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Los Angeles

Modeling the Uncertain Future of a Threatened Habitat:
Climate Change and Urban Growth in California Sage Scrub

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Biology

by

Erin Coulter Riordan

2013

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ABSTRACT OF THE DISSERTATION

Modeling the Uncertain Future of a Threatened Habitat:
Climate Change and Urban Growth in California Sage Scrub

by

Erin Coulter Riordan

Doctor of Philosophy in Biology

University of California, Los Angeles, 2013

Professor Philip W. Rundel, Chair

The combined impacts of climate change and land use are projected to drive unprecedented rates of environmental change and biodiversity loss this century. Given the rapidly growing human populations in mediterranean-climate systems, land use may pose a more immediate threat to biodiversity than climate change, however, the relative future impact of each driver remains largely unaddressed. Focusing on California sage scrub (CSS), a plant association of considerable diversity, endemism, and threatened status in the mediterranean-climate California Floristic Province, I investigate the future threats of projected land use and climate change on CSS distribution and diversity. California sage scrub is highly reduced and fragmented in distribution and contains a large number of threatened and endangered species that may be particularly vulnerable to further habitat loss from future land use and climate change.

My objectives are to (1) assess the role of climate in shaping current patterns of CSS species and floristic group distributions at a regional scale, (2) predict changes in the distribution of CSS species and growth forms, testing whether niche, geographic, or bioclimatic factors explain the magnitude of species response to projected climate change and identifying potential future impacts on CSS community structure and diversity, and (3) compare the relative threats of projected land use and climate change on CSS in California to better understand how threats may vary spatially and temporally. Using a species distribution modeling approach, I modeled the contemporary climate relationship and future (mid- and late-century) geographic distributions of 33 dominant CSS shrub species assuming two possible climate change trajectories (warmer wetter and warmer drier) and two dispersal scenarios (unlimited dispersal and no dispersal). Habitats loss from future land use was calculated from projected land use overlays (objective 3).

Current models reveal climate is a strong predictor of individual CSS species and floristic group distributions at regional scales. Modeling at a floristic group level provides important information about the differences in current climatic niches within CSS, highlighting the potential for community-level modeling approaches to investigate plant distribution patterns. Under projected climate change, I predict two overall patterns in CSS habitat change consistent across climate change trajectories: southern habitat contraction and northern habitat expansion. By late-century (2080s) species habitat losses will range from moderate (unlimited dispersal) to severe (no dispersal), with succulent species showing minimal habitat loss and overall net habitat gains (unlimited dispersal). Individual shifts in the distribution of CSS species translate to considerable community restructuring and diversity shifts at northern and southern extents of CSS, with implications for future CSS management and conservation.

I find the degree of threat posed by climate change relative to land use depends upon

dispersal scenario, with land use and climate change posing similar future threats under no dispersal scenarios and land use posing a greater future threat under unlimited dispersal scenarios. Impacts will also vary spatially between Central Coast and South Coast California Ecoregions, with high CSS habitat and diversity losses from both land use and climate change predicted in the South Coast even under best-case unlimited dispersal scenarios, but considerable habitat gains and increased diversity predicted in the Central Coast. Furthermore, I find that regions of the South Coast that are currently intact but projected to undergo future anthropogenic conversion will have disproportionately high losses in CSS species richness driven by climate change. These findings highlight the potential for land use and climate change to have compounding negative impacts on CSS and emphasize the necessity to include analyses of both drivers in conservation and resource management planning.

The dissertation of Erin Coulter Riordan is approved.

Victoria Sork

Thomas Welch Gillespie

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2013

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PRESENTATIONS

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CHAPTER 1

MODELING THE DISTRIBUTION OF A THREATENED HABITAT: THE CALIFORNIA SAGE SCRUB[†]

ABSTRACT

Aim: Using predictive species distribution and multivariate ecological niche modeling, our objectives are: (1) to identify important climatic drivers of distribution at regional scales of a locally complex and dynamic system: California sage scrub, (2) to map suitable sage scrub habitat in California, and (3) to distinguish between bioclimatic niches of floristic groups within sage scrub to assess the conservation significance of analyzing such species groups.

Location: Coastal mediterranean-type shrublands of southern and central California.

Methods: Using point localities from georeferenced herbarium records, we modeled the potential distribution and bioclimatic envelopes of 14 characteristic sage scrub species and three floristic groups (south-coastal, coastal–interior disjunct and broadly distributed species) based upon current climate conditions. Maxent was used to map climatically suitable habitat, while principal components analysis followed by canonical discriminant analysis were used to distinguish between floristic groups and visualize species and group distributions in multivariate ecological space.

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Results: Geographic distribution patterns of individual species were mirrored in the habitat suitability maps of floristic groups, notably the disjunct distribution of the coastal–interior species. Overlap in the distributions of floristic groups was evident in both geographic and multivariate niche space; however, discriminant analysis confirmed separability of floristic groups based on bioclimatic variables. Higher performance of floristic group models compared to sage scrub as a whole suggests that groups have differing climate requirements for habitat suitability at regional scales and that breaking sage scrub into floristic groups improves the discrimination between climatically suitable and unsuitable habitat.

Main conclusions: The finding that presence-only data and climatic variables can produce useful information on habitat suitability of California sage scrub species and floristic groups at a regional scale has important implications for ongoing efforts of habitat restoration for sage scrub. In addition, modeling at a group level provides important information about the differences in climatic niches within California sage scrub. Finally, the high performance of our floristic group models highlights the potential a community-level modeling approach holds for investigating plant distribution patterns.

INTRODUCTION

Recent advances in ecological niche modeling are proving to be valuable tools for ecosystem conservation and management. Bioclimatic envelope models, which relate species distributions to climate, are becoming widely applied to identify climatically suitable habitat and predict both current and future species ranges (Box 1981, Busby 1986, Kadmon et al. 2003, Pearson and Dawson 2003, Beaumont et al. 2005, Manthey and Box 2007, McKenney et al. 2007). Such an approach, which considers climatic variables as primary drivers of species

distribution, can be particularly powerful at continental and global scales where climate is often the major driver of species distribution (Franklin 1995, Guisan and Zimmermann 2000, Pearson et al. 2004, Luoto et al. 2007). The appropriateness of bioclimatic envelope modeling, however, is less clear in particularly dynamic systems where non-climatic factors are known to have strong influences on species distributions. We assess the ability of bioclimatic envelope models to predict current regional distributional patterns of California sage scrub, a highly dynamic system at local scales whose considerable diversity, endemism, and threatened status make this vegetation type a conservation priority in California (Davis et al. 1994, Feldman and Jonas 2000).

California sage scrub forms an ecologically significant plant association distributed along the coast and semiarid interior of southern California, as well as scattered areas along the central California coast (Rundel 2007). The characteristic feature of sage scrub is the dominance of drought-deciduous shrubs, in contrast to the more widespread evergreen chaparral shrublands. Drought-deciduous species lose much to all of their foliage in summer, as soil water availability declines, and grow new leaves with the onset of fall rains. Sage (*Salvia*) species exemplify this life form and are common but not invariably present. The complex, mosaic-like distribution patterns typical of California sage scrub are governed by factors acting at multiple spatial scales. Topography, geological substrate, soil, disturbance, and species interactions contribute to local distribution patterns, while climate appears to be a major driver of regional patterns (Harrison et al. 1971, Parsons and Moldenke 1975, Parsons 1976, Kirkpatrick and Hutchinson 1980, Westman 1981b, 1983, Zedler et al. 1983, Keeley and Keeley 1984, Malanson and Westman 1991, Callaway and Davis 1993, Franklin 1995, Meentemeyer et al. 2001). Urbanization, recreational development, and alteration of natural disturbance regimes have caused widespread

loss and fragmentation of this unique vegetation type, with only about 10% of its original extent remaining (Rundel 2007). This loss of sage scrub habitat has led to the listing of 11 mammal, 26 bird, and 10 reptile species as threatened or endangered (Keeley and Swift 1995). It is not surprising therefore that restoration and preservation of sage scrub have become important but controversial conservation issues because of economic land values in its range of occurrence (Feldman and Jonas 2000).

While vegetation modeling has long been employed both as a predictive and descriptive tool to better understand the complex relationship between plant species and their environment, many modeling approaches require spatial information on species presence and absence across an environmental landscape. Reliable absence data are frequently neither documented nor available and often conservation biologists must rely upon presence-only museum or herbarium records to provide information on species distributions (Loiselle et al. 2003, Graham et al. 2004, Elith and Leathwick 2007). Nevertheless, herbarium records are proving to be a valuable tool for predictive distribution modeling, especially in the light of recent modeling developments adapted to such presence-only datasets (Elith et al. 2006, Elith and Leathwick 2007, Miller et al. 2007, Loarie et al. 2008, Loiselle et al. 2008). Beyond analyses using single species records, modeling distributions at a community or species assemblage level can help overcome problems posed by biased and incomplete datasets and yield more complete information for habitat suitability compared to individual species modeling (review in Franklin 1995, review in Guisan and Zimmermann 2000, Cawsey et al. 2002, Ferrier et al. 2002, Ferrier and Guisan 2006, review in Austin 2007).

Our objectives in this study are to utilize the distributions of both individual species and species assemblages to understand biogeographical and floristic patterns in California sage scrub.

Using both predictive distribution and bioclimatic niche modeling, we aim to: (1) identify important climatic drivers of California sage scrub distribution at regional scales, (2) map climatically suitable sage scrub habitat in California as an aid to restoration, and (3) distinguish between floristic groups within sage scrub to assess whether groups occupy different bioclimatic niches. By using herbarium specimens and methods of analysis that do not require absence data, we analyze climatic drivers of sage scrub distribution over a much larger geographical range than has previously been investigated. Through these analyses we demonstrate the conservation significance of understanding bioclimatic niches at both the species-level and level of floristic group within a distinct ecological community.

MATERIALS AND METHODS

Species records

We chose 14 characteristic sage scrub woody and semi-woody species to model the bioclimatic envelope for California sage scrub (Table 1.1). We obtained species occurrence point localities from georeferenced herbarium specimen records from the online database of the Consortium of California Herbaria (<http://ucjeps.berkeley.edu/consortium/>), which compiles records from 16 participating institutions in California. All subspecies and varieties were lumped with the associated species (see Cawsey et al. 2002). Prior to modeling, all records were mapped and examined to identify and exclude any records of cultivated plants, errors in georeferencing, obvious misidentifications, and duplicate collections. The number of records used to model individual species ranged from 34 to 619 (Table 1.1).

A priori, we categorized the 14 species into one of three floristic groups based on their known patterns of geographic distribution: (1) south-coastal California, (2) coastal–interior

disjunct, and (3) broadly distributed (Table 1.1). We then modeled the potential distribution of both individual species and floristic groups. The seven species representing the south-coastal group were shrubs and subshrubs with ranges restricted to coastal southern California, typically occurring from Santa Barbara southwards into north-western Baja California. The species modeled were *Encelia californica*, *Eriogonum cinereum*, *Isocoma menziesii*, *Mirabilis californica*, *Salvia apiana*, *Salvia leucophylla*, and *Salvia mellifera*. Coastal–interior species have a disjunct pattern of distribution, occurring both along the southern California coast and inland along the western margin of the desert. This group was represented by *Croton californicus*, *Encelia farinosa*, and *Isomeris arborea*. The third group contained common sage scrub species whose individual ranges of distribution were broad and well outside the occurrence of the sage scrub community. The species modeled were *Artemisia californica*, *Eriogonum fasciculatum*, *Lotus scoparius*, and *Mimulus aurantiacus*. We selected three species from each of these groups to present more detailed species-level habitat suitability maps. Taxonomy follows Hickman (1993).

Climate data

Bioclimatic variables were obtained from WorldClim (version 1.4; <http://www.worldclim.org>), a set of global climate coverages derived from weather station monthly mean temperature and precipitation data (Hijmans et al. 2005). These 19 bioclimatic variables represent biologically meaningful climate conditions (Nix 1986): annual trends, seasonality, and extremes. The climate coverages used for this analysis were interpolated to 30 arc-second (~1 km) resolution. Given California’s mediterranean-type climate, certain bioclimatic variables are highly correlated. For example, annual precipitation, precipitation of

the wettest month and precipitation of the coldest quarter are all highly correlated ($r > 0.99$). Furthermore, predictive distribution models can be sensitive to selection and number of predictor variables (Beaumont et al. 2005). In order to avoid model over-fitting and minimize the number of highly correlated environmental variables, we examined a correlation matrix of all bioclimatic variables and chose a subset where all correlation coefficients were less than 0.85. The eleven variables retained for modeling were: (1) annual mean temperature, (2) mean diurnal range, (3) isothermality ($100 * \text{mean diurnal range} / \text{annual temperature range}$), (4) mean temperature of the wettest quarter, (5) mean temperature of the driest quarter, (6) mean temperature of the warmest quarter, (7) mean temperature of the coldest quarter, (8) annual precipitation, (9) precipitation of the driest month, (10) precipitation seasonality, and (11) precipitation of the warmest quarter.

Species distribution modeling

We used Maxent (version 3.1.0), a maximum entropy algorithm (Phillips et al. 2006), to model the potential distributions of sage scrub species and floristic groups. Maxent is a general-purpose machine-learning method that calculates probability distributions based on incomplete information (Phillips et al. 2006) and does not require absence data, making it appropriate for modeling species distributions based on presence-only herbarium records. When estimating species distributions, Maxent finds the probability of maximum entropy (closest to uniform), with the constraint that the expected value of each environmental feature is that of the empirical average for that feature (Phillips et al. 2006). Although only recently applied to species distribution modeling, Maxent has among the highest performance of many frequently used modeling techniques (Elith et al. 2006) and has a number of advantages over other methods, such as high performance with both spatially biased data (Loiselle et al. 2008) and limited species

occurrence records (Pearson et al. 2007). This modeling approach, however, can result in high habitat suitability predictions outside the present ‘realized’ distribution (Phillips et al. 2006).

We ran three sets of Maxent models to identify climatically suitable habitat at three different levels: (1) California sage scrub as a whole (all species occurrence records combined), (2) floristic groups, and (3) individual species. We included all of the above 11 bioclimatic variables in all models. At each level of analysis, we created 10 random partitions of the point localities with 60% of points for model training and 40% for model testing. For each model run, 10,000 background pixels were selected at random as “pseudo-absences”, the maximum number of iterations was 500, the convergence threshold was set to 10^{-5} , and regularization was set to “auto” allowing Maxent to set the amount of regularization automatically based on our locality and environmental data (Phillips et al. 2006). Potential distribution maps were produced using all point localities 1900 to present and the logistic output format from Maxent (Phillips and Dudík 2008).

We evaluated the spatial accuracy of model predictions of individual species and groups using both threshold dependent and threshold independent tests. As a threshold dependent test, we used the extrinsic omission rate, defined as the fraction of test localities falling outside the predicted area, at a fixed 10% cumulative probability threshold. We also provide the proportional area, the fraction of all pixels predicted suitable by the model, at the same threshold. A one-tailed binomial test was used to determine if models had a lower omission rate than that of a random prediction. A two-tailed Wilcoxon rank sum test was used to determine if species and group models differed in terms of omission rate. We chose to examine model omission rate because, with presence-only data, maintaining low model omission rates is key in producing useful predictions of a species’ potential distribution (Anderson et al. 2003).

To evaluate overall model performance, we used two threshold independent measures: the area under the Receiver Operating Characteristic (ROC) curve (AUC) of the test localities and the test gain. The ROC curve measures a model's ability to correctly predict presence and absence, plotting the model sensitivity (1 – false negative, or omission, rate) against 1 – specificity (false positive, or commission, rate). The AUC represents the probability that a presence site will be ranked above an absence. With presence-only data and pseudo-absences, the resulting AUC statistic can be interpreted as the probability that a presence site is ranked above a random background site (Phillips et al. 2006). AUC scores can range from 0 to 1.0, with a random prediction scoring 0.5. We used a one-tailed Wilcoxon signed-rank test to determine if model performance was higher than that of random prediction (0.5), in terms of AUC. To determine whether modeling floristic groups separately increased overall performance from modeling sage scrub as a whole, we performed a one-tailed Wilcoxon rank sum test for each floristic group's AUC scores compared to AUC scores of sage scrub models.

In light of recent critiques (Araujo et al. 2006), a mention of AUC's potential limitations is merited. Namely, that AUC is sensitive to the total spatial extent of the model (high AUC scores can result when the area used to draw pseudo-absence records is much larger than that of the predicted distribution) and weights commission and omission errors equally (Lobo et al. 2008, Peterson et al. 2008). Despite these limitations, AUC can provide important information on relative model performance when species predictions and study area are maintained at the same scales (see Wisz et al. 2008). Given the similarity of species ranges and the conservation of study area in our study, we consider that AUC can still provide important information to compare overall performance models. To compensate for potential weaknesses in AUC measures, we include an additional metric of overall (threshold independent) performance, the

test gain (Phillips 2005).

When Maxent generates a probability distribution, it starts at uniform distribution (gain = 0) and performs a number of iterations to adjust feature weights and maximize the likelihood of presence at the sample locations, called the training gain (Phillips 2005). The test gain is the average log probability of the presence samples used to test the model. For example, if the model test gain is 2, the average likelihood of a test presence locality is $\exp(2)$ (about 7.4) times greater than that of a random background pixel (Phillips 2005). This value is analogous to deviance, a measure of goodness of fit, used to assess performance of generalized linear and additive models (Phillips 2005) and has been used as another measure of overall model performance (Buermann et al. 2008, Yost et al. 2008). To test whether higher level floristic groups models compared to all sage scrub had increased performance in terms of test gain, we performed a one-tailed Wilcoxon rank sum test.

Niche modeling

Ordination is frequently used in ecology to characterize species or community trends with respect to environmental descriptors (James and McCulloch 1990, Legendre and Legendre 1998). We use principal components analysis (PCA) followed by canonical linear discriminant analysis (CDA) (Stata 10.0 © StataCorp LP, College Station, TX, USA), to distinguish between floristic groups based on bioclimatic variables and to depict their bioclimatic niches in two-dimensional space. Discriminant analysis has long been applied to ecological niche and species distribution modeling (Green 1971, Williams 1983, Lowell 1991, Gavilan and Fernández-González 1997, Manel et al. 1999, Guisan and Zimmermann 2000, Spichiger et al. 2004, Abella and Covington 2006) and has been used to both reduce dimensionality of multivariate datasets

and identify variables that best differentiate between groups (Williams 1983, James and McCulloch 1990). As discriminant analysis produces functions from linear combinations of the predictor variables, the effectiveness of this approach is greatest when attributes are normally distributed and linearly related. However, even in violation of these assumptions, discriminant analysis can be a valuable tool for visualizing complex relationships in two-dimensional space (James and McCulloch 1990).

To reduce dimensionality and correlations between variables within our database, we first performed PCA on our 11 bioclimatic variables for all point localities using a correlation matrix. Given the correlation among temperature and precipitation variables across species localities, we performed two separate PCAs, one on temperature variables and the other on precipitation variables, to minimize the inclusion of correlated variables in a single model. The resulting first two axes from both temperature and precipitation PCAs (temp1, temp2, rain1, rain2) were retained for subsequent canonical discriminant analysis. Separability of floristic groups was investigated by comparing the mean discriminant scores of the three groups using Wilk's (λ) goodness of fit statistic, which is also a measure of model performance. By following PCA with canonical discriminant analysis, we were able to reduce the dimensionality of our dataset and investigate the relationship between sage scrub distribution and climate in reference to our *a priori* floristic group classification (Anderson and Willis 2003).

