100 m versus \sim 12.5 x 12.5 km). Using higher resolution data than the one I used here (e.g. 25 m) might still result in different amounts of suitable habitat gained or lost as fine scale models that capture the topoclimate effects show markedly different range loss and extinction estimates than coarse scale models for some species (see Randin et al., 2009; Triverdi et al., 2009). However, I would argue that the different results are in part due to the finer resolution climatic and environmental data I used (as proposed by Seo et al., 2009) as the modeling conditions used by Loarie et al. (2008) were similar to the ones used in this study.

High-resolution climate data allowed me to obtain more accurate estimates of present suitable habitat (Seo et al., 2009) at a scale that is appropriate for analysis

of the NCCP areas. However, while my results for future suitable habitat are refined from those of previous studies I cannot claim higher accuracy in my projections. Predictive performance of future projections from SDMs is likely to be lower and more variable than what the accuracy estimates for performance based on current distributions suggest (Dobrowski et al., 2011). Nevertheless, this modeling effort using high-resolution environmental data takes into account the effects of topography on local climate (for both present and future), which is not addressed when averaging environmental variables over large areas. Because topoclimate and soil conditions control the local conditions organisms experience (Bailey 1996; Dobrowski, 2010), the resulting predictions are more precise and spatially-explicit than coarse-grained predictions, although still affected by the uncertainties evaluated in this study.

I found the average magnitude of projected centroid shift to be in agreement with that of coarser-resolution studies (e.g., Iverson and Prasad, 1998; Loarie et al., 2008) suggesting that data resolution does not highly influence centroid shift estimates. At the same time these results suggest that predicted climate change patterns could alter the suitable habitat area for these 19 species by 2080. The need to disperse long distances might be problematic for several of the genera considered, e.g. *Arctostaphylos, Ceanothus,* and *Xylococcus*, that have propagules that are unspecialized for widespread dispersal and whose dispersal distance is not much greater than the species' own canopy diameter (Keeley and Davis, 2007).

Effects of climate change on different PFTs and range sizes

I found that the PFT most affected by predicted climate change impacts was obligate seeders rather than resprouters, which is in contrast to my initial hypothesis. While this could be a biological signal, it could also be an artifact of the range classification for the species in each PFT. There are two small range and two large range obligate seeder species, while there are five large range and two small range resprouting species. It could be that the effect of the small range species is not counterbalanced by the large range species for obligate seeders. This might account for obligate seeders being more affected than resprouters because as hypothesized earlier small range species tend to occur in localized climatic conditions that have been predicted to shrink more than areas with dominant climate types. Nonetheless, it cannot be ignored that if the reduction in suitable habitat for obligate seeders is a biological signal, reduction in suitable habitat compounded with slow recruitment due to fire dependency, impacts of altered fire regimes (Regan et al., 2010), and short dispersal distances, make conservation planning for obligate seeders a priority.

While small range species do not lose suitable habitat on average, it seems like the climatic conditions for them do not increase either. On the other hand the dominant climate types associated with large range species seem to become more common possibly facilitating the expansion of the common species at the expense of the rare species.

Climate and Land Use Change in NCCP areas

In its current configuration, the NCCP network is ineffective to protect climatically suitable habitat for the species that I examined. If I only take into account the six rare species for which suitable habitat was not predicted to disappear, three of them lose protected habitat while their habitat increases overall but outside the protected areas. To effectively protect species' suitable habitat in the future (at least as much suitable habitat as is currently protected) currently ineffective conservation areas could be replaced by new ones that achieve more for conservation (Fuller et al., 2010) and/or additional conservation areas need to be created in areas that are robust to uncertainty (Carvalho et al., 2011).

Consensus predictions like the ones I present here are well suited to inform these decisions as they identify areas that are selected consistently in different scenarios and offer the least investment risk as proposed by Carvalho et al. (2011). An additional way to protect species' suitable habitat area at a future time would be to implement integrated land management that allows for the protection of species outside of protected areas (Araújo et al., 2011). However, the conservation of a particular target species needs to be done without endangering or weakening the communities that already exist in either new or already established conservation areas.