RESULTS

Species distribution modeling

At all three levels of analysis (sage scrub as a whole, floristic groups, and individual species), models had high performance (Table 1.2). For all model runs, both the extrinsic

omission rates at the 10% cumulative threshold and AUC scores were highly statistically significant compared to a random prediction ($P < 0.0001$, one-tailed binomial test of omission rates; $P < 0.001$, one-tailed Wilcoxon signed-rank test of AUC), suggesting that climate variables alone provide important information about sage scrub habitat requirements at a regional scale (Table 1.2). In addition, models of floristic groups had higher overall performance than our model for sage scrub as a whole, which included localities for all species. Both AUC scores and test gains of floristic group models were significantly higher than those of all sage scrub ($P < 0.001$ for all comparisons, one-tailed Wilcoxon rank sum test). This suggests that breaking California sage scrub into floristic groups improves the discrimination between climatically suitable and unsuitable habitat. AUC scores of individual species models were similar to and mostly significantly higher than those of floristic group models, with the exception of *Salvia mellifera*, *Mimulus aurantiacus* and *Isomeris arborea* (Table 1.2). In the case of *M. aurantiacus*, the group model actually performed better ($P = 0.0001$, one-tailed Wilcoxon rank sum test). Trends in the model test gain generally agree with those for the AUC scores, indicating that all species, except for *M. aurantiacus*, had better performance than their associated floristic groups (all $P < 0.025$, one-tailed Wilcoxon rank sum test).

At the 10% cumulative threshold value, all models had low omission rates, indicating that only a small percentage of test points fell outside the area predicted as suitable (Table 1.2). Of the group-level models, all sage scrub had a significantly lower omission rate than either the broad or coastal–interior disjunct models ($P < 0.001$, two-tailed Wilcoxon rank sum test). The south-coastal model, however, had a lower omission rate and highest performance at this particular threshold ($P = 0.0001$). Floristic group models tended to have higher or equal spatial accuracy (lower omission rates) than species specific models. The only exception was *Mirabilis*

californica, which had a significantly lower omission rate than that of the south-coastal group model ($P = 0.02$). The proportional predicted area at this threshold represents the fraction of the total study area for each modeled group or species. Group models tended to predict a larger fraction of the study area as suitable compared to the individual groups models (Table 1.2). The proportional predicted area was significantly smaller for all species compared to that of their associated floristic groups (all $P < 0.05$, two-tailed Wilcoxon rank sum), with the exception of *M. aurantiacus* ($P = 0.20$). Thus, group models appear to perform better than species models in terms of minimizing omission rates at our chosen threshold, but predict a larger area.

For our distribution maps, we used Maxent's logistic output, which represents the probability of species or group presence based on the environmental variables (Phillips et al. 2006). For each grid cell in our study region, the probability of presence ranges from 0 to 1.0. These modeled distributions can be interpreted as the potential distributions of the species or group of interest with respect to climate. They show the area where a species ought to occur given the current climate conditions and known species distribution. Visual inspection shows that there is broad agreement between the mapped predicted distribution and observed occurrences for both floristic groups and individual species (Figs 1.1–1.4). We have presented maps for three representative species of each group: south-coastal (Fig. 1.2), coastal–interior disjunct (Fig. 1.3), and broadly distributed species (Fig. 1.4). Similar patterns are evident in the habitat suitability maps for floristic groups (Fig. 1.1) and individual species (Figs 1.2–1.4). Notably, Maxent is able to identify the uniquely disjunct distribution of the coastal–interior species (Fig. 1.3).

Niche modeling

Principal components analyses of the bioclimatic variables for all sage scrub occurrences reduced the dimensionality of our dataset to four composite bioclimatic variables. Principal component analyses of temperature variables produced two major axes, temp1 and temp2, that explained 49% and 34%, respectively, (83% cumulatively) of the variation in temperature variables in sage scrub occurrences. Similarly, PCA of the precipitation variables produced two major axes, rain1 and rain2, that explained 52% and 32%, respectively, (84% cumulatively) of the variation in precipitation values in sage scrub occurrences.

Further examination of the factor loadings of bioclimatic variables on PCA axes (Table 1.3) reveals that these resulting four axes (temp1, temp2, rain1, and rain2) represent seasonal climatic trends in California. The bioclimatic variables with the greatest loadings on Temp1 are annual mean temperature (Bio 1), mean temperature of the driest quarter (Bio 9), and mean temperature of the warmest quarter (Bio10). Thus, temp1 can be interpreted as a measure of summer temperature severity. The bioclimatic variables with the greatest loading on temp2 are mean diurnal temperature range (Bio2) and mean temperature of the coldest quarter (Bio11). This axis can thus be interpreted as winter temperature severity. Precipitation of the driest month (Bio 14) and warmest quarter (Bio18) have the greatest loadings for rain1, which can be interpreted as a measure of summer drought. Finally, annual precipitation has the greatest contribution to axis rain2. As California has a winter rainfall regime, this axis can be interpreted as a measure of both annual and winter precipitation.

These four axes were used as the variables to distinguish between floristic groups in a subsequent canonical discriminant analysis (CDA). CDA produced two discriminant functions, explaining 91% and 9% of the total climatic variance in sage scrub, and differentiating between

the three floristic groups. The CDA model correctly distinguished and categorized 45% of broad observations, 62% of south-coastal observations, and 52% of coastal–interior disjunct observations. This level of misidentification probably reflects the high degree of overlap between species and groups where ranges intersect. Despite these misidentification rates, floristic groups were distinct in their climatic envelopes.

Mean discriminant scores of south-coastal, coastal–interior disjunct, and broadly distributed floristic groups differed significantly ($P < 0.0001$, Wilk's lambda; Fig. 1.5), suggesting that floristic groups within sage scrub are climatically distinguishable. The canonical structure of each function (Table 1.3) shows the contribution of each of the four composite climate variables. Rain2 (annual precipitation) and temp1 (summer temperature severity) contributed most to the first function, while rain1 (summer drought) and temp2 (winter temperature severity) contributed most to the second function. Overlap of floristic groups in the CDA ordination plot (Fig. 1.5) appears to reflect their overlap in geographic distribution.

Mean discriminant scores of individual species were plotted against bioclimatic variables to show the relationship between known geographic distribution and climate (Fig. 1.6). The first discriminant function best differentiated coastal–interior disjunct species from both south-coastal and broadly distributed species. Coastal–interior disjunct species had higher scores for the first discriminant function, which corresponds to more extreme summer temperatures (temp1) and low annual rainfall (rain2). The second discriminant function best differentiated south-coastal from both disjunct and broadly distributed species. South-coastal species tended to score lower on the second discriminant axis than either coastal–disjunct or broadly distributed species. A lower score corresponds to milder winter temperature conditions (temp2) and summer drought (rain1).

DISCUSSION

The restoration and conservation of sage scrub and its associated rare and endangered species have become issues of increasing concern as pressures from urbanization, recreational development, and alteration of fire regimes and air pollution continue in southern California. These changes in land-use and disturbance have led to a loss of nearly 90% of the original extent of sage scrub habitat. Moreover, many of the remaining areas of sage scrub habitat occur on private lands (Davis et al. 1994, Feldman and Jonas 2000).

As many aspects of land-use in southern California date back to the Spanish ranchos of the late 18th century through the 19th century of Euro-American settlement, the original extent of sage scrub distribution remains poorly understood. Bioclimatic niche modeling can thus play two roles in restoration efforts. One role is to identify climatically suitable areas where sage scrub once existed but is no longer present today because of land use changes. The other role, and perhaps one for discussion among resource managers, is for the identification of areas where sage scrub might be restored even if we have no information that it once occurred there.

At the regional state-wide scale considered in our study, climate variables produced high performing models predicting California sage scrub distributions. This suggests that climate variables and presence-only herbarium records can provide important information about habitat suitability, even for species and groups with locally dynamic and complex distributional patterns, such as California sage scrub. Within sage scrub, we identified three floristic groups whose differing geographic distribution patterns appear to be strongly influenced by climatic variables. Canonical discriminant analysis confirms that south-coastal, coastal-interior disjunct, and broadly distributed groups are climatically distinguishable, in spite of high geographic and

climatic overlap. High floristic group model performance compared to all sage scrub models further supports the notion that there are at least three climatically distinct floristic groups within sage scrub.

Coastal–interior disjunct species are particularly distinguishable from the two other groups, occupying areas that may include much more severe summer temperatures and low annual rainfall and lying outside of areas mapped as sage scrub. These results are consistent with designations of distinct southern–interior sage scrub floristic groups, such as the Riversidian flora, which has been described by a number of studies (Kirkpatrick and Hutchinson 1977, Westman 1981b, 1983, Davis et al. 1994). South coastal species tend to occur in areas with less severely cold winters, probably related to their proximity to the coast, yet still occur in areas with considerable summer drought. Individual species models within the south-coastal group tended to have the highest test gains and AUC scores relative to all other species, with *Eriogonum cinereum* having the highest model performance. This is probably a reflection of the more restricted ranges of these species compared to species in the two other floristic groups. Conservation plans need to address the different climatic requirements of floristic groups within sage scrub.

Our results are in agreement with previous investigations that have identified species assemblages and floristic groups within California sage scrub (Kirkpatrick and Hutchinson 1977, Westman 1981b, 1983, Malanson 1984, Davis et al. 1994). Floristic designations of communities termed Venturan, Diegan, and Riversidian sage (Kirkpatrick and Hutchinson 1977, Westman 1981b, 1983, Davis et al. 1994) tend to correspond to climatic gradients in precipitation and summer evaporative stress, as well as pollution (Westman 1981b). Individual species distributions, however, often reveal preference to substrate, topography, and sensitivity

to disturbance regimes (Rundel 2007). Although our analysis does not incorporate these drivers, our results show similar relationships between climate and the geographical distribution of floristic groups. With respect to sage scrub restoration, climate-based models, such as those we produce, are a necessary step in identifying the climatic requirements of species and floristic groups, as well as respective suitable areas at a regional scale. Additional information about species-specific requirements for substrate, topography, disturbance, etc., can then further aid in identifying locations with the highest likelihood of successful restoration.

Community-level analyses are much less frequently used than individual species distributions in assessing habitat suitability, yet can provide important information that may not be available in species-level models assuming that species within these assemblages respond to similar climatic controls. The inclusion of extrinsic omission rates as a measure of model performance highlights another benefit of a group-based modeling approach that was not apparent from the threshold independent AUC and test gain measures of model performance. Group models tended to have similar, if not lower, omission rates than that of associated species models. This indicates that, in terms of omission rates, floristic group models provide adequate predictions of their associated species, at least in our system. There is a drawback in that floristic group models also had larger proportional predicted areas. For individual species within the group, a group model may likely over-predict the distribution specific to individual species.

Such community models, however, are subject to criticism as Clementsian views of communities as “organisms” (Clements 1936). Community composition is expected to change under changing climate conditions that impact individual species differently, and thus simple community models may not give sufficient consideration to individual species’ requirements (see Ferrier and Guisan 2006). Nevertheless, modeling species assemblages, or communities, under

current climate conditions, can still be a very powerful approach, yielding more complete information for habitat suitability and biodiversity especially when locality data at species levels are insufficient (review in Franklin 1995, review in Austin 1998, review in Guisan and Zimmermann 2000, Cawsey et al. 2002, Ferrier et al. 2002, Ferrier and Guisan 2006). Though not included in our models, there are many species endemic to California that are poorly represented in herbarium collections (Loarie et al. 2008). A community level approach to investigating plant distributional patterns, such as ours, is likely to be particularly useful for such species with biased or incomplete occurrence data.

Undoubtedly, there are other factors that are important in determining species distributions that were not included in our analysis. Substrate (Kirkpatrick and Hutchinson 1980, Westman 1981b, 1983), topography (Franklin 1998, 2003), disturbance, including fire (Kirkpatrick and Hutchinson 1980, Keeley and Keeley 1984, Malanson 1984), and biotic interactions (Louda 1983) all play important roles in shaping species ranges in California sage scrub. At coarse spatial scales, however, such variables become less influential relative to climate (see Franklin 1995, see Guisan and Zimmermann 2000, Pearson et al. 2004, Luoto et al. 2007). Bioclimatic variables, such as those used in our analysis, are closely related to the physiological tolerances of species and directly influence species distributions (Franklin 1995, Guisan and Zimmermann 2000). Furthermore, relationships with factors such as biotic interactions or substrate act at smaller spatial scales, and thus cannot be adequately modeled from point locations derived from herbarium records.

Finally, bioclimatic modeling is not without limitations. Some of these include the assumption that the current species distribution is in equilibrium with the current climate and that the ecological niche is conserved over the time-scale of interest (Pearson and Dawson 2003). In

addition, such an approach does not consider species adaptations. These assumptions are likely to be particularly important when modeling predicted shifts in species distributions over long time periods, or under rapidly changing climatic conditions. Recent results, however, suggest that niche conservatism for plant species is a valid assumption at least over moderate time periods, even despite profound changes in climate and environmental condition (Martínez-Meyer and Peterson 2006). Thus, we find bioclimatic modeling to be a useful approach given the temporal and spatial scales considered in our study, even for such a dynamic system as California sage scrub.

In conclusion, species distribution and ecological niche modeling hold great potential for aiding the conservation and future preservation of sage scrub communities and species in California by improving the success of restoration efforts through selection of appropriate habitat areas and by allowing better prediction of the impacts of future climate change on these distributions (E. Riordan, unpublished data). Loarie et al. (2008) projected a striking decrease in many endemic plant taxa distributions in response to climate change, especially along central coast areas of the California Floristic Province. These areas may become important refugia for declining species unable to migrate in response to climate change. All three floristic groups we identify within California sage scrub have current species distribution ranges coinciding with portions of California's central and southern coasts, especially the broadly distributed floristic group. Due to its distribution along California's central and southern coasts and coincidence with some of the refugia sites projected by Loarie et al. (2008), conservation of sage scrub habitats will be of particular significance in protecting biodiversity in California's Floristic Province.

Table 1.1. Characteristics and floristic grouping of the modeled California sage scrub species. Taxonomy follows Hickman (1993), with updated (Baldwin et al. 2012) names in parentheses.

Taxon name	n	Family	Growth form	Habitat
South-coastal	1128			
<i>Encelia californica</i>	114	Asteraceae	Shrub	Coastal scrub
<i>Eriogonum cinereum</i>	34	Polygonaceae	Shrub	Beaches, coastal bluffs
<i>Isocoma menziesii</i>	167	Asteraceae	Subshrub	Sandy soils coastal and inland
<i>Mirabilis californica</i> (<i>Mirabilis laevis</i> var. <i>crassifolia</i>)	186	Nyctaginaceae	Subshrub	Grassy areas, chaparral, dunes, dry rocky areas and washes
<i>Salvia apiana</i>	242	Lamiaceae	Shrub/subshrub	Dry slopes, coastal sage scrub, chaparral, yellow-pine forest
<i>Salvia leucophylla</i>	91	Lamiaceae	Shrub	Dry, open hills
<i>Salvia mellifera</i>	294	Lamiaceae	Shrub	Coastal sage scrub, lower chaparral
Coastal-interior disjunct	567			
<i>Croton californicus</i>	213	Euphorbiaceae	Subshrub	Sandy soils, dunes washes
<i>Encelia farinosa</i>	176	Asteraceae	Shrub	Coastal scrub, stony desert hillsides
<i>Isomeris arborea</i>	178	Brassicaceae	Shrub	Coastal bluffs, hills, desert washes, flats
Broadly distributed	1626			
<i>Artemisia californica</i>	158	Asteraceae	Shrub/subshrub	Coastal scrub, chaparral, dry foothills, especially near coast
<i>Eriogonum fasciculatum</i> (all varieties)	386	Polygonaceae	Shrub	Dry slopes, washes, canyons in scrub
<i>Lotus scoparius</i> (<i>Acmispon</i> <i>glaber</i>)	463	Fabaceae	Subshrub	Chaparral, roadsides, coastal sand, desert slopes, flats, washes
<i>Mimulus aurantiacus</i> (all varieties)	619	Phrymaceae	Shrub/ subshrub	Rocky hillsides, cliffs, canyon slopes, disturbed areas, borders of chaparral, open forest

Table 1.2. Means of proportional predicted area (Area) and test omission rates (OR) at the 10% cumulative threshold, area under the receiver operating characteristic curve (AUC), and test gains for all models of sage scrub species and three floristic groups: south-coastal California, coastal–interior disjunct, and broadly distributed. All performance metrics are based on the 10 random data partitions (60% train, 40% test) generated for each species and group.

	Area	OR	AUC	Test gain
All	0.402	0.0542	0.900	1.335
South-coastal	0.157	0.0420	0.956	2.154
<i>Encelia californica</i>	0.052	0.0693	0.980	2.983
<i>Eriogonum cinereum</i>	0.028	0.0400	0.997	4.697
<i>Isocoma menziesii</i>	0.065	0.0749	0.973	2.849
<i>Mirabilis californica</i>	0.113	0.0632	0.967	2.618
<i>Salvia apiana</i>	0.128	0.0307	0.965	2.323
<i>Salvia leucophylla</i>	0.110	0.0978	0.964	2.383
<i>Salvia mellifera</i>	0.129	0.0813	0.959	2.300
Coastal-interior disjunct	0.284	0.0936	0.913	1.653
<i>Croton californicus</i>	0.206	0.1029	0.933	1.889
<i>Encelia farinosa</i>	0.135	0.0999	0.944	2.157
<i>Isomeris arborea</i>	0.304	0.0999	0.904	1.792
Broadly distributed	0.301	0.0772	0.910	1.472
<i>Artemisia californica</i>	0.118	0.0691	0.958	2.222
<i>Eriogonum fasciculatum</i>	0.028	0.0400	0.952	2.105
<i>Lotus scoparius</i>	0.208	0.0749	0.942	1.955
<i>Mimulus aurantiacus</i>	0.284	0.1115	0.893	1.297

Table 1.3. Factor loadings of bioclimatic variables for principal component analysis axes (Temp1, Temp2, Rain1, Rain2) and canonical structure of discriminant functions (CDA1, CDA2).

Variable or axis	Temp1	Temp2
Annual mean temperature	0.919	0.353
Mean diurnal range	0.368	-0.716
Isothermality	-0.492	0.615
Mean temperature wettest quarter	0.588	0.657
Mean temperature driest quarter	0.888	-0.282
Mean temperature warmest quarter	0.954	-0.254
Mean temperature coldest quarter	0.396	0.884
	Rain1	Rain2
Annual precipitation	0.334	0.886
Precipitation driest month	0.822	0.228
Precipitation seasonality	-0.665	0.677
Precipitation warmest quarter	0.918	-0.0352
	CDA1	CDA2
Rain1	0.148	0.885
Rain2	-0.908	0.117
Temp1	0.856	-0.176
Temp2	-0.020	-0.811

Figure 1.1. Occurrence localities (a–c) and Maxent predicted distributions (d–f) for the three floristic elements: (a, d) south-coastal California; (b, e) coastal–interior disjunct; (c, f) broadly distributed.

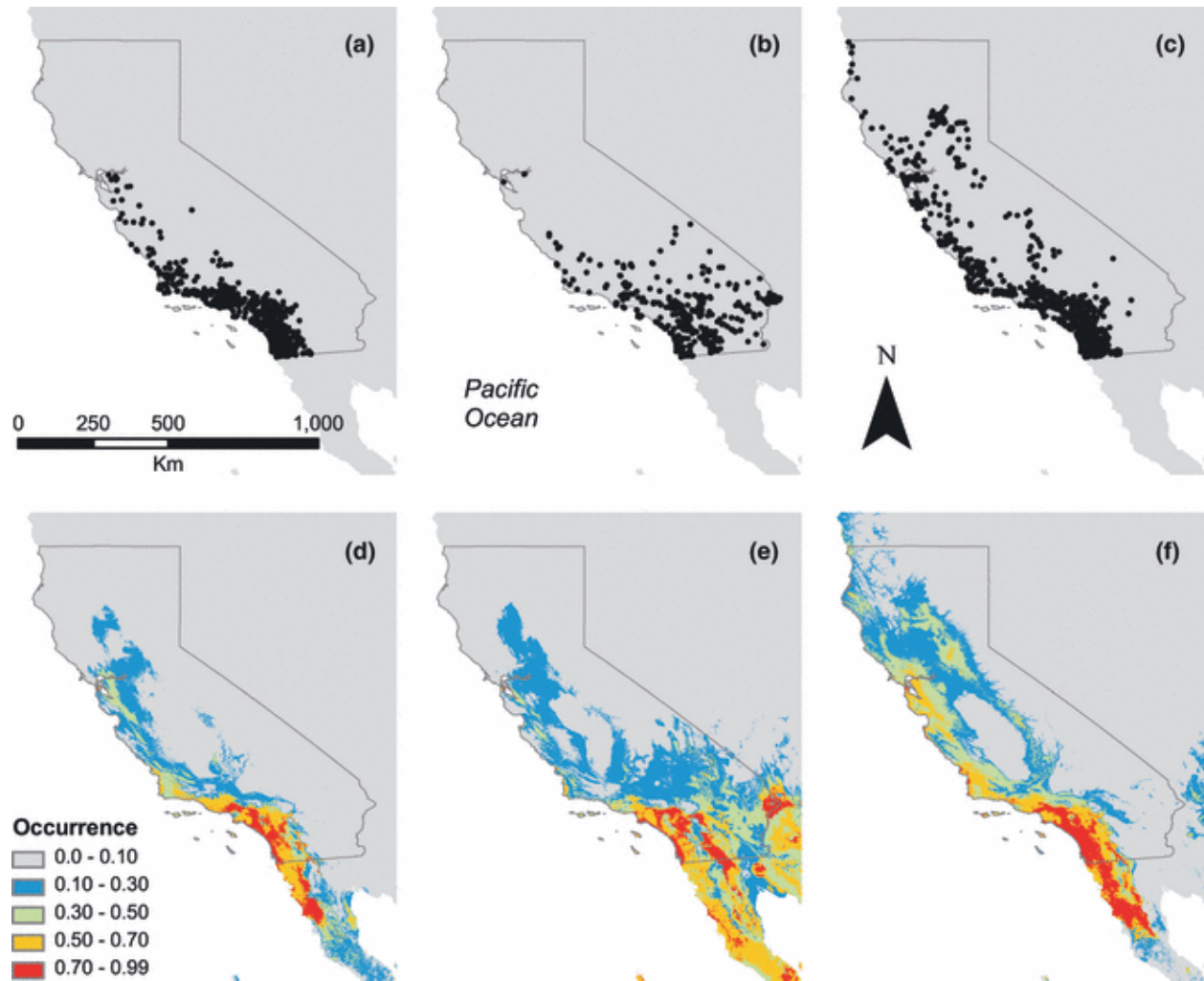


Figure 1.2. Occurrence localities (a–c) and Maxent predicted distributions (d–f) for three representative south-coastal California sage scrub species: (a, d) *Isocoma menziesii*; (b, e) *Encelia californica*; (c, f) *Salvia leucophylla*.

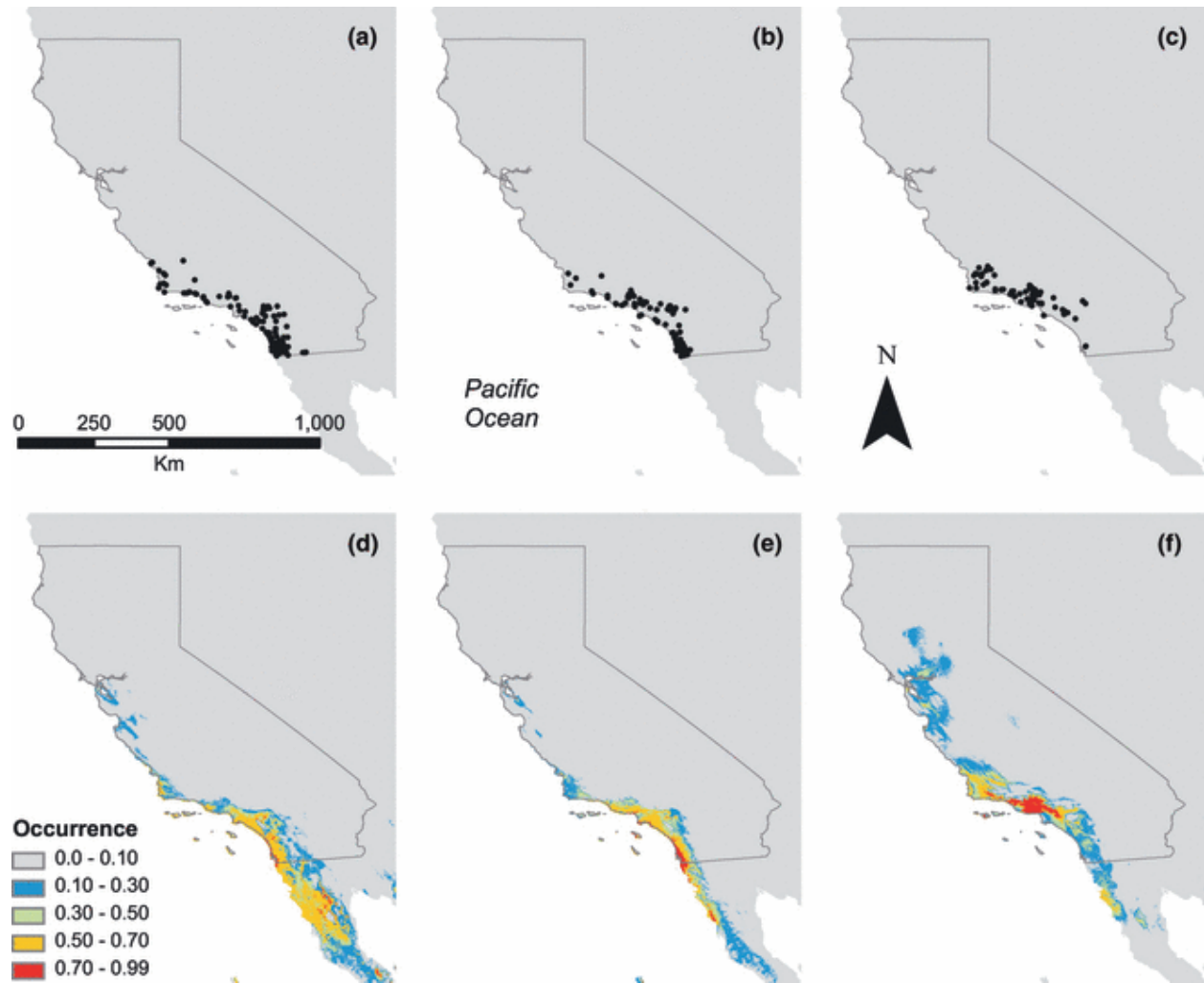


Figure 1.3. Occurrence localities (a–c) and Maxent predicted distributions (d–f) for three coastal–interior disjunct sage scrub species in California: (a, d) *Encelia farinosa*; (b, e) *Croton californicus*; (c, f) *Isomeris arborea*.

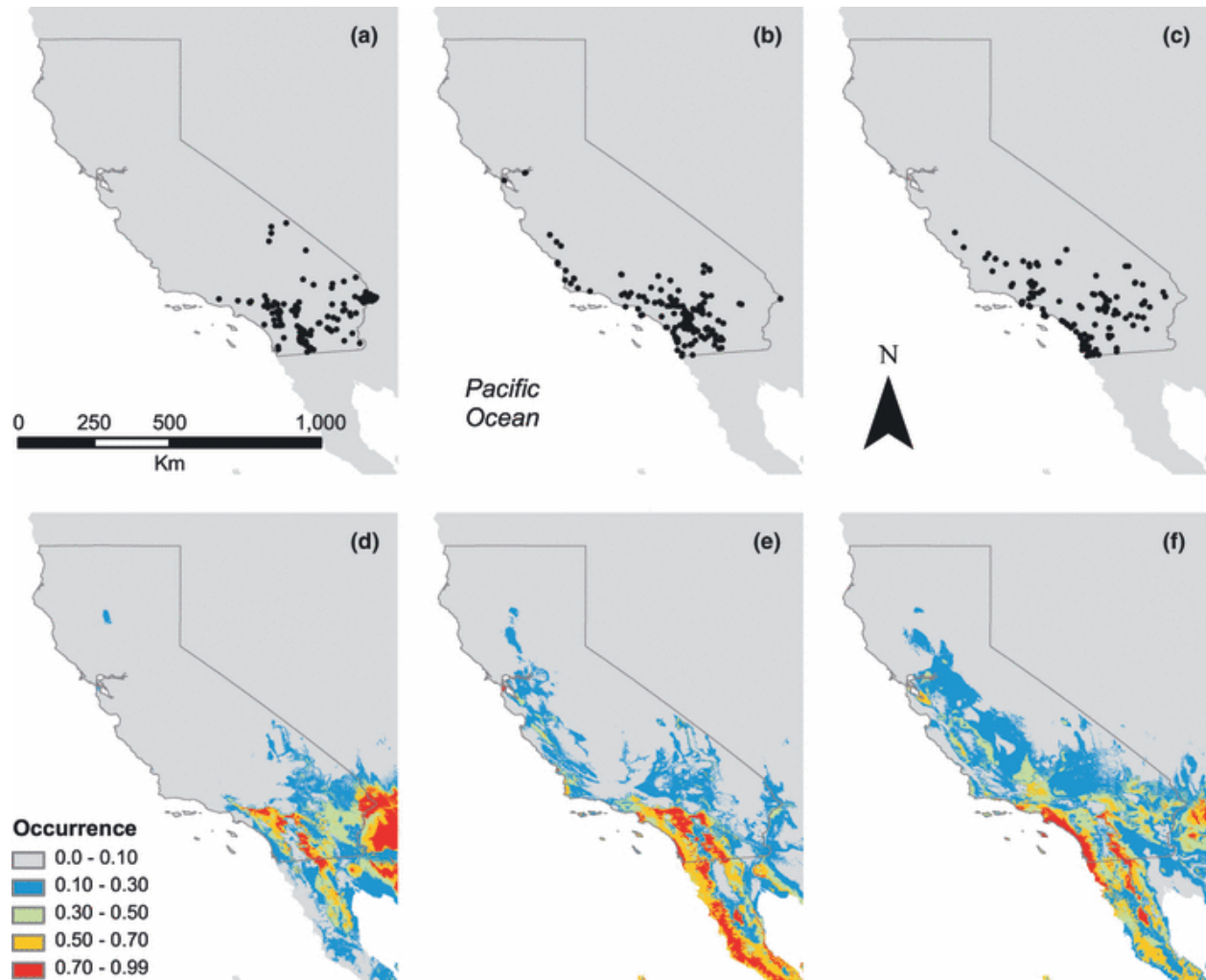


Figure 1.4. Occurrence localities (a–c) and Maxent predicted distributions (d–f) for three broadly distributed sage scrub species in California: (a, d) *Eriogonum fasciculatum*; (b, e) *Lotus scoparius*; (c, f) *Mimulus aurantiacus*.

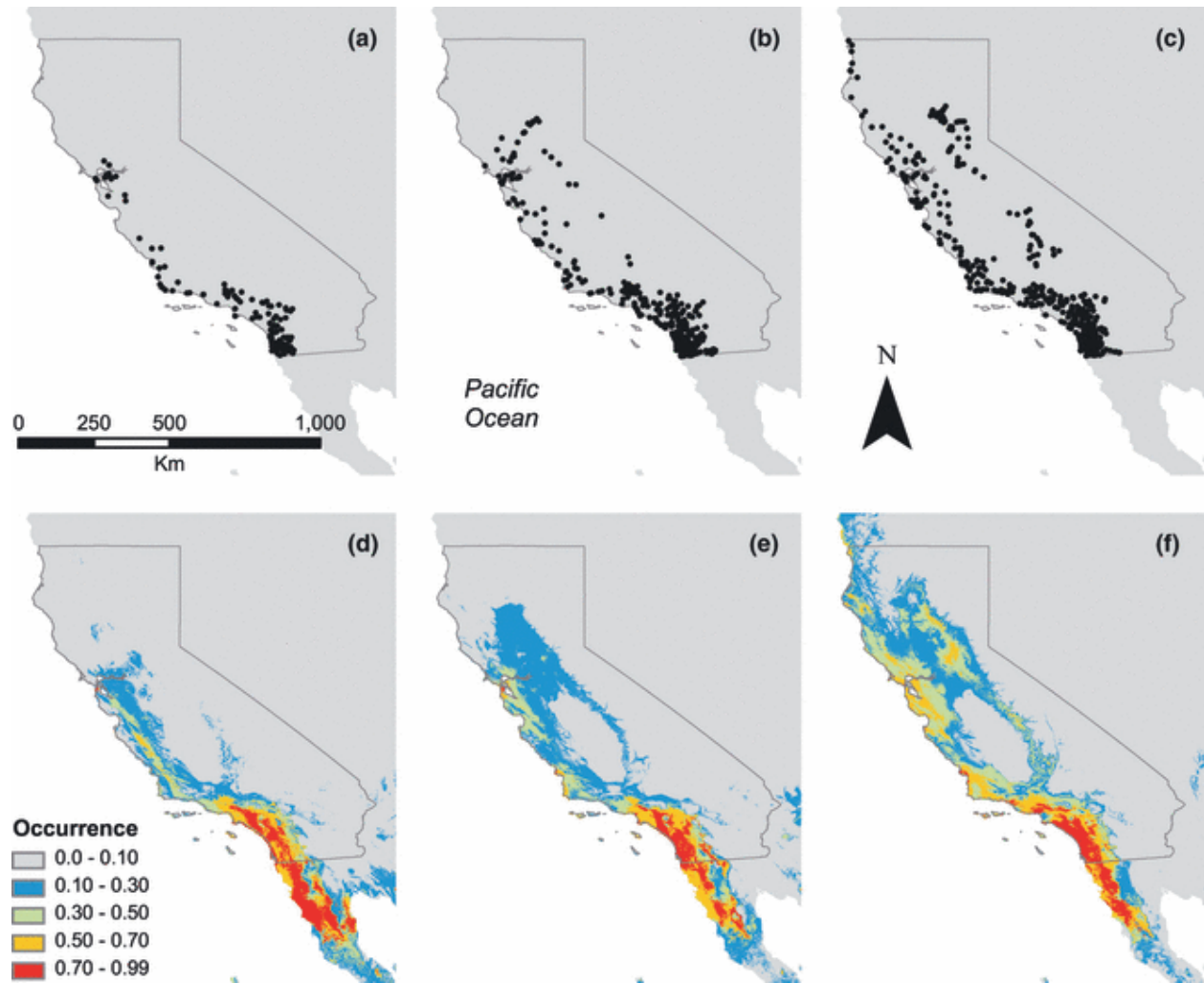


Figure 1.5. Canonical discriminant analysis ordinations of (a) three floristic groups in California sage scrub: south-coastal (•), coastal–interior disjunct (Δ), and broadly distributed (○) groups, and (b) individual species. Symbols and species abbreviations as follows: south-coastal (•) *Encelia californica* (enc), *Eriogonum cinereum* (erc), *Mirabilis californica* (mic), *Isocoma menziesii* senso varieties (ism), *Salvia apiana* (saa), *Salvia leucophylla* (sal), *Salvia mellifera* (sam); coastal-interior disjunct (Δ) *Croton californicus* (crc), *Encelia farinosa* (enf), *Isomeris arborea* (isa); and broadly distributed (○) *Artemisia californica* (arc), *Eriogonum fasciculatum* (erf), *Lotus scoparius*, (los), *Mimulus aurantiacus* (mia).