In this study I considered the two major threats to vegetation in MTEs and to the Southwest ecoregion in particular -- climate change and land use change (as urban development). My results are in contrast to those of Sala et al. (2000). For
my study species the habitat loss due to predicted climate change impact was far larger than the loss due to predicted patterns of land use change. Even though the land use change modeling is asynchronous with the climate change modeling, I propose that the difference observed is likely a difference in the effects of these two drivers in the region instead of an artifact of the modeling process. The rate of development slows down and levels off by 2030 (see Syphard et al., 2011b) and even if the effects of urban growth are doubled (which is highly unlikely), land use change becomes the driving factor of change for only one additional species. These results highlight the need to conduct regional analyses to better understand the relative importance of the drivers of biodiversity change and consequently provide better information for the creation or revision of conservation management plans.

Uncertainty

SDMs are correlative models built on current distributions that do not account for physiological tolerances, dispersal limitations or demographic processes affecting species' migration (reviewed by Franklin 2010b). Additionally SDMs implicitly assume equilibrium between the current distribution and the environment, that the variables included in the models reflect the niche requirement of a species, and niche conservationism (Wiens et al., 2009). Despite these limitations, the relationship between climate and plant distributions is well established (Holdridge, 1947). Therefore, the capacity of SDMs to use current

information in conjunction with the projections of climate models can inform decision-making by conservationists and resource managers (Wiens et al., 2009).

I addressed the uncertainty that is introduced by using different modeling techniques (Pearson et al., 2006), thresholds (cut-off of occurrence probability value) (Thuiller, 2004), climate change models (Beaumont et al., 2008; Buisson, 2010), and emission scenarios (Thuiller, 2004) with consensus forecasting, which reflects the central tendency of selected forecasts and increases the agreement between projected and observed range shifts (Araújo et al., 2005; Araújo and New, 2007; Marmion et al., 2009).

These results were consistent with previous studies in this and other MTEs (Klausmeyer and Shaw, 2009; Fitzpatrick et al., 2008; Midgley et al., 2002; Benito Garzon et al., 2008) and the California Floristic Province (Loarie et al., 2008) that found that the projected variation in suitable area estimates differed according to emissions scenarios and climate models. I also evaluated a best (low threshold) and a worst (high threshold) case scenario. However, it should be noted that the criterion I used for low threshold (Maximum Sensitivity $+$ Specificity) can substantially overestimate the range of low prevalence species while the high threshold criterion (MaxKappa) has been found to portray unbiased estimates of species prevalence (Freeman and Moisen, 2008). The difference between the high and low emission scenario was the greatest source of uncertainty, meaning that, depending on the trend of greenhouse gas increase by the end of the century we could see two very different outcomes for the

distribution of climatically suitable habitat for plant species in the ecoregion. However, current atmospheric measurements (Raupach et al., 2007; Canadell et al., 2007) indicate that we are on track to surpass even the medium-high emission scenario (A2) that was used in this study. If this is the case the projections from the medium-high emission scenario are more likely than those from the low emission scenario (B1), and would in turn become a best-case scenario since they could be surpassed. The combination of the more plausible high threshold criterion with a more likely medium-high emission scenario by the end of the century suggests that the most severe results (high threshold/medium-high emission scenario) portray the more likely picture of future conditions.

In conclusion, my analysis, based on high-resolution environmental data and a consensus forecasting, provides a refinement to a study of global change risk factors. In contrast to the results from the global study, these results indicate that the relative importance of climate change as a driver of biodiversity change in this region is larger (not smaller) than that of land use change. Regional assessments of the dynamics of the drivers of biodiversity change would provide further understanding of those dynamics, and are necessary to provide useful and meaningful information to inform management plans at this scale.

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Tables

Table 1. Summary of study species and results of species distribution models.