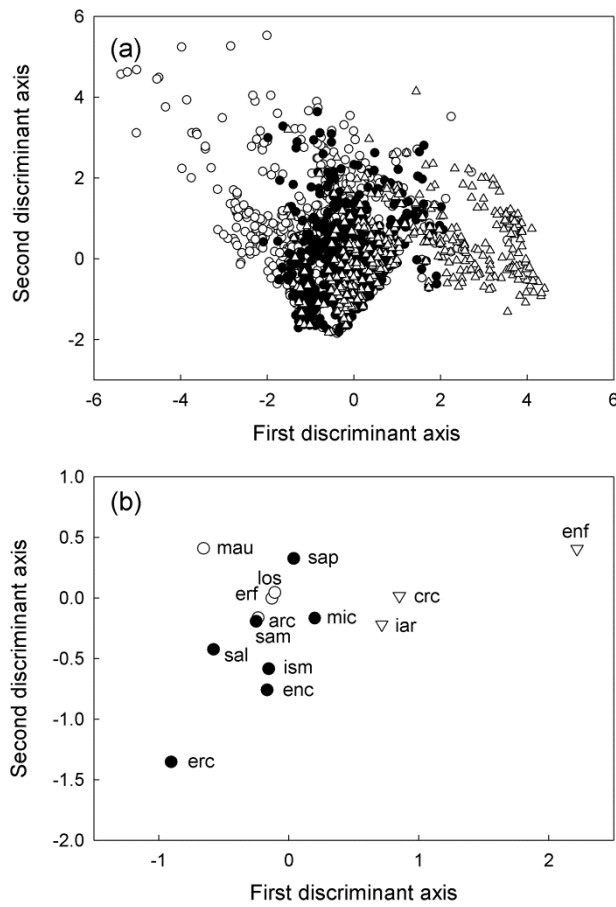
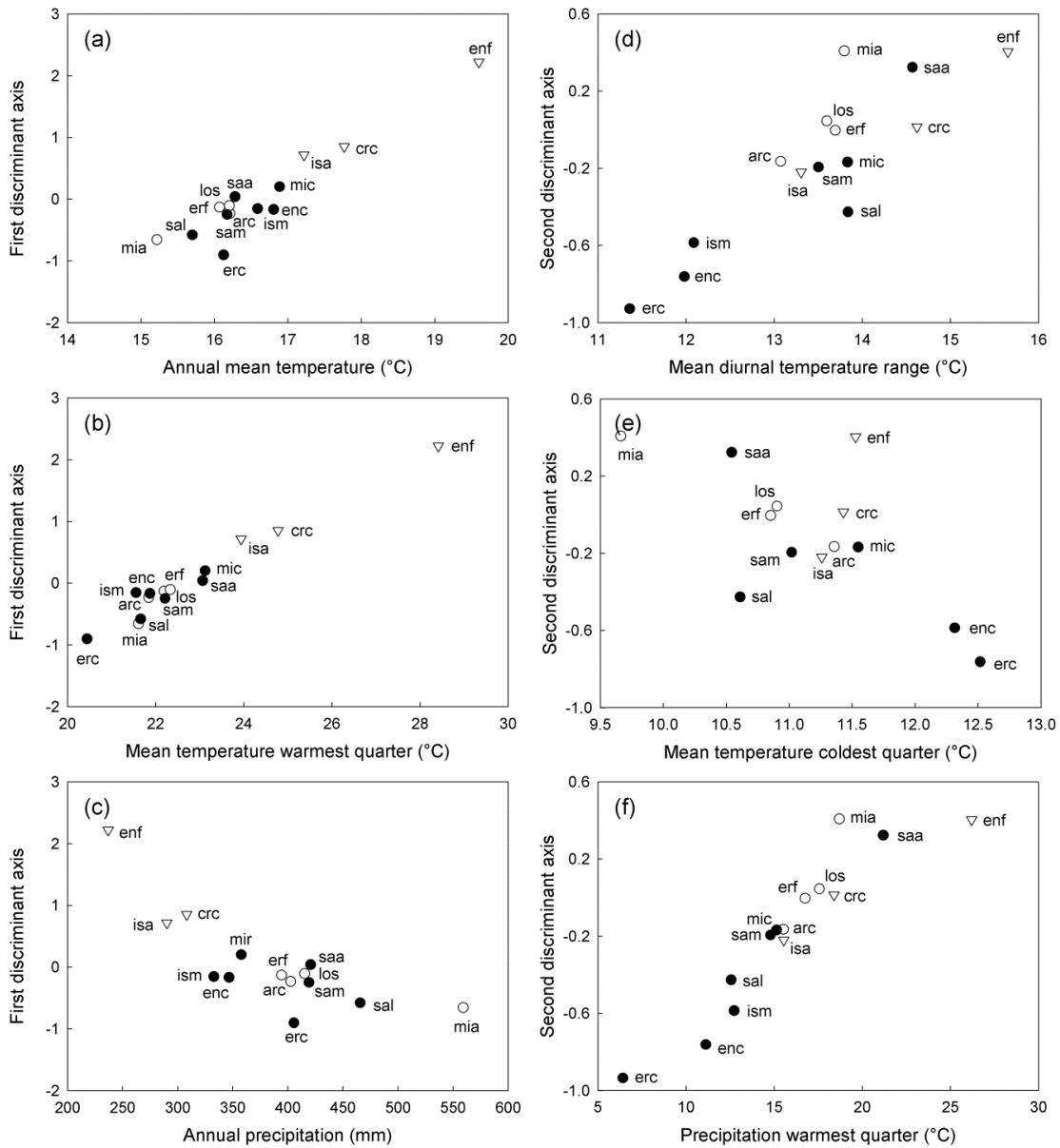


Figure 1.6. Plots of mean species canonical discriminant scores versus bioclimatic variables showing the relationship between the first discriminant axis and (a) annual precipitation, (b) maximum temperature of the warmest month, (c) precipitation seasonality; the second discriminant axis and (d) precipitation of warmest month, (e) minimum temperature of the coldest month, (f) mean diurnal temperature range. Symbols as follows: south-coastal (●) *Encelia californica* (enc), *Eriogonum cinereum* (erc), *Mirabilis californica* (mic), *Isocoma menziesii* (ism), *Salvia apiana* (saa), *Salvia leucophylla* (sal), *Salvia mellifera* (sam); coastal–interior disjunct (Δ) *Croton californicus* (crc), *Encelia farinosa* (enf), *Isomeris arborea* (isa); and broadly distributed (○) *Artemisia californica* (arc), *Eriogonum fasciculatum* (erf), *Lotus scoparius*, (los), *Mimulus aurantiacus* (mia).



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CHAPTER 2

DIFFERENTIAL GROWTH FORM RESPONSES TO PROJECTED CLIMATE CHANGE IN A THREATENED, MEDITERRANEAN-CLIMATE SHRUBLAND

ABSTRACT

Understanding how individual species and groups of species may respond to projected climate change can provide insight into how communities and diversity will restructure in the face of global change. Using a predictive species distribution modeling framework, we assess the sensitivity of 33 plant species to projected climate in California sage scrub (CSS), a diverse and highly threatened mediterranean-climate shrubland. We hypothesize that growth forms within CSS, which vary in prevalence within CSS along moisture and temperature gradients, will differ in response to climate change. Within growth form groups, we test whether geographic distribution (latitudinal range), bioclimatic niche breadth, and severity of projected climate change explain the sensitivity, or magnitude, of species response to projected climate change. Finally, we identify potential future impacts on CSS community structure and diversity under climate change driven by differential species responses. Overall, we find two patterns of habitat change for CSS: northern habitat expansion and southern habitat contraction. Species habitat losses will range from moderate (unlimited dispersal) to severe (no dispersal) for drought deciduous and evergreen species. Succulent species, in contrast, show a different pattern of considerable habitat gains (unlimited dispersal) and relatively low sensitivity to habitat loss. Bioclimatic niche breadth, latitudinal range, and climatic anomalies best explain habitat gains,

with broadly ranging species showing greatest projected habitat increases. We predict that wide ranging species will have the greatest projected habitat gains under future climate scenarios and succulent species will expand in range under changes of increasing aridity. Individual shifts in the distribution of CSS species translate to considerable changes in both future community structure and diversity with high community restructuring at northern and southern extents of CSS. Our findings suggest climate change will have greatest implications of CSS conservation and management in northwestern Baja California and coastal southern California, where community restructuring coincides with large declines in CSS diversity driven by southern habitat contraction of many CSS species.

INTRODUCTION

Global climate change poses a significant ecological threat this century, causing dramatic shifts in species distributions, altering species interactions and community structure, and ultimately impacting patterns of biodiversity and ecosystem functioning. Temperatures have already warmed by 1°C over the past century (global average), driving widespread shifts in the geographic distributions of species across taxa (Walther et al. 2002, Parmesan and Yohe 2003, Parmesan 2006), and are projected to continue rising as high as 4°C by 2100 (Meehl et al. 2007). As species respond to changing conditions and novel climates, non-analogue species compositions may characterize future communities (Williams et al. 2007a, Stralberg et al. 2009, Sheldon et al. 2011, Wiens et al. 2011). Although species are expected to respond individually to changing conditions (Huntley 1991), groups of species with shared characteristics or properties (e.g., plant functional types, growth forms, life forms) may respond similarly to environmental change (Lavorel et al. 1997, Suding et al. 2008). Therefore, predictions of the

response to climate change in both individual species and groups of species can provide insight into how communities and diversity may restructure in the face of global change (Woodward and Diament 1991, Grime et al. 2000, Voigt et al. 2007, Suding et al. 2008).

Species distribution models, which define a species range with respect to predictive environmental variables such as climate (Guisan and Zimmermann 2000, Guisan and Thuiller 2005), are valuable tools for predicting species responses to projected climate change. While uncertainties exist in the trajectories of both climate change and species response (Beaumont et al. 2008), species distribution models provide important insight into how species may respond to future climate change, identifying species at risk to habitat loss and extinction and predicting future changes in diversity (Thomas et al. 2004, Araujo et al. 2005, Williams et al. 2007a, Thuiller et al. 2008). Many studies use species distribution models to forecast range shifts of species under climate change, however, a species distribution modeling framework can also be used to test hypotheses of factors thought to influence the sensitivity of species to climate change, lending understanding to what drives the variability in response to climate change predicted across species and systems (Thuiller et al. 2005, Broennimann et al. 2006, Williams et al. 2007b).

Varied responses of individual species to climate change may be explained, at least in part, by the geographic distribution and environmental niche of a species. Assuming a positive relationship between species abundance and range size, restricted range species will have a greater risk of extinction (Brown 1984) and potentially greater susceptibility to extinction from habitat loss under climate change compared to widespread (large range) or generalist (broad niche) species. Recent studies have shown increased vulnerability to climate change in restricted range species and species with narrow niche breadth (Thuiller et al. 2005, Broennimann et al.

2006, Williams et al. 2007b). Additionally, the severity of climate change, and thus the velocity of species movements required to track changing climate, is varied geographically (Loarie et al. 2009). Indeed, high habitat losses are predicted for species with narrow ranges or bioclimatic niches that occur in geographic areas having large projected changes in future climate (Thuiller et al. 2005, Broennimann et al. 2006).

Focusing on California sage scrub (CSS), a diverse and highly threatened shrubland in the mediterranean-climate California Floristic Province of North America, we investigate the response of individual species and growth form groups to projected climate change to understand how this sensitive community may shift and restructure under scenarios of global change. Mediterranean-climate ecosystems, which contain over 20% of known vascular plant diversity in only slightly more than 2% of the land area on Earth (Cowling et al. 1996), are at particular risk of future biodiversity loss (Sala et al. 2000, Underwood et al. 2009). Considerable species losses and range reductions have been predicted across the five mediterranean-climate regions (Midgley et al. 2002, Fitzpatrick et al. 2008, Yates et al. 2010) including the California Floristic Province (Loarie et al. 2008). California sage scrub is currently highly reduced and fragmented in distribution with as little as 10% of its original extent intact (Westman 1981a, Minnich and Dezzani 1998, Taylor 2004, Rundel 2007) and contains a large number of threatened and endangered species (O'Leary 1990, DeSimone 1995), which may be particularly vulnerable to further habitat loss under climate change.

California sage scrub, which occurs in varied community compositions primarily distributed along the coast of southern California, USA to northwestern Baja California, Mexico (Kirkpatrick and Hutchinson 1977, Axelrod 1978, Westman 1981b, a, 1983, Davis et al. 1994, review in Rundel 2007), provides a test-bed to investigate how differential responses of species

and growth form groups under climate change may drive changes in patterns of community composition and diversity. Although CSS is typically characterized by dominant drought-deciduous shrubs, both evergreen and succulent species are significant and often locally dominant elements. Evergreen, sclerophyllous species may locally dominate CSS communities where ground water is available whereas drought-deciduous shrub species (e.g., *Salvia* species) dominate the majority of communities with low water availability, lower latitudes and elevations, and steep slopes (Mooney and Dunn 1970, Harrison et al. 1971, Miller and Poole 1979). Succulent species, typically tolerant of high temperatures and drought (Nobel and Zutta 2008), become increasingly prominent in CSS communities in northwestern Baja California known as maritime succulent scrub (Westman 1983, Rundel 2007, Garcillán et al. 2012), but are restricted in the north by an intolerance of fire and lower winter temperatures. Given the differences in temperature and drought tolerance of growth forms in CSS, differential species and growth form responses to climate change could have profound impacts on CSS communities and diversity.

The magnitude of projected climate change varies geographically across the distribution of CSS, which will likely influence the spatial patterns in CSS response to climate change. The coastal plains of southern California and northwestern Baja California, areas harboring high CSS diversity and endemism, are expected to contract significantly, becoming replaced by novel, warmer and drier conditions (Klausmeyer and Shaw 2009, Ackerly et al. 2010). Thus, climate change poses a particularly high threat to critical areas of high CSS diversity and endemism. Additionally, the southern limit of CSS in Baja California marks the transition of mediterranean-climate in North America to more arid, desert conditions and corresponding sharp floristic transition (Shreve 1936). Marginal sage scrub communities occurring at this transition may be more susceptible to climate change impacts and the future persistence of species in these

communities will determine the dynamics of this transition zone (Thuiller et al. 2008).

Given the high conservation priority of CSS and large economic expense associated with its protection in California, predictions of projected climate change impacts on CSS distribution and diversity are critical for conservation planning this century, but only a few studies focused on a restricted number of species have addressed climate change in CSS (Malanson and Westman 1991, Westman 1991). Using a predictive species distribution modeling framework, we assess the sensitivity of 33 key CSS species to climate change to better understand how the ecosystem may restructure under climate change. Such climate-based species distribution models have recently been shown to provide important information on habitat requirements of individual CSS species, as well as to distinguish between different floristic elements, or species assemblages, within CSS (Riordan and Rundel 2009).

We hypothesize that growth forms, which vary in prevalence within CSS along moisture and temperature gradients, will differ in response to climate change. Within growth form groups, we test whether geographic distribution (latitudinal range), bioclimatic niche breadth, and severity of projected climate change explain the sensitivity, or magnitude, of species response to projected climate change. Finally, we investigate the spatial pattern of potential change in CSS community structure and diversity under climate change driven by differential species responses, highlighting areas of conservation concern under future change.

METHODS

Study system

California sage scrub is a highly threatened, diverse plant association in the California Floristic Province characterized by dominant drought-deciduous shrubs (e.g., *Salvia* species) and

a diverse herbaceous understory with a variable component of evergreen and succulent shrubs. California sage scrub is distributed along a gradient of increasing temperature and aridity in coastal areas from the San Francisco Bay Area in California, USA (38° N) southwards to El Rosario (30° N) in northwestern Baja California, Mexico (Shreve 1936, Epling and Lewis 1942, Westman 1983, Rundel 2007), where mediterranean-type climate transitions to more arid, desert conditions (Shreve 1936). California sage scrub has high conservation priority, providing habitat for over 100 plant and animal species currently considered threatened, endangered, or of special conservation concern (O'Leary 1990, DeSimone 1995). Anthropogenic impacts, however, have already caused widespread loss and fragmentation of this unique vegetation type (Westman 1981a, Minnich and Dezzani 1998, Taylor 2004, Rundel 2007), and projected use and climate change will likely drive further habitat and species losses.

Climate in California is expected shift substantially, with general circulation models (GCMs) predicting temperature increases of 1.35°C to 5.8°C statewide by 2100 (Hayhoe et al. 2004). In southern California, temperatures will rise on average 1.6°C (low emission SRES B1 scenario) to 4.4°C (high emission SRES A2 scenario) by 2100 (Cayan et al. 2008). Although varied in direction and magnitude of response, precipitation will also change with projections of mean annual precipitation for southern California ranging from losses of up to 26% (high emission SRES A2 scenario) to gains of up to 8% (low emission SRES B1 scenario) averaged across the region (Cayan et al. 2008). Under projected climate change, mediterranean-climate in the coastal plains of southern California and northwestern Baja California is expected to contract significantly, becoming replaced by novel, warmer and drier conditions (Klausmeyer and Shaw 2009, Ackerly et al. 2010).

Modeling approach

We modeled current and future climatically suitable habitat for 33 dominant CSS shrub species representing drought-deciduous (15 species), evergreen (11 species), and succulent (seven species) growth forms that collectively span the Central and South Coast Ecoregions in California, USA and the Northwestern Baja California Mediterranean-Climate Ecoregion in Mexico (Fig. 2.1, Table 2.1). We grouped semi-evergreen species, such as *Eriogonum fasciculatum*, with evergreen species and the drought-deciduous stem photosynthetic *Adolphia californica* with drought-deciduous species. While studies of CSS focus overwhelmingly on California, often truncating species occurrences at the U.S. – Mexico border, we include species and occurrences from northwestern Baja California spanning the full range of CSS and including maritime succulent scrub. In doing so, we minimize the chance of over-predicting habitat losses under climate change, which often arises when a restricted range of occurrence records (e.g., due to political boundaries) is used to model species distributions (Barbet-Massin et al. 2010).

We searched the following databases for herbarium records for CSS species in both California and Baja California: the Consortium of California Herbaria (CCH; <http://ucjeps.berkeley.edu/consortium>), the Southwest Environmental Information Network (SEINet; <http://swbiodiversity.org/seinet>), the Global Biodiversity Informatics Facility (GBIF; <http://www.gbif.org>), the San Diego Natural History Museum's Baja Flora (<http://www.sdnhm.org>), and the Red Mundial de Información sobre Biodiversidad (REMIB; http://www.conabio.gob.mx/remib/doctos/remib_esp.html). Prior to modeling, we mapped all records to identify and exclude cultivated plants, errors in georeferencing, obvious misidentifications and duplicate collections. Only records collected from 1950 to present were retained for modeling, as earlier occurrence records may represent climates that do not reflect

current climate conditions.

We chose seven bioclimatic variables from the Worldclim climate database (<http://www.worldclim.org>; Hijmans et al. 2005) to represent annual trends, seasonality, and extremes in climate: annual mean temperature, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation seasonality, precipitation of the warmest quarter, and precipitation of the coldest quarter. Variables were selected that both minimized correlations among variables and maximized contribution to model predictions. Worldclim climate layers are derived from interpolated weather station monthly mean temperature and precipitation data collected from 1950 to 2000 (Hijmans et al. 2005).

We selected late-century (2080s) future climate projections from two global circulation models (GCMs) to represent two possible trajectories of climate change under the A1B Special Report on Emission Scenarios (SRES) storyline: (1) a warmer wetter future (CCCMA CGC 3.1) and a warmer drier future (NCAR CCSM 3.0). The A1B storyline reflects a moderate-high future emissions scenario characterized by rapid economic growth, global population that peaks in mid-century and declines thereafter, rapid technological innovation, balanced energy sources, and active management of resources (Meehl et al. 2007). Downscaled climate data for the seven corresponding bioclimatic variables were downloaded from the International Center for Tropical Agriculture's climate change program (CIAT; <http://www.ccafs-climate.org>), which downscaled original GCM output data from the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) (Meehl et al. 2007) and created a 30-year average for late century (2080s: 2070-2100). All climate data, current and future, were at 30-arcsec (ca. 1 km) spatial resolution. While finer resolution climate data exist for California, such as the Parameter-elevation Regressions on Independent Slopes Model (PRISM) dataset, these datasets only cover

the United States and exclude Baja California.

Current climatically suitable habitat for individual CSS species was modeled from herbarium record locations and current climate data using the maximum entropy modeling algorithm Maxent (version 3.3.3; Phillips et al. 2006). Maxent, which does not require absence data and has high performance with spatially biased data (Elith et al. 2006, Phillips et al. 2006, Loiselle et al. 2008), is appropriate for modeling CSS species distributions from presence-only herbarium records. Additionally, the maximum entropy modeling framework of Maxent is particularly useful for modeling CSS, as the current, fragmented distribution of the vegetation type may reflect local anthropogenically driven extirpations rather than environmental limits.

Current species-climate models were trained with all herbarium records then projected onto downscaled future climate layers from the two GCMs. We ran a 10-fold cross-validation replication for each species model to estimate overall model performance (Appendix 2.1) measured by the area under the receiving operator characteristics curve (AUC). This metric ranges from 0.5 (random prediction) to 1 (maximum prediction) and can be interpreted as the probability that a presence site is ranked above a random background site when using presence-only data (Phillips et al. 2006). Each model run was performed using the same 10,000 randomly selected pixels across the study area as “pseudo-absences” with a maximum set of iterations of 500, a convergence threshold of 10^{-5} , and “auto” regularization allowing Maxent to set the amount of regularization automatically based on our locality and environmental data (Phillips et al. 2006).

We created binary current and future habitat maps (0 = unsuitable, 1 = suitable) from Maxent’s logistic output using the maximum sensitivity plus specificity threshold (Liu et al. 2005) assuming two possible dispersal scenarios: a best-case, unlimited dispersal scenario where

species can colonize any future suitable habitat, and a worst-case, no dispersal scenario where species cannot disperse to future suitable habitat outside areas modeled as currently climatically suitable.

CSS response to climate change

We characterized the predicted CSS species responses to climate change as follows: (1) total percent loss in species habitat, (2) percent gain in species habitat, (3) total change in habitat measured as the Euclidean distance of loss and gain ($\sqrt{loss^2 + gain^2}$), (4) the shift in the geographic centroid of modeled species distribution, and (5) the shift in median elevation of modeled species distributions. We calculated the percent habitat loss (no dispersal scenario) and gain (unlimited dispersal scenario) for each CSS species as the percent change in the number pixels modeled as suitable habitat from current to late-century (2080s). We calculated the geographic shift in species distributions as the distance between the geographic centroids of modeled current and future suitable habitat. We calculated the shift in elevation of species distribution as the difference in median elevations of modeled current and future suitable habitat. We tested for differences in species predicted responses between warmer wetter and warmer drier climate scenarios within growth form groups using the nonparametric paired Wilcoxon signed rank test. To test whether different growth forms within CSS vary in their predicted response to climate change, we performed one-way analyses of variance (ANOVAs) for each response variable.

Geographic and bioclimatic explanation of CSS sensitivity to climate change

We geographically characterized current species distributions by their latitudinal range,

measured as the latitudinal (N-S) distance (km) between the northern-most and southern-most herbarium record localities. To estimate the breadth of a species current bioclimatic niche, we performed a Principal Component Analysis (PCA) on the seven bioclimatic variables across species localities after first scaling variables to have unit variance. For each species, we calculated the bioclimatic niche breadth as the variance in PCA scores along the first principal component axis. To quantify the severity of projected climate change across the current distribution of a species, we calculated the anomalies in temperature (annual) and precipitation (annual and winter) as the mean difference between future and current climate conditions at herbarium record localities. We then investigated the relationship between the projected habitat loss and gain of CSS species and geographic and bioclimatic predictors for individual growth form groups using stepwise multiple linear regressions.

Climate change impacts on CSS community and diversity

To examine the potential change in the geographic pattern of CSS diversity in California and Baja California driven by projected climate change, we estimated current and future CSS shrub species richness by overlaying the binary habitat suitability maps of our 33 modeled species. For future richness, we assumed a complete loss of species from areas with future suitability falling below the maximum sensitivity plus specificity threshold and complete persistence or gain of species in areas with future suitability above the threshold. We estimated future richness for both no dispersal and unlimited dispersal scenarios. We calculated the absolute change in CSS species richness and the relative (percent) change in CSS species richness from current to future (2080s). We also calculated the per-pixel similarity of CSS species assemblages across the study area using the Jaccard similarity index:

$$J = 100 \times \frac{A}{A + B + C}$$

Where for a given pixel, A is the number of species with suitable habitat for both current and future models, B is the number of species with suitable habitat under current models only, and C is the number of species with suitable habitat under future models only. We compared changes in species richness and community similarity across three ecoregions spanning the current distribution of CSS: the Central Coast California Ecoregion (Central Western California in Baldwin et al. 2012), the South Coast California Ecoregion (Southwestern California in Baldwin et al. 2012), and the Northwestern Baja California Mediterranean-Climate Ecoregion (INEGI et al. 2008) (ecoregions shown in Fig. 2.1). All spatial analyses and model visualizations were performed in ArcMap 10 (ESRI, Redlands, CA, USA).

RESULTS

CSS response to climate change

Under the future climate scenarios selected for this study, warmer wetter and warmer drier trajectories, changes in temperature and precipitation will vary geographically across the range of CSS (Fig. 2.2). The warmer wetter (CCCMA CGC 3.1) scenario projects the most severe warming at southern latitudes of CSS's current distribution with increases in precipitation most notably at the northern extent of CSS and drying across southern California and the Baja California peninsula. The warmer wetter (NCAR CCSM 3.0) future scenario, in contrast, projects increasing warming and drying with increasing latitudes and the most severe changes in temperature and precipitation at the northern extent of CSS.

Maxent models had high performance across CSS species: median AUC score of 0.977 (range: 0.904–0.992) (Appendix 2.1). Overall, our predictions of CSS response to climate

change were similar across warmer wetter and warmer drier future climate scenarios (Table 2.2; Figure 2.3), but varied with species. We predict a wide range in both habitat losses and gains for CSS species by late century (Appendix 2.2). Assuming no dispersal, species will experience maximum habitat losses of a median 46.06% (19.08–98.48) to 40.27% (4.7–97.36%) under warmer wetter and warmer drier future climate scenarios, respectively (Table 2.2). Fourteen of the 33 shrub species considered in our study will have >50% habitat loss under at least one future climate scenario. However, climate change will also drive the expansion of climatically suitable habitat for many CSS species, especially at the northern extent of current species distributions. Assuming CSS species can disperse fully into newly available habitat (unlimited dispersal), we predict maximum habitat gains of a median 22.06% (0–111.94%) under a warmer wetter future and 34.40% (1.97–122.88%) under a warmer drier future. Thus, after accounting for habitat losses under unlimited dispersal scenarios, CSS species will experience more moderate habitat losses with a median predicted net habitat change of -19.01% (-98.48% to 91.86%) under a warmer wetter future and -2.65% (-95.57% to 118.19%) net habitat change under a warmer drier future. Assuming unlimited dispersal, we predict only five of 33 species will experience > 50% net habitat loss under at least one future climate scenario, while 16 species will experience a net gain in habitat under at least one future climate scenario.

We also predict variable shifts in both the geographic centroid of CSS species distributions and the median elevation across modeled species ranges (Appendix 2.3). We predict the greatest shift in geographic centroid under unlimited dispersal scenarios, with median shifts of 162 km (12–404 km) and 201 km (28–548 km) under warmer wetter and warmer drier future scenarios, respectively (Table 2.2). In addition, species will undergo significantly greater geographic shifts in distribution under a warmer drier future climate compared to a warmer

wetter future climate ($P < 0.01$; paired Wilcoxon signed rank test). While modeled elevation shifts are highly variable across climate and dispersal scenarios, with species projected to shift both upslope and downslope (Table 2.2), we predict the greatest median elevation shift assuming unlimited dispersal (warmer wetter $P < 0.001$ and warmer drier $P < 0.05$; paired Wilcoxon signed rank test).

Shrub growth forms, drought-deciduous, evergreen, and succulent, also vary in their sensitivity to habitat change under future climate scenarios (Table 2.3). While we find considerable overlap in predicted habitat losses and gains for evergreen and drought deciduous species, with most species showing greater habitat losses than gains, we predict a notably different pattern of response in succulent species (Fig. 2.4). We predict succulent species will have significantly less habitat loss than evergreen species (warmer wetter and warmer drier future scenarios) and drought-deciduous species (warmer drier future scenario only) and greater habitat gains than either growth form assuming unlimited dispersal (warmer drier future scenario only) (Table 2.4, Fig. 2.5). Assuming unlimited dispersal, we predict net habitat gains in succulent species in contrast to net habitat losses for both drought-deciduous and evergreen species. Drought-deciduous and evergreen species will respond similarly in terms of predicted habitat losses and gains, regardless of climate scenario (all $P > 0.60$; Tukey's HSD; Table 2.4). Interestingly, we do not predict a significant difference in the total habitat change, measured as the Euclidean distance of loss and gain, among growth form groups (Fig. 2.5) ($P > 0.16$ both climate scenarios; ANOVA).

In addition, we predict that the greatest habitat losses will occur under a warmer wetter future climate, with evergreen and succulent species having significantly higher losses under a warmer wetter climate compared to a warmer drier climate ($P < 0.05$; paired Wilcoxon signed

rank test). We do not, however, find any significant differences in either the predicted shift in geographic distribution centroid or median elevation among different the growth forms (all $P > 0.307$; ANOVA).

Geographic and bioclimatic explanation of CSS sensitivity to climate change

Niche breadth, measured as the variance of species scores along the first PCA axis of bioclimatic variables (Table 2.5), had a strong positive correlation with annual temperature seasonality in both drought-deciduous and evergreen species (Table 2.6), but not succulent species. In succulent species, niche breadth was most strongly correlated with the minimum temperature of the coldest month (negative relationship) and precipitation of the coldest quarter (positive relationship). In addition, niche breadth was highly correlated with latitudinal range of a species (Pearson's $r=0.879$), but only for drought-deciduous species. Growth forms did not differ significantly in their bioclimatic niche breadth ($P = 0.394$; ANOVA).

Range size, niche breadth, and severity of climate change had significant relationships with projected habitat loss and gain for CSS species under future climate scenarios (Table 2.7). When analyzing CSS species collectively, we find that both anomalies in temperature (warmer wetter and warmer drier future scenarios) and summer precipitation (warmer drier scenario only) had a significant positive relationship with future habitat loss: greater changes in future climate translated to greater projected habitat losses. Habitat gains were most strongly related to the latitudinal range of a species (positive relationship; warmer wetter and warmer drier future scenarios) and anomalies in annual precipitation (negative relationship; warmer drier future scenario only). Thus, a greater latitudinal range translated to greater habitat gains for CSS shrub species.

The explanatory relationships for habitat loss and gain of individual growth forms, showed similar patterns with some differences across and within climate scenarios (Table 2.7). For drought-deciduous species under a warmer wetter future, anomalies in temperature was the most significant predictor of projected habitat loss (positive relationship), whereas none of the geographic or climatic variables considered in our study were significantly related to drought-deciduous shrub habitat loss under a warmer drier future. Similarly, anomalies in temperature (positive relationship) and latitudinal range (negative relationship) were significant predictors of habitat loss for evergreen species, but only under a warmer wetter future: the narrower the latitudinal distribution of a species, the greater the habitat loss. For succulent species, niche breadth was positively correlated with habitat loss, but only under the warmer drier future scenario. However, bioclimatic niche breadth in succulent species was positively correlated with anomalies in temperature under a warmer drier future scenario (Pearson's $r = 0.779$).

When considering habitat gain across growth form groups, latitudinal range had a significant positive relationship with habitat gain under both warmer wetter and warmer scenarios for all growth forms with the exception of drought-deciduous species under the warmer wetter scenario (Table 2.7). In this case, niche breadth (positive relationship) in combination with anomalies in temperature (negative relationship) and annual precipitation (negative relationship) were the best predictors of habitat gain. Niche breadth and latitudinal range in drought-deciduous species are highly correlated. Somewhat surprisingly, niche breadth had a negative relationship with habitat gain for evergreen species under both future climate scenarios. Overall, the larger the latitudinal range (evergreen, succulent species) or niche breadth (drought-deciduous species only) of a species, the greater the projected habitat gain under climate change.

Climate change impacts on CSS community and diversity

We predict two patterns of habitat change for CSS species consistent across both future climate scenarios; southern habitat contraction (unlimited and no dispersal) and northern habitat expansion (unlimited dispersal); which could, in turn, drive differential changes in CSS diversity along coastal California and northwestern Baja California ecoregions (Fig. 2.6). Current modeled CSS shrub species richness is greatest in the South Coast California and Northwestern Baja California Mediterranean-Climate Ecoregions, with a median modeled richness of 14 species and 19 species, respectively, compared to a median richness of 8 species in the Central Coast California Ecoregion (Table 2.8, Fig. 2.7). Both southern ecoregions are predicted to undergo considerable declines in species richness even under best-case, unlimited dispersal scenarios (Fig. 2.8). In the South Coast Ecoregion, we predict relative losses in species richness of 27–29% (unlimited dispersal) to 35–38% (no dispersal). We predict similar losses in the Northwestern Baja California Mediterranean-Climate Ecoregion: 26–31% (unlimited dispersal) to 37–41% (no dispersal). The Central Coast Ecoregion, in contrast, has a much different predicted pattern of future diversity. Assuming no dispersal, species richness losses will be much less severe than either of the two more southern ecoregions, with only a 9–11% decline in median relative species richness across the ecoregion (Table 2.8, Fig. 2.8). Assuming unlimited dispersal, we predict notable increases (53–55%) in median species richness, consistent across both warmer wetter and warmer drier future climate scenarios.

As individual species shift in distribution in response to climate change, we predict that CSS community composition will also change. Regions with the lowest future community similarity, and thus greatest projected change in species composition, will be the California Central Coast Ecoregion (unlimited dispersal) where CSS shrub species ranges will potentially

expand into future climatically suitable habitat, and the southern portion of the Northwestern Baja California Mediterranean-Climate Ecoregion, where CSS shrub species ranges will potentially contract with declining precipitation and increasing temperatures (Table 2.8, Fig. 2.6). Under no dispersal scenarios we predict less severe community restructuring, indicated by greater similarities in species composition between current and future communities. Similarity will still be relatively low, however, at the southern limit of CSS in northwestern Baja California and extending into the mediterranean-desert climate transition zone.

DISCUSSION

With climate change expected to drive cascading ecological impacts on species to ecosystems, a better understanding of the factors influencing species sensitivity to projected climate change will be critical for the effective conservation and management of biodiversity under global change. Differential responses of individual species and groups of species (e.g., plant functional types, growth forms) will likely cause significant restructuring of communities and shifts in biodiversity (Williams et al. 2007a, Stralberg et al. 2009, Sheldon et al. 2011, Wiens et al. 2011) before the end of the century. Focusing on California sage scrub, a threatened mediterranean-climate shrubland of high conservation significance, we predict climate change will have a varied impact across CSS, with species and growth forms showing a large range in both predicted habitat gains and losses under future climate scenarios. Our findings suggest that these variable species responses could have profound impacts on the diversity and community structure within California sage scrub, which will likely have major implications for the large number of sensitive species dependent upon CSS for habitat (O'Leary 1990, DeSimone 1995).

Among dominant shrub growth forms in CSS, we predict differential responses to

projected climate change, with succulent species showing a distinctly different pattern of large habitat gains combined with minimal habitat losses under future climate scenarios compared to the overall net losses predicted for many drought-deciduous and evergreen species. Currently, succulent species increase in prevalence in CSS communities with increasing aridity, becoming dominant features of maritime succulent scrub in northwestern Baja California and southern areas of San Diego County in California (Westman 1983, Harper et al. 2010). Many of these species span the semiarid transitional zone between mediterranean and Sonoran Desert climates, extending into the Vizcaino Desert. *Agave shawii* and *Bergerocactus emoryi*, both predicted to undergo habitat expansions with future climate change, are indicative of transitional zone plant associations (Peinado et al. 1995). Our findings suggest a possible northward shift in the mediterranean-desert climate transition zone, a region marked by some of the highest levels of endemism across the peninsula due to co-occurrence of both mediterranean and desert floristic elements (Peinado et al. 1995, Peinado et al. 2008). Our analyses of projected community change indicate high levels of species turnover in the transition zone, where the habitat contraction of many drought-deciduous and evergreen species coincides with the habitat expansion of many succulent species. With many succulent species intolerant of fire, the northern extent of habitat expansion for succulents will be influenced by fire occurrence under future climate scenarios, which occurs at higher frequency in southern California compared to northwestern Baja California. Some succulent species, however, such as mound-forming *Opuntia* species, *Bergerocactus emoryi*, and *Agave shawii*, are moderately tolerant of fire.

Although drought deciduous and evergreen growth forms typically vary in dominance within CSS communities along gradients of water availability (Mooney and Dunn 1970, Harrison et al. 1971, Miller and Poole 1979), we find high overlap in species projected response

to climate change between growth forms. Currently, evergreen species tend to increase in prevalence in CSS with increasing elevation and increasing latitudes along the central California coast where they become dominant (Harrison et al. 1971, Westman 1983). Drought-deciduous species dominate in areas of lower water availability; lower latitudes and elevation, lower precipitation inputs, and areas of poor soil moisture; although they are capable of surviving at higher elevations and greater water availability when released from competition with taller evergreen chaparral shrubs. Accordingly, we expected evergreen species to show greater habitat gains under a warmer wetter future climate scenario, particularly along the central coast of California, and drought deciduous species to show greater northern expansion under a warmer drier future climate scenario.

The similarity in modeled response of evergreen and drought-deciduous growth forms to climate change may be due to the degree of variability in phenological traits and water relations within our growth form groupings. Many drought-deciduous species, such as *Salvia mellifera*, show patterns of seasonal leaf dimorphism, retaining smaller leaves through summer months when larger leaves are abscised under high drought stress (Nilsen and Muller 1981, Westman 1981c). Within the evergreen grouping we include semi-evergreen species such as *Eriogonum fasciculatum*, which lose some leaves under summer drought stress. Although typically less tolerant of low water availability, evergreen species have highly variable water relations with some overlap with drought-deciduous species (Poole and Miller 1975, Miller and Poole 1979, Gill and Mahall 1986). Thus, our growth form groupings contain variable trait compositions which may lead to variable responses to climate change within groupings (Lavorel and Garnier 2002). In addition, our climate-based models do not include other factors related to moisture availability, such as edaphic conditions or species rooting depth, which influence fine-scale

differences between drought-deciduous and evergreen species at local rather than regional scales (Miller and Poole 1979). We predict >100% habitat gain in the deeply rooted evergreen species *Rhus integrifolia* under climate change, a response more similar to the succulent species than the over evergreen species we modeled. The 1 km spatial resolution of our analyses may also fail to capture finer-scale topographic differences in climate, or ‘topoclimate’ (Ackerly et al. 2010), and may contribute to the similarities in modeled responses to climate change among growth forms. For example, drought deciduous and evergreen species may differ in distribution on north versus south-facing slopes within a 1 km grid cell.

Whereas previous studies have found significant relationships between habitat loss and niche breadth, range size, and climate anomalies (Thuiller et al. 2005, Broennimann et al. 2006, Williams et al. 2007b), we found only weak relationships between such variables and predicted CSS habitat loss. We find much stronger explanatory relationships between habitat gain and the geographical distribution (latitudinal range) and niche breadth of a species, as well as the severity of climate change across the current distribution of a species. Species with large predicted habitat gains are those typically widespread with large current latitudinal ranges and include *Opuntia littoralis*, *Echinocereus maritimus*, *Rhus integrifolia*, *Mimulus aurantiacus*, *Artemisia californica*, *Acmispon glaber*, *Encelia californica*, and *Agave shawii*. We did find that narrowly distributed species also had greater sensitivity to habitat losses under climate change, but this relationship was only significant for evergreen species under a warmer wetter scenario. As expected, anomalies in future climate were related to CSS species sensitivity to climate change, and had a negative relationship with habitat gain and a positive relationship with habitat loss.

We predict climate change impacts will vary geographically across CSS with two broad

patterns of species habitat change consistent across climate change trajectories: southern habitat contraction and northern habitat expansion. Although precipitation is projected to increase in central and northern California under the warmer wetter future climate scenario, drier conditions are projected for southern California and the Baja California peninsula under both warmer wetter and warmer drier future climate scenarios, likely accounting for the similarity in predicted CSS responses under the two different climate change trajectories. As individual species lose habitat in the south and gain habitat in the north, we predict a high degree community restructuring at both northern and southern extents of CSS. Dispersal will likely play key roles in shaping the trajectory of response to climate change for individual species and communities: offsetting habitat losses projected under climate change for individual species but also facilitating high species turnover and restructuring in CSS communities, particularly along the central coast of California.