Obligate seeders (OS), herbs (HERB), resprouting shrubs (RESPRSHR),

subshrubs (SUBSHR). PFT: Plant Functional Type. AUC: Area Under the Curve.

Table 2. Projected percent area change for 19 species in the Southwest ecoregion of the California Floristic Province under two different climate change models (PCM and GFDL), emissions scenarios (A2 and B1), and thresholds (high and low) applied to predicted probabilities of species occurrence to define suitable habitat.

Table 3. Projected percent current area of suitable habitat that is also predicted to be suitable by the end of the century (stable area) for 19 species in the Southwest ecoregion of the California Floristic Province under two different climate change models (PCM and GFDL), emission scenarios (A2 and B1), and thresholds (high and low) applied to predicted probabilities of species occurrence to define suitable habitat.

Table 4. Projected current and future suitable habitat for nine small range species in the Southwest ecoregion of the California Floristic Province. Protected area is the portion of the suitable habitat, either present or future, inside a Natural Community Conservation Planning area. Total area includes suitable habitat that is outside of the subregion that contains the protected areas. The protected habitat percent change is the change (in percentage) of suitable habitat inside the protected areas between now and the end of the century.

Table 5. Average suitable habitat gained or lost by nine rare species (Table 1) present within the NCCP areas in the Southwest ecoregion of the California Floristic Province. The average was calculated from two different climate change models (PCM and GFDL), emissions scenarios (A2 and B1), using the high threshold to predicted probabilities of species occurrence to define suitable habitat**.**

Figures

Figure 1. Map showing the location of the California Floristic Province (dotted black line) within the State of California (dotted black line on gray background) US, the Natural Community Conservation Planning areas (NCCP) (diagonal gray lines), and the Southwest ecoregion (solid gray) within the California Floristic Province**.** The combined effects of climate and land use

change analysis (analysis shown in Table 4 and Fig. 8) were performed in the area within the solid black lines.

Figure 2. Boxplots for projected change in climatically suitable habitat area for 19 species in the Southwest ecoregion of the California Floristic Province showing the differences in projections for plants grouped by PFTs (HERB: herbs; OS: obligate seeder; RESPRSHR: resprouting shrubs; SUBSHR: subshrubs). High and Low Threshold results are shown (cut-off of occurrence probability value). Each boxplot shows the smallest observation (maximum amount of suitable habitat loss), lower quartile $(Q1)$, median $(Q2)$, upper quartile $(Q3)$, and largest observation (maximum amount of suitable habitat gain). Hollow circles above or below the boxplot are outliers.

Figure 3. Boxplots showing the projected species centroid shift (km) for 19 species in the Southwest ecoregion of the California Floristic Province under two different climate change models (PCM and GFDL), emission scenarios (A2 and B1), and thresholds (High and Low) applied to predicted probabilities of species occurrence to define suitable habitat. Each boxplot shows the smallest observation (minimum distance the species centroid was predicted to shift), lower quartile $(Q1)$, median $(Q2)$, upper quartile $(Q3)$, and largest observation (maximum distance the species centroid was predicted to shift). Hollow circles above or below the boxplot are outliers.

Figure 4. Boxplots for projected change in climatically suitable habitat area for 19 species in the Southwest ecoregion of the California Floristic Province showing the differences in response for species grouped by range size class (Large/common, and Small/rare). Each boxplot shows the smallest observation (maximum amount of suitable habitat loss), lower quartile (Q1), median (Q2), upper quartile (Q3), and largest observation (maximum amount of suitable habitat gain). Hollow circles above or below the boxplot are outliers.

Figure 5. Projected area gained or lost by rare species in a) San Diego County Multiple Species Conservation Plan Area; b) San Diego County Multiple Habitat Conservation Open Space Plan Area; c) All other NCCP areas in the Southwest, in response to projected climate change by 2080. The average and standard deviation were calculated from two different climate change models (PCM and GFDL), emission scenarios (A2 and B1), using the high threshold to predicted probabilities of species occurrence to define suitable habitat.