The greater dispersal capacities of species with small, wind dispersed seeds (e.g., *Artemisia californica*, *Encelia californica*, *Eriogonum fasciculatum*, *Mimulus aurantiacus*) (Wells 1962), may facilitate the northward expansion of CSS under climate change, however, successful establishment in newly available habitat will depend upon a number of factors. California sage scrub has a dynamic relationship with chaparral and grasslands, which currently occupy northern areas of potential suitable habitat, along with existing patches of CSS. Climate is an important predictor of CSS distribution at regional scales (Riordan and Rundel 2009), but topography, geological substrate, soil, disturbance and species interactions play significant roles in determining local patterns of CSS establishment and distribution (Wells 1962, Harrison et al. 1971, Parsons and Moldenke 1975, Parsons 1976, Kirkpatrick and Hutchinson 1980, Westman 1981b, 1983, Zedler et al. 1983, Keeley and Keeley 1984, Malanson and Westman 1991,

Callaway and Davis 1993, Franklin 1995, Meentemeyer et al. 2001). For example, fire can facilitate the establishment of CSS within chaparral, but too short of a return interval can lead to conversion to exotic grasslands (Keeley and Keeley 1984, Keeley et al. 2005, see review in Rundel 2007). Nitrogen deposition from pollution can further reinforce the conversion of CSS to grasslands (Padgett et al. 1999, Talluto and Suding 2008), and may therefore impede the successful colonization of new habitat by CSS. Large seeded species (e.g., *Aesculus parryi*) with greater dispersal limitation may be unable to successfully track changing climatic conditions. In addition, land use and habitat fragmentation pose formidable barriers to species expansion and limit the extent to which CSS species will realistically expand in range in response to climate change. A more nuanced model of dispersal incorporating the dispersal distances of individual species as well as geographic and anthropogenic barriers to dispersal would help refine the results presented in this study.

Perhaps most significant for CSS conservation are our predictions of considerable biodiversity declines for coastal southern California and northwestern Baja California even under best-case unlimited dispersal scenarios. These regions, particularly northwestern Baja California, have remarkably high floristic diversity and endemism, not just for CSS, but globally (Westman 1981a, Peinado et al. 1995, Riemann and Ezcurra 2005). There is minimal protection for the large number (> 130) of endemic plants in northwestern Baja California (Riemann and Ezcurra 2005), many of which have restricted or local ranges and may be particularly vulnerable to climate change. Our findings further highlight the need to focus conservation efforts within northwestern Baja California.

We also find high potential for diversity and community change at the southern limit of CSS at the mediterranean-climate to Sonoran Desert transition zone. The mediterranean-desert

climate transition zone, which contains many isolated endemics, has been identified as an important refuge of many Tertiary relics (Axelrod 1978, Peinado et al. 1995). Marginal sage scrub communities occurring at this transition contain the ‘trailing edge’ (Thuiller et al. 2008) of many species distributions expected to contract with climate change. Plant populations within this region may not be in equilibrium with climatic conditions and may be more susceptible to climate change impacts. The persistence of species in these communities under climate change may determine the dynamics of the transition zone.

Climate change in coastal southern California and northwestern Baja California will likely compound the high degree of habitat loss and fragmentation from other anthropogenic activities that currently characterize the region. While our analyses focus on climate change, current anthropogenic land use practices across coastal California (Westman 1981a, Minnich and Dezzani 1998, Taylor 2004, Rundel 2007) and northwestern Baja California (Bullock 1999, Escofet and Espejel 1999, Riemann and Ezcurra 2005, Underwood et al. 2009) have already driven substantial conversion of CSS habitat. Therefore, the actual degree of CSS habitat loss will be much greater than our predictions, when factoring in current and future land use.

While species distribution models can provide valuable insight into the potential shifts of species under climate change and subsequent impacts on communities and diversity, a mention of their limitations (Araujo and Guisan 2006) is warranted. The correlative modeling approach used in this study assumes a static relationship between species and their environment, where species are at equilibrium with current climatic conditions (Guisan and Zimmermann 2000, Pearson and Dawson 2003, Guisan and Thuiller 2005). These models do not account for the ability of a species to acclimate or adapt to changing environmental conditions. Nor do they capture the local adaptations to environmental conditions within populations across a species

range which could lead to different relationships with climate and responses to climate change at the limits of a species current distribution (Thuiller et al. 2008, Sork et al. 2010). A large degree of uncertainty is associated with species distribution models, both in the trajectories of future climate change and the modeled response of species (Beaumont et al. 2008). We chose two future scenarios for California climate to reflect two possible trajectories of climate change across our study region. Our results should be interpreted as illustrating the potential impact of climate change on CSS, but should not exclude other possible future scenarios.

In conclusion, we predict a varied response to climate change across the distribution of CSS. Dispersal will be necessary to offset species habitat losses under climate change but may, in turn, lead to increased community-level restructuring. We predict that wide ranging species will have the greatest projected habitat gains under future climate scenarios and succulent species will expand in range under changes of increasing aridity. The mediterranean-desert climate transition zone of the Baja California Peninsula may exhibit a northwards shift, with unknown impacts for the large number of endemics currently distributed within the transition zone and northwards in the mediterranean-climate region of Baja California. Restructuring of CSS communities and CSS diversity declines could have serious implications for the large number of sensitive species within sage scrub. Our findings highlight CSS conservation priorities for both southern California and northwestern Baja California but also bring to light potential concerns for current protected areas: as species shift in distribution to track suitable conditions under climate change, protected areas may not support the species and ecosystems they were originally intended to protect (Araujo et al. 2011). Thus, we advocate for the adoption of an adaptive management approach to CSS conservation, where projections of species and community responses to climate change can be incorporated into management strategies.

Table 2.1. List of California sage scrub species with number of herbarium records used in models, growth habitat, and distribution. Species with a rare, endangered, or threatened status in either California or Baja California are indicated by an asterisk. Distribution abbreviations: NCo = North California Coast, CCo = Central California Coast, SCo = South California Coast, SNF = California Sierra Nevada Foothills, NWBC = Mediterranean-climate Northwestern Baja California, BCD = Baja California Desert. Taxonomy follows Baldwin et al. (2012).

Taxon name	N	Family	Growth Form	Distribution
<i>Acmispon glaber</i>	603	Fabaceae	Drought-deciduous subshrub	CCo, SCo, SNF, NWBC, BCD
<i>Adolphia californica</i> *	90	Rhamnaceae	Drought-deciduous shrub (stem photosynthetic)	SCo, NWBC, BCD
<i>Aesculus parryi</i>	41	Sapindaceae	Drought-deciduous shrub to small tree	NWBC, BCD
<i>Agave shawii</i> *	44	Agavaceae	Succulent shrub (rosette)	SCo, NWBC, BCD
<i>Artemisia californica</i>	242	Asteraceae	Drought-deciduous shrub	CCo, SCo, NWBC, BCD
<i>Bahiopsis laciniata</i>	176	Asteraceae	Drought-deciduous shrub	SCo, NWBC, BCD
<i>Bergerocactus emoryi</i> *	28	Cactaceae	Succulent shrub	SCo, NWBC
<i>Ceanothus verrucosus</i> *	86	Rhamnaceae	Evergreen shrub	SCo, NWBC
<i>Cneoridium dumosum</i>	117	Rutaceae	Evergreen shrub	SCo, NWBC, BCD
<i>Cylindropuntia prolifera</i>	79	Cactaceae	Succulent shrub	SCo, NWBC, BCD
<i>Dudleya edulis</i>	58	Crassulaceae	Succulent perennial	SCo, NWBC
<i>Echinocereus maritimus</i>	44	Cactaceae	Succulent shrub	NWBC, BCD
<i>Encelia californica</i>	204	Asteraceae	Drought-deciduous shrub	CCo, SCo, NWBC, BCD
<i>Ericameria ericoides</i>	85	Asteraceae	Evergreen shrub	CCo, SCo
<i>Eriogonum fasciculatum</i> (coastal vars.)	665	Polygonaceae	Evergreen shrub	CCo, SCo, NWBC, BCD
<i>Ferocactus viridescens</i> *	34	Cactaceae	Succulent shrub	SCo, NWBC
<i>Hazardia squarrosa</i>	223	Asteraceae	Evergreen shrub	CCo, SCo, NWBC, BCD
<i>Hesperoyucca whipplei</i>	226	Agavaceae	Evergreen shrub (rosette)	CCo, SCo, SNF, NWBC, BCD
<i>Isocoma menziesii</i>	313	Asteraceae	Evergreen shrub	CCo, SCo, NWBC, BCD

Table 2.1. Cont.

Taxon name	N	Family	Growth Form	Distribution
<i>Malosma laurina</i>	218	Anacardiaceae	Evergreen shrub	SCo, NWBC, BCD
<i>Mimulus aurantiacus</i>	793	Phrymaceae	Drought-deciduous shrub	NCo, CCo, SCo, SNF, NWBC, SNF
<i>Mirabilis laevis var. crassifolia</i>	289	Nyctaginaceae	Drought-deciduous subshrub	CCo, SCo, NWBC, BCD, SNF
<i>Opuntia littoralis</i>	79	Cactaceae	Succulent shrub	SCo, NWBC, BCD
<i>Ornithostaphylos oppositifolia</i> *	47	Ericaceae	Evergreen shrub	SCo, NWBC
<i>Ptelea aptera</i> *	38	Rutaceae	Drought-deciduous shrub to small tree	SCo, NWBC, BCD
<i>Rhus integrifolia</i>	196	Anacardiaceae	Evergreen shrub	SCo, NWBC, BCD
<i>Ribes speciosum</i>	138	Grossulariaceae	Drought-deciduous shrub	CCo, SCo, NWBC
<i>Rosa minutifolia</i> *	29	Rosaceae	Drought-deciduous shrub	SCo, NWBC
<i>Salvia apiana</i>	305	Lamiaceae	Drought-deciduous shrub	CCo, SCo, NWBC, BCD
<i>Salvia leucophylla</i>	60	Lamiaceae	Drought-deciduous shrub	CCo, SCo, NWBC
<i>Salvia mellifera</i>	325	Lamiaceae	Drought-deciduous shrub	CCo, SCo, NWBC
<i>Salvia munzii</i> *	58	Lamiaceae	Drought-deciduous shrub	SCo, NWBC, BCD
<i>Xylococcus bicolor</i>	189	Ericaceae	Evergreen shrub	SCo, NWBC, BCD

Table 2.2. Median loss in species habitat, shift in elevation, shift in distribution centroid, and change in species richness relative to current modeled richness across the study area under projected climate change (2080). Values reported are medians (range: min to max).

Scenario	Dispersal	Habitat loss (%)	Centroid shift (km)	Elevation shift (m)
Warmer wetter	no	-46.06 (-98.48 to -19.08)	96 (12 to 401)	-11 (-129 to 389)
	yes	-19.01 (-98.48 to 91.86)	162 (12 to 404)	39 (-129 to 243)
Warmer drier	no	-40.27 (-97.36 to -4.7)	62 (8 to 379)	-23 (-280 to 300)
	yes	-2.65 (-95.57 to 118.19)	201 (28 to 458)	15 (-244 to 276)

Table 2.3. Summary table of ANOVAs on CSS habitat change by growth form group. Total habitat change is calculated as the Euclidean distance of percent habitat loss and percent habitat gain. DF = degrees freedom, SS = sum of squares, MS = Mean of squares. Growth form abbreviations: DD = drought-deciduous, EG = evergreen, SUC = succulent. Dispersal scenarios: ND = no dispersal, UD = unlimited dispersal. Significance *P*: NS > 0.1 • > 0.05 > * > 0.01 > ** > 0.001 > *** > 0.

Scenario	Response	Factor	DF	SS	MS	F-ratio	P-value	
Warmer wetter (ND)	Loss	Growth form	2	2377	1188.6	3.93	0.0304	*
		Residuals	30	9068	302.3			
Warmer wetter (UD)	Gain	Growth form	2	4651	2326	3.06	0.0619	•
		Residuals	30	22829	761			
Warmer wetter (UD)	Total change	Growth form	2	97	48.5	0.103	0.903	NS
		Residuals	30	14184	472.8			
Warmer drier (ND)	Loss	Growth form	2	5065	2532.5	9.28	< 0.001	***
		Residuals	30	8188	272.9			
Warmer drier (UD)	Gain	Growth form	2	10469	5235	8.75	0.001	***
		Residuals	30	17948	598			
Warmer drier (UD)	Total change	Growth form	2	1631	815.3	1.92	0.164	NS
		Residuals	30	12724	424.1			

Table 2.4. Mean differences in habitat change between growth form groups (Tukey's HSD Honest Significance Difference test on ANOVA). Growth form abbreviations: DD = drought-deciduous, EG = evergreen, SUC = succulent. Dispersal scenarios: ND = no dispersal, UD = unlimited dispersal. Significance P : NS > 0.10 > • > 0.05 > * > 0.01 > ** > 0.001 > *** > 0.

Scenario	Response	Pair	Mean difference (95% CI)	Significance
Warmer wetter (ND)	Loss	EG-DD	-4.76 (-21.77 to 12.26)	NS
		SUC-DD	18.11 (-1.51 to 37.73)	•
		SUC-EG	22.87 (2.15 to 43.59)	*
Warmer wetter (UD)	Gain	EG-DD	-9.71 (-36.70 to 17.29)	NS
		SUC-DD	23.00 (-8.13 to 54.13)	NS
		SUC-EG	32.71 (-0.17 to 65.59)	•
Warmer drier (ND)	Loss	EG-DD	-1.68 (-17.85 to 14.49)	NS
		SUC-DD	29.54 (10.90 to 48.18)	**
		SUC-EG	31.22 (11.53 to 50.91)	**
Warmer drier (UD)	Gain	EG-DD	-0.14 (-24.08 to 23.79)	NS
		SUC-DD	43.51 (15.91 to 71.11)	**
		SUC-EG	43.65 (14.50 to 72.81)	**

Table 2.5. Bioclimatic variable loadings of the first principal component axis, explaining 44.9% of the climatic variance in current CSS species occurrences.

Bioclimatic variable	PC axis 1
BIO1 Annual mean temperature	0.273
BIO4 Temperature seasonality (SD*100)	-0.515
BIO5 Maximum temperature of warmest month	-0.340
BIO6 Minimum temperature of coldest month	0.524
BIO15 Precipitation seasonality (Coefficient of Variation)	0.310
BIO18 Precipitation of warmest quarter	-0.321
BIO19 Precipitation of coldest quarter	-0.265

Table 2.6. Relationship (Pearson's correlation coefficient) between the niche breadth of a species and bioclimatic variables for different growth forms in CSS. DD = drought-deciduous, EG = evergreen, SUC = succulent. Values in bold indicate variables having the strongest correlation with niche breadth.

Bioclimatic variable	DD	EG	SUC
BIO1 Annual mean temperature	-0.674	-0.086	-0.713
BIO4 Temperature seasonality (SD*100)	0.812	0.814	0.602
BIO5 Maximum temperature of warmest month	0.282	0.693	-0.283
BIO6 Minimum temperature of coldest month	-0.665	-0.689	-0.901
BIO15 Precipitation seasonality (Coefficient of Variation)	-0.099	-0.546	0.137
BIO18 Precipitation of warmest quarter	0.688	0.539	0.724
BIO19 Precipitation of coldest quarter	0.718	0.170	0.820

Table 2.7. Relationship between geographic, niche, and climatic variables and projected CSS habitat change (loss and gain) inferred from multiple regression models. Growth form abbreviations: DD = drought-deciduous, EG = evergreen, SUC = succulent. Significance P : NS > 0.10 > • > 0.05 > * > 0.01 > ** > 0.001 > *** > 0.

Scenario	Growth Form	Latitudinal Range	Niche Breadth	Temp anomalies (annual)	PPT anomalies (annual)	PPT anomalies (summer)	DF	R ² adj.	F	P
Habitat loss										
Warmer wetter	All	NS	NS	Positive ***	NS	NS	1,31	0.324	16.3	***
	DD	NS	NS	Positive **	NS	NS	1,13	0.382	9.64	**
	EG	Negative *	NS	Positive **	NS	NS	2,8	0.594	8.32	*
	SUC	NS	NS	NS	NS	NS	-	-	-	-
Warmer drier	All	NS	NS	Positive ***	NS	Positive *	2,30	0.284	7.36	**
	DD	NS	NS	NS	NS	NS	-	-	-	-
	EG	NS	NS	NS	NS	NS	-	-	-	-
	SUC	NS	Positive *	NS	NS	NS	1,5	0.507	7.17	*
Habitat Gain [†]										
Warmer wetter	All	Positive *	NS	NS	NS	NS	1,30	0.173	7.48	*
	DD	NS	Positive ***	Negative **	Negative *	NS	3,11	0.878	34.6	***
	EG	Positive ***	Negative *	NS	NS	NS	2,7	0.818	21.2	**
	SUC	Positive *	NS	NS	NS	NS	1,5	0.561	8.66	*
Warmer drier	All	Positive **	NS	Negative**	NS	NS	2,29	0.313	8.04	**
	DD	Positive ***	NS	NS	NS	NS	1,13	0.653	27.4	***
	EG	Positive **	Negative*	NS	NS	NS	2,7	0.752	10.1	**
	SUC	Positive *	NS	NS	NS	NS	1,5	0.589	9.59	*

[†]Habitat gain analyses exclude *Rhus integrifolia* (outlier).

Table 2.8. Median species richness (Richness), percent change in species richness relative to current modeled richness (Relative Δ richness), and Jaccard percent community similarity (Similarity) under projected (2080) climate change. Values reported are medians (range: min to max).

Ecoregion	Climate scenario	Dispersal	Richness	Relative Δ richness	Similarity
Central Coast CA	Current	•	8 (0 to 28)	• •	• •
	Warmer wetter	No	7 (0 to 26)	-9 (-100 to 0)	90 (0 to 100)
		Yes	14 (0 to 31)	55 (-100 to 1900)	46 (0 to 100)
	Warmer drier	No	6 (0 to 27)	-11 (-100 to 0)	88 (0 to 100)
		Yes	15 (0 to 32)	53 (-100 to 2400)	36 (0 to 100)
	South Coast CA	Current	•	14 (0 to 33)	• •
Warmer wetter		No	8 (0 to 27)	-38 (-100 to 0)	61 (0 to 100)
		Yes	11 (0 to 28)	-29 (-100 to 900)	50 (0 to 100)
Warmer drier		No	8 (0 to 27)	-35 (-100 to 0)	65 (0 to 100)
		Yes	11 (0 to 30)	-27 (-100 to 1100)	53 (0 to 100)
NW Baja		Current	•	19 (0 to 33)	• •
	Warmer wetter	No	9 (0 to 28)	-41 (-100 to 0)	58 (0 to 100)
		Yes	13 (0 to 31)	-26 (-100 to 1400)	42 (0 to 100)
	Warmer drier	No	9 (0 to 29)	-37 (-100 to 0)	62 (0 to 100)
		Yes	11 (0 to 32)	-31 (-100 to 900)	50 (0 to 100)

Figure 2.1. Study area and herbarium record locations for the 33 modeled CSS shrub species. California Central Coast and South Coast Ecoregions (Baldwin et al. 2012) and Northwestern Baja California Mediterranean-Climate Ecoregion (INEGI et al. 2008) are shown in gray.

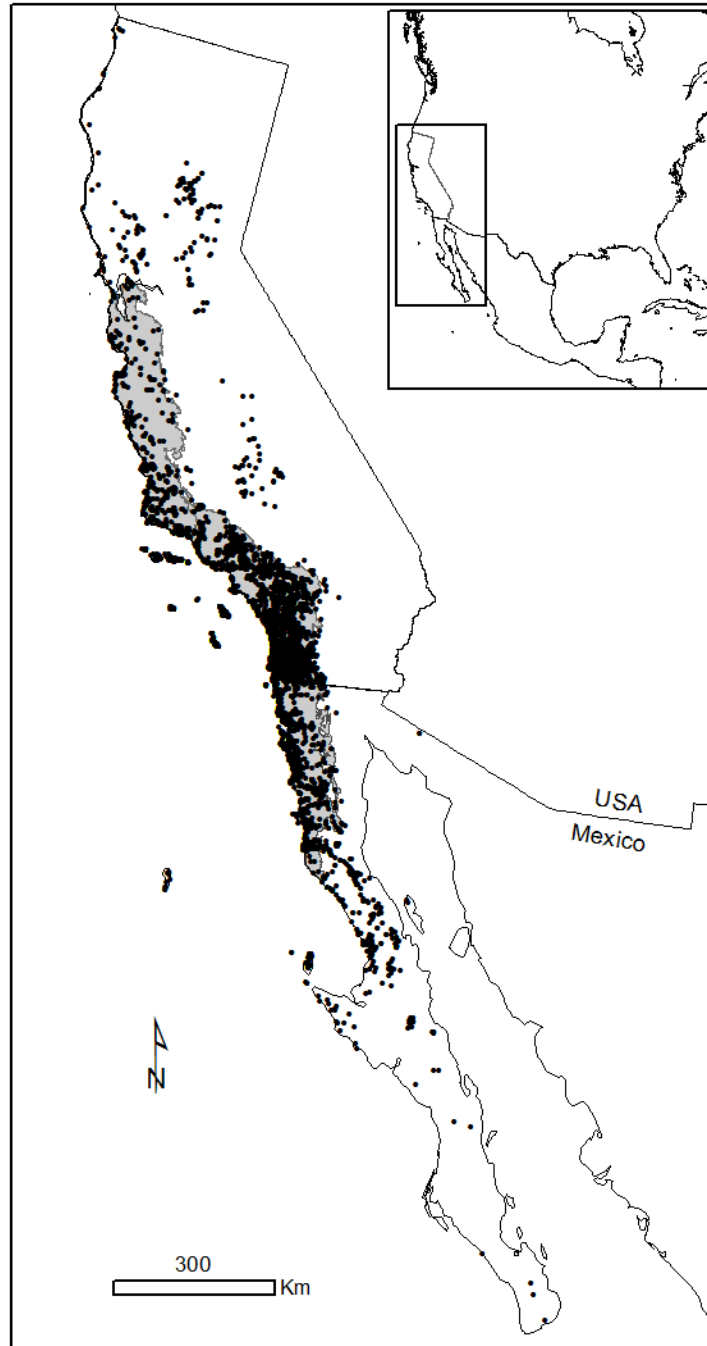


Figure 2.2. Geographic pattern of climate change across current CSS shrub localities for warmer wetter (CCCMA CGC 3.1) and warmer drier (NCAR CCSM 3.0) future (2080) climate scenarios. Anomalies in annual mean temperature (Δ Temperature: future – current) and annual precipitation (Δ PPT: future – current) are plotted against latitude in decimal degrees. Drought-deciduous species shown in light gray, evergreen in dark gray, succulent in black.

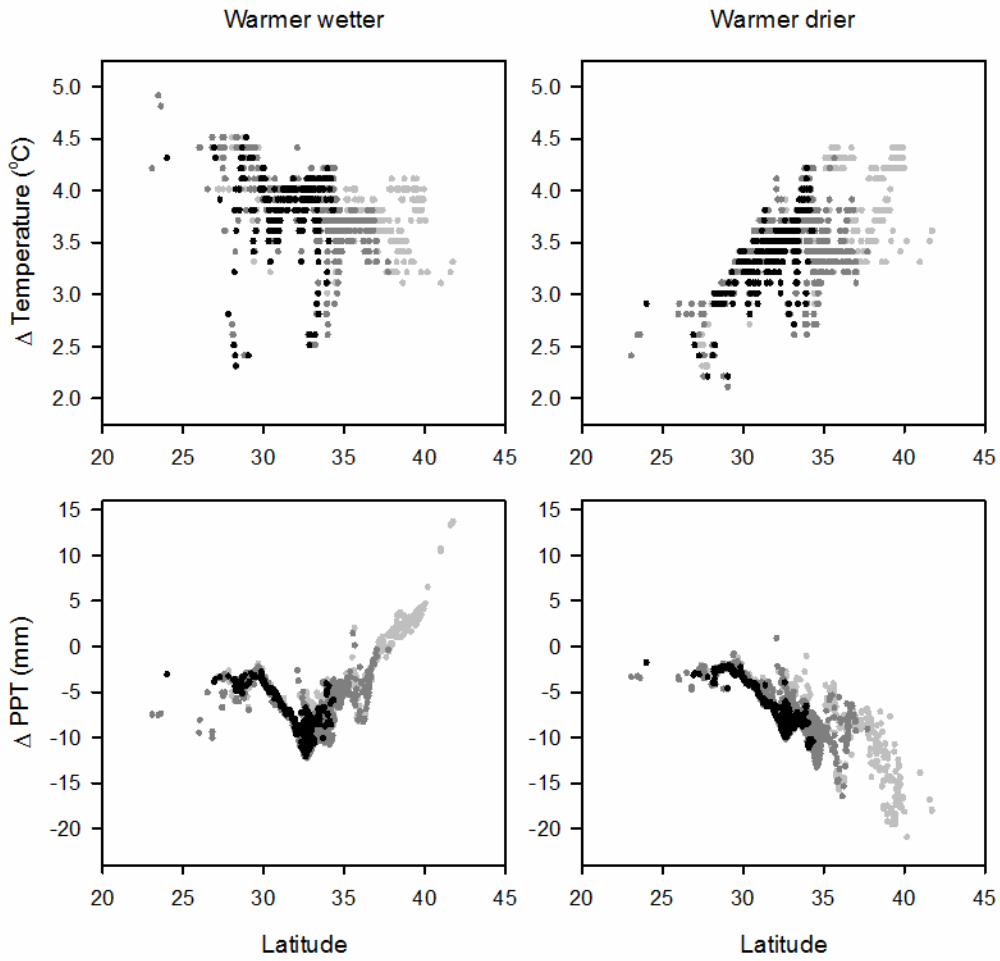


Figure 2.3. Percent habitat loss (top), shift in distribution centroid (middle), and median shift in elevation (bottom) of CSS shrub species under projected (2080) climate change. No dispersal scenarios are shown in dark gray, unlimited dispersal scenarios in light gray.

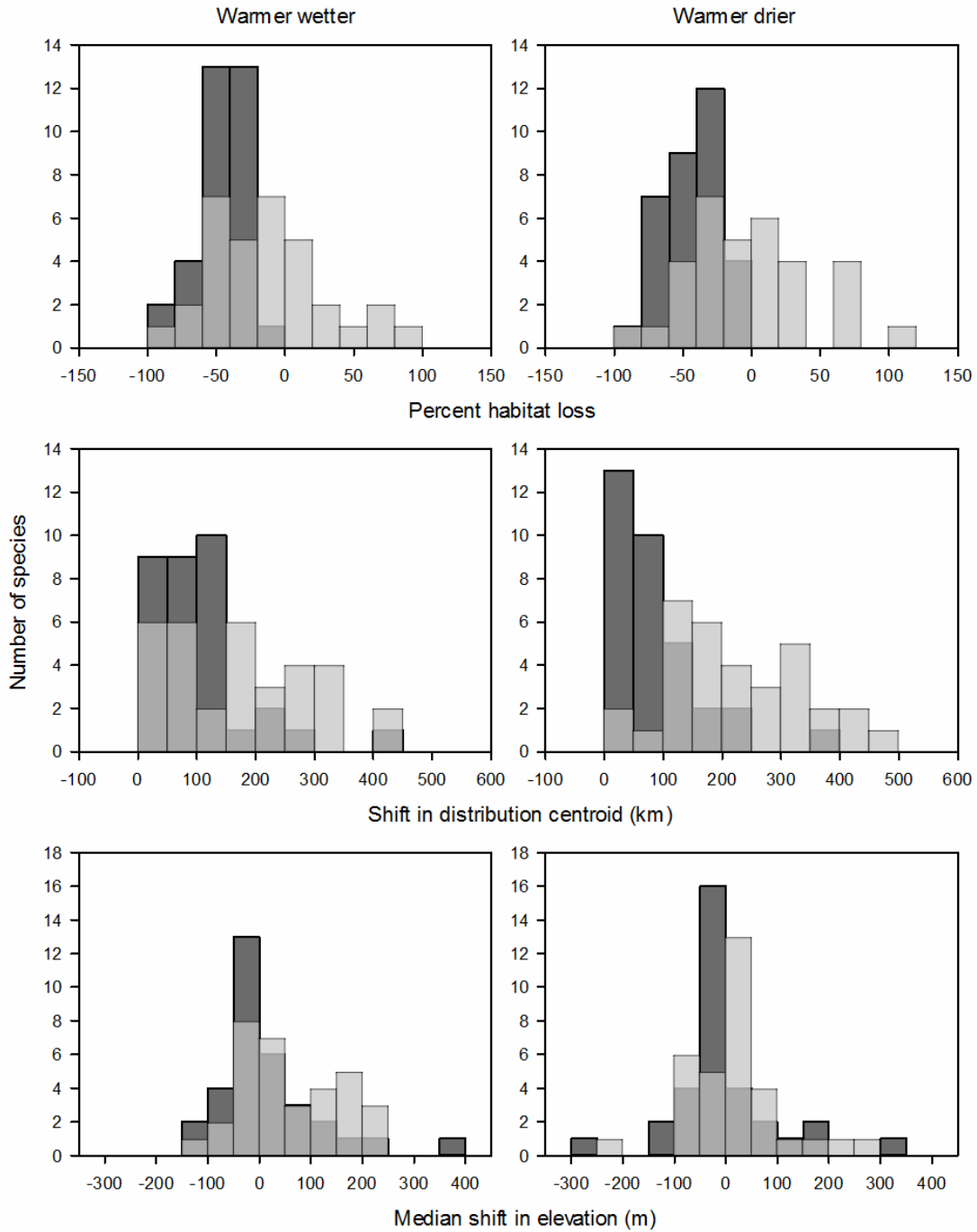


Figure 2.4. Scatter plots of predicted habitat loss versus habitat gain for CSS shrub species under two future climate scenarios. Growth form groups: drought deciduous (open circles), evergreen (gray circles), succulent (black circles). Reference line indicates percent gain = percent loss.

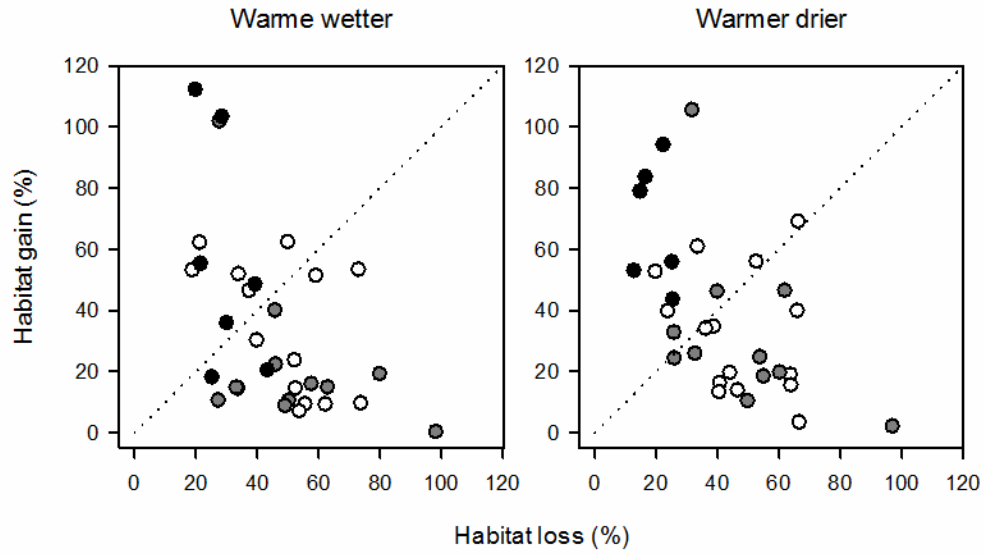


Figure 2.5. Predicted percent habitat loss, percent habitat gain, and total habitat change in habitat under projected (2080) climate change for CSS shrub species by growth form group. Growth forms: DD = drought-deciduous, EG = evergreen, SUC = succulent. Dispersal scenarios: ND = no dispersal, UD = unlimited dispersal. Letters indicate significant differences in habitat change between growth form groups ($P < 0.05$; Tukey's HSD test).

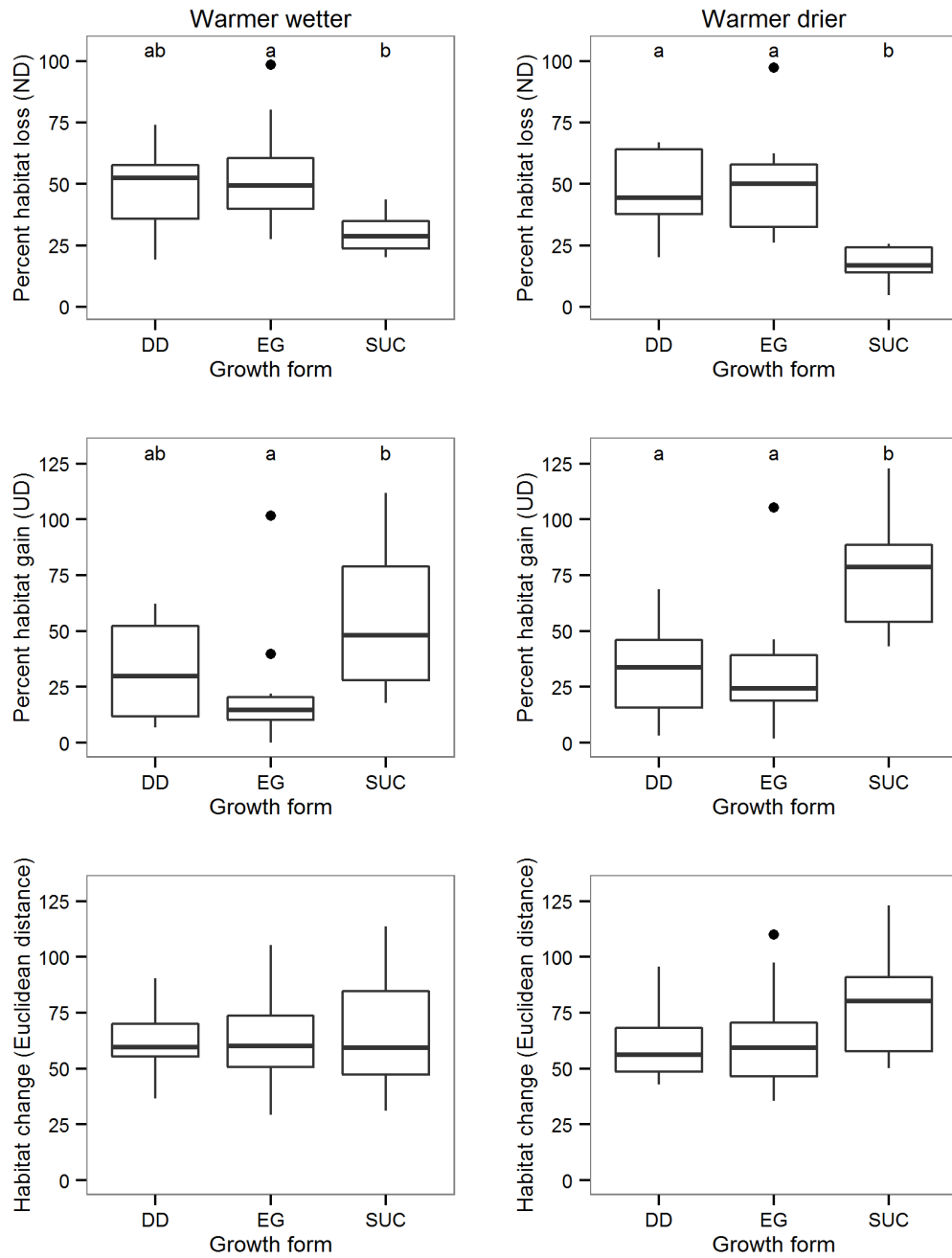
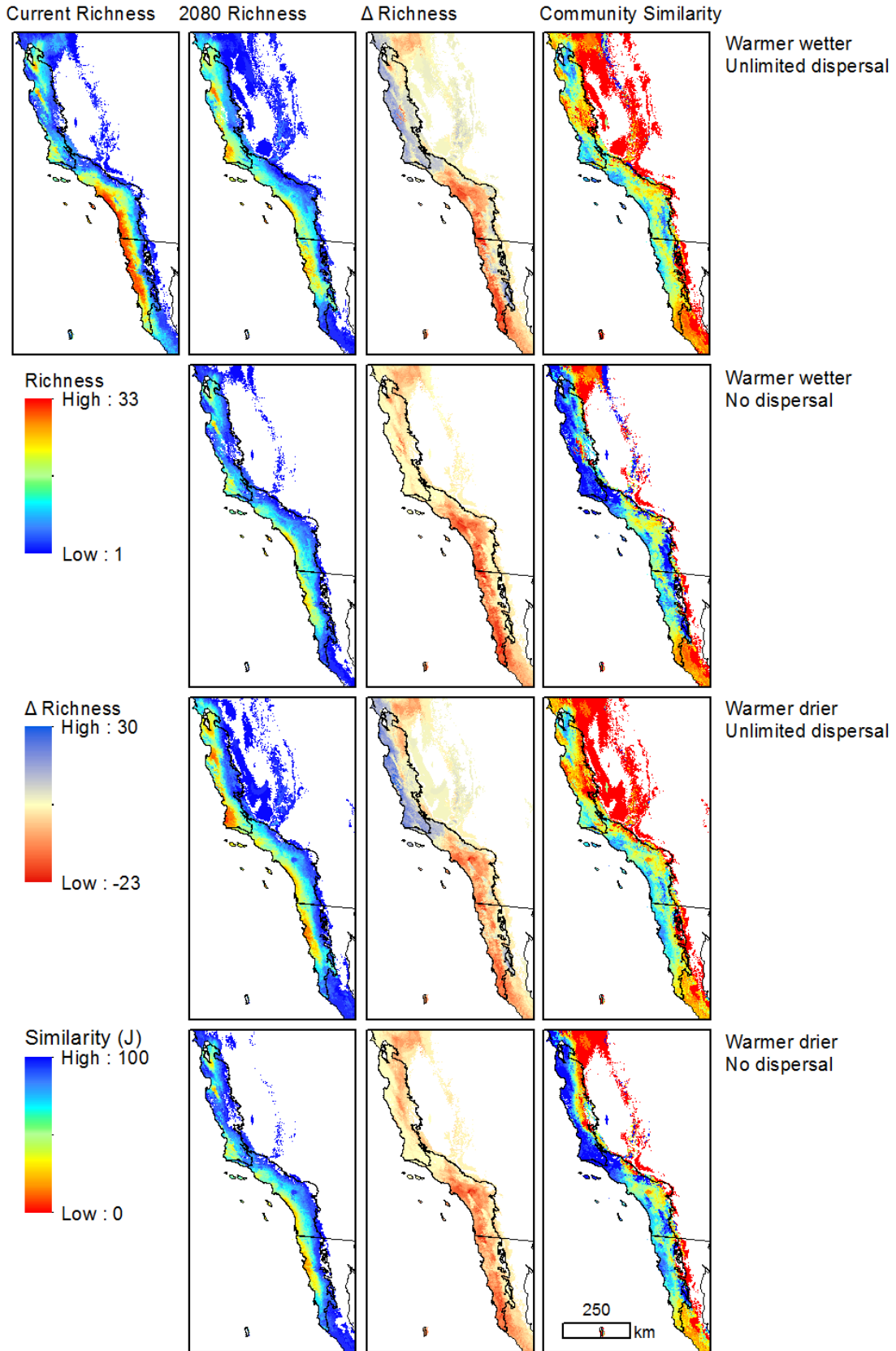


Figure 2.6. Modeled current and future (2080) predicted species richness, change in species richness, and community similarity (Jaccard index) under projected climate. Ecoregions are shown with a black outline.