Figure 6. Boxplots for projected change in climatically suitable habitat area for 19 species in the Southwest ecoregion of the California Floristic Province, calculated from two different climate change models (PCM and GFDL), emission scenarios (A2 and B1), showing the differences in predicted area using two thresholds (High and Low) as cut-off of occurrence probability values. Each boxplot shows the smallest observation (maximum amount of suitable habitat loss), lower quartile (Q1), median (Q2), upper quartile (Q3), and largest observation (maximum amount of suitable habitat gain). Hollow circles above or below the boxplot are outliers.

Figure 7. Boxplots for projected change in climatically suitable habitat area for 19 species in the Southwest ecoregion of the California Floristic Province a) differences projected under GFDL vs PCM climate models, b) differences projected using A2 and B1 emission scenarios. High and Low Threshold results

are shown (cut-off of occurrence probability value) in both figures. Each boxplot shows the smallest observation (maximum amount of suitable habitat loss), lower quartile (Q1), median (Q2), upper quartile (Q3), and largest observation (maximum amount of suitable habitat gain). Hollow circles above or below the boxplot are outliers.

APPENDIX A

AREA UNDER THE CURVE (AUC) COEFFICIENT FOR THE MODELS USED TO CREATE CONSENSUS MAPS TO CALCULATE SUITABLE HABITAT. THE VARIABLE IMPORTANCE (BY RANK) IS SHOWN FOR THE VARIABLES USED TO CREATE THE MODELS. IN GENERALIZED ADDITIVE MODELS (GAM) VARIABLE IMPORTANCE IS CALCULATED BY COMPARING THE CHANGE IN DEVIANCE BETWEEN TWO MODELS

TO A CHI-SQUARE DISTRIBUTION WITH DEGREES OF FREEDOM EQUAL TO THE DEGREES OF FREEDOM BETWEEN THE TWO MODELS. IN RANDOMFOREST (RF) VARIABLE IMPORTANCE IS CALCULATED AS THE REDUCTION OF PREDICTIVE ACCURACY AFTER A RANDOM PERMUTATION OF THE VALUES ASSUMED BY EACH PREDICTIVE VARIABLE. IN MAXENT VARIABLE IMPORTANCE IS A HEURISTIC ESTIMATE OF RELATIVE CONTRIBUTIONS OF THE ENVIRONMENTAL

VARIABLES TO THE MODEL. TMX: MAXIMUM TEMPERATURE OF WARMEST PERIOD, GRW: GROWING DAYS ABOVE 5° C, PPT: ANNUAL

PRECIPITATION, TSE: TEMPERATURE SEASONALITY, PWQ: PRECIPITATION WARMEST QUARTER, ARI: ARIDITY INDEX, DEPL: SOIL DEPTH, AWCL: SOIL AVAILABLE WATER CAPACITY, PHL: SOIL PH, SLOPE: SLOPE ANGLE DERIVED FROM DIGITAL ELEVATION MODEL, SUMRAD: POTENTIAL SUMMER SOLSTICE SOLAR INSOLATION.

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APPENDIX B

PROJECTED AREA GAINED OR LOST BY RARE SPECIES IN A) SAN DIEGO COUNTY MULTIPLE SPECIES CONSERVATION PLAN AREA; B) SAN DIEGO COUNTY MULTIPLE HABITAT CONSERVATION OPEN SPACE PLAN AREA; C) ALL OTHER NCCP AREAS IN THE SOUTHWEST, IN RESPONSE TO PROJECTED CLIMATE CHANGE BY 2080. THE MEAN AND STANDARD DEVIATION WERE CALCULATED FROM TWO DIFFERENT CLIMATE CHANGE MODELS (PCM AND GFDL) AND EMISSION SCENARIOS (A2 AND B1) USING THE LOW THRESHOLD TO PREDICTED PROBABILITIES OF SPECIES OCCURRENCE TO DEFINE SUITABLE HABITAT.