2.7. Histograms of current (solid lines) and predicted future 2080 (dashed line) species richness by percent land area in each ecoregion; California Central Coast (top), California South Coast (middle), and Northwestern Baja California Mediterranean-climate (bottom) Ecoregions.

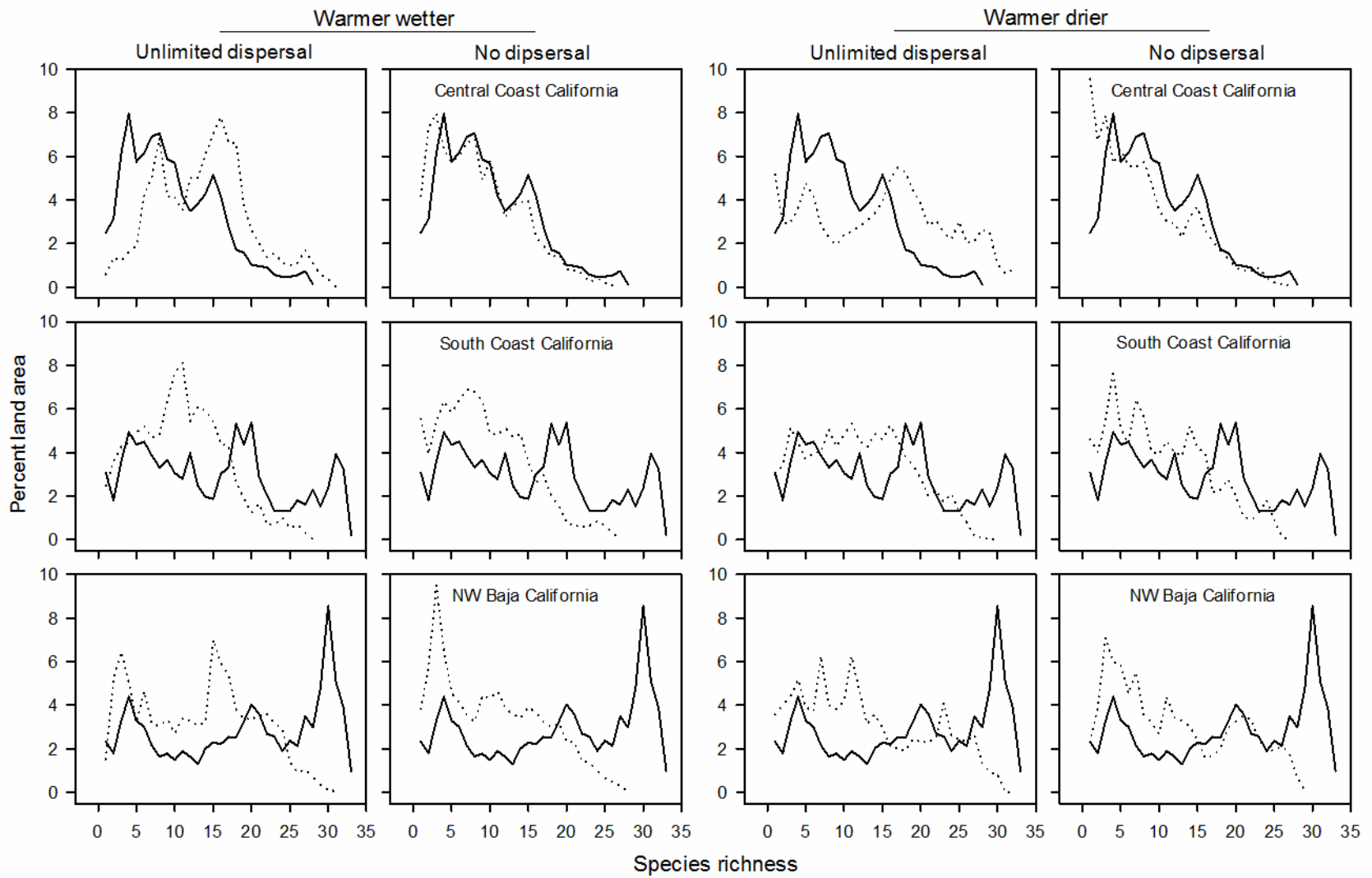
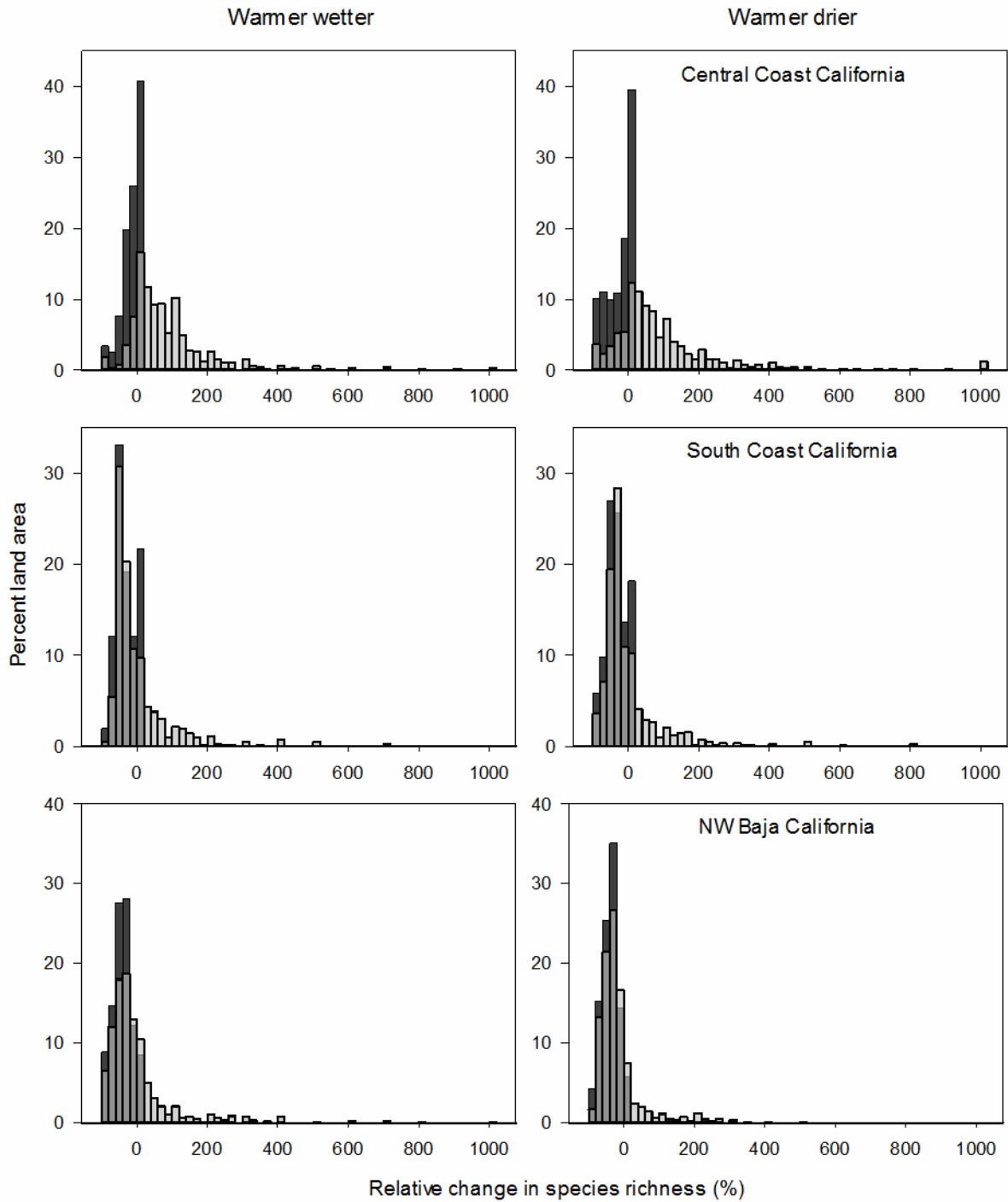


Figure 2.8. Histograms of predicted future (2080) percent change in species richness, relative to current modeled richness, by ecoregion land area assuming no dispersal (dark gray bars) and unlimited dispersal (light gray bars).



Appendix 2.1. Median Maxent model performance (n = 10) and logistic threshold for habitat suitability for CSS species. Overall model performance is measured by the threshold-independent area under the receiver operating characteristic curve (AUC). Model suitability threshold is the maximum training sensitivity plus specificity threshold.

Species	Median AUC (range)	Threshold (range)
<i>Acmispon glaber</i>	0.927 (0.905–0.942)	0.215 (0.1821–0.2381)
<i>Adolphia californica</i>	0.981 (0.916–0.985)	0.0721 (0.0350–0.276)
<i>Aesculus parryi</i>	0.988 (0.962–0.995)	0.0544 (0.0372–0.0637)
<i>Agave shawii</i>	0.989 (0.945–0.996)	0.0772 (0.0367–0.3065)
<i>Artemisia californica</i>	0.957 (0.934–0.976)	0.191 (0.151–0.224)
<i>Bahiopsis laciniata</i>	0.968 (0.925–0.983)	0.108 (0.0985–0.207)
<i>Bergerocactus emoryi</i>	0.989 (0.974–0.999)	0.0437 (0.0281–0.289)
<i>Ceanothus verrucosus</i>	0.988 (0.970–0.995)	0.0931 (0.0476–0.137)
<i>Cneoridium dumosum</i>	0.974 (0.957–0.989)	0.118 (0.0536–0.229)
<i>Cylindropuntia prolifera</i>	0.987 (0.903–0.993)	0.0963 (0.0587–0.153)
<i>Dudleya edulis</i>	0.985 (0.973–0.994)	0.233 (0.155–0.256)
<i>Echinocereus maritimus</i>	0.986 (0.972–0.991)	0.209 (0.194–0.226)
<i>Encelia californica</i>	0.969 (0.955–0.979)	0.119 (0.0985–0.133)
<i>Ericameria ericoides</i>	0.991 (0.985–0.995)	0.0910 (0.0602–0.110)
<i>Eriogonum fasciculatum</i>	0.923 (0.913–0.945)	0.241 (0.217–0.261)
<i>Ferocactus viridescens</i>	0.992 (0.978–0.998)	0.0367 (0.0294–0.149)
<i>Hazardia squarrosa</i>	0.960 (0.923–0.967)	0.124 (0.106–0.163)
<i>Hesperoyucca whipplei</i>	0.933 (0.880–0.952)	0.246 (0.165–0.273)
<i>Isocoma menziesii</i>	0.958 (0.948–0.962)	0.132 (0.0884–0.162)
<i>Malosma laurina</i>	0.964 (0.949–0.975)	0.103 (0.0603–0.136)
<i>Mimulus aurantiacus</i>	0.904 (0.890–0.922)	0.256 (0.211–0.274)
<i>Mirabilis laevis var. crassifolia</i>	0.944 (0.922–0.952)	0.154 (0.136–0.184)
<i>Opuntia littoralis</i>	0.978 (0.934–0.986)	0.103 (0.0837–0.166)
<i>Ornithostaphylos oppositifolia</i>	0.988 (0.982–0.994)	0.280 (0.254–0.366)
<i>Ptelea aptera</i>	0.990 (0.976–0.996)	0.170 (0.100–0.190)
<i>Rhus integrifolia</i>	0.977 (0.970–0.981)	0.118 (0.0587–0.173)
<i>Ribes speciosum</i>	0.977 (0.968–0.984)	0.0942 (0.0504–0.276)
<i>Rosa minutifolia</i>	0.991 (0.953–0.998)	0.167 (0.135–0.240)
<i>Salvia apiana</i>	0.948 (0.939–0.967)	0.232 (0.214–0.262)
<i>Salvia leucophylla</i>	0.982 (0.923–0.993)	0.0826 (0.0710–0.238)
<i>Salvia mellifera</i>	0.965 (0.946–0.972)	0.136 (0.113–0.195)
<i>Salvia munzii</i>	0.989 (0.975–0.994)	0.106 (0.0795–0.120)
<i>Xylococcus bicolor</i>	0.977 (0.963–0.986)	0.104 (0.0848–0.125)

Appendix 2.2. Modeled current climatically suitable habitat (Current Area) and future (2080) percent habitat loss, percent habitat gain and percent net habitat change under projected climate change. Species habitat loss and gain were calculated from no dispersal and unlimited dispersal scenarios, respectively. Net habitat change corresponds to unlimited dispersal scenarios.

Species	Current Area (km ²)	Warmer wetter			Warmer drier		
		Loss	Gain	Net change	Loss	Gain	Net change
<i>Acemispom glaber</i>	90882	-19.08	52.92	33.84	-24.10	39.49	15.38
<i>Adolphia californica</i>	47004	-74.06	9.33	-64.73	-64.08	18.64	-45.44
<i>Aesculus parryi</i>	47182	-55.84	9.01	-46.83	-46.85	13.62	-33.24
<i>Agave shawii</i>	54301	-39.55	48.19	8.64	-16.85	83.37	66.52
<i>Artemisia californica</i>	51006	-21.55	61.89	40.34	-20.05	52.39	32.34
<i>Bahiopsis laciniata</i>	66141	-52.43	23.42	-29.01	-39.10	34.40	-4.70
<i>Bergerocactus emoryi</i>	12845	-21.79	55.06	33.27	-15.07	78.68	63.61
<i>Ceanothus verrucosus</i>	23851	-63.13	14.53	-48.61	-60.59	19.39	-41.19
<i>Cneoridium dumosum</i>	36549	-50.51	10.19	-40.33	-32.99	25.59	-7.41
<i>Cylindropuntia prolifera</i>	27492	-30.29	35.59	5.30	-25.46	55.53	30.08
<i>Dudleya edulis</i>	29063	-43.60	20.15	-23.45	-25.69	43.21	17.52
<i>Echinocereus maritimus</i>	23381	-28.69	103.01	74.31	-4.70	122.88	118.19
<i>Encelia californica</i>	52507	-34.17	51.66	17.49	-33.77	60.61	26.84
<i>Ericameria ericoides</i>	14678	-27.54	10.29	-17.25	-26.14	32.46	6.32
<i>Eriogonum fasciculatum</i>	101166	-57.91	15.66	-42.24	-55.27	18.15	-37.12
<i>Ferocactus viridescens</i>	27281	-25.47	17.86	-7.61	-13.10	52.73	39.63
<i>Hazardia squarrosa</i>	83089	-49.27	8.55	-40.73	-50.18	10.03	-40.15
<i>Hesperoyucca whipplei</i>	83246	-46.31	22.06	-24.25	-54.18	24.41	-29.77
<i>Isocoma menziesii</i>	75557	-33.45	14.44	-19.01	-26.24	24.05	-2.19
<i>Malosma laurina</i>	67739	-46.06	39.67	-6.39	-40.27	45.84	5.57
<i>Mimulus aurantiacus</i>	116088	-50.15	62.11	11.97	-66.63	68.76	2.14
<i>Mirabilis laevis</i> var. <i>crassifolia</i>	84400	-59.33	51.08	-8.25	-52.94	55.69	2.75
<i>Opuntia littoralis</i>	39924	-20.08	111.94	91.86	-22.67	93.85	71.18
<i>Ornithostaphylos oppositifolia</i>	19692	-98.48	0.00	-98.48	-97.36	1.79	-95.57
<i>Ptelea aptera</i>	21291	-62.46	9.00	-53.46	-66.94	3.18	-63.76
<i>Rhus integrifolia</i>	34323	-27.91	101.55	73.64	-32.03	105.22	73.19
<i>Ribes speciosum</i>	54151	-33.85	14.13	-19.72	-41.07	15.95	-25.12
<i>Rosa minutifolia</i>	22150	-53.95	6.72	-47.23	-40.87	13.05	-27.82
<i>Salvia apiana</i>	60772	-73.31	53.09	-20.22	-66.37	39.51	-26.86
<i>Salvia leucophylla</i>	86527	-40.09	29.92	-10.18	-64.29	15.20	-49.09
<i>Salvia mellifera</i>	62394	-37.57	46.09	8.52	-36.45	33.80	-2.65
<i>Salvia munzii</i>	29767	-52.71	14.14	-38.57	-44.33	19.33	-25.00
<i>Xylococcus bicolor</i>	42323	-80.14	18.92	-61.22	-62.31	46.14	-16.17

Appendix 2.3. Predicted shifts in the median elevation (m) and geographic centroid (km) of suitable habitat under projected climate change (2080) assuming no dispersal (ND) and unlimited dispersal (UD) scenarios.

Species	Median elevation shift (m)				Centroid shift (km)			
	Warmer wetter		Warmer drier		Warmer wetter		Warmer drier	
	ND	UD	ND	UD	ND	UD	ND	UD
<i>Acmispon glaber</i>	27	-2	67	47	55	168	20	177
<i>Adolphia californica</i>	-34	-56	-40	-76	210	297	193	346
<i>Aesculus parryi</i>	-26	21	-20	4	237	228	228	297
<i>Agave shawii</i>	79	129	30	33	150	249	61	310
<i>Artemisia californica</i>	-5	119	-26	15	74	147	34	207
<i>Bahiopsis laciniata</i>	-36	-14	-25	-18	142	260	126	308
<i>Bergerocactus emoryi</i>	-29	39	-18	6	62	55	39	162
<i>Ceanothus verrucosus</i>	-105	-97	-108	-97	96	162	115	210
<i>Cneoridium dumosum</i>	-39	-48	-58	-70	21	45	53	144
<i>Cylindropuntia prolifera</i>	-19	51	-11	35	144	151	125	256
<i>Dudleya edulis</i>	16	74	-77	-95	12	43	35	158
<i>Echinocereus maritimus</i>	54	159	7	33	104	152	17	111
<i>Encelia californica</i>	-21	24	-28	9	176	334	174	403
<i>Ericameria ericoides</i>	7	19	22	41	19	46	49	151
<i>Eriogonum fasciculatum</i>	212	226	105	4	41	71	30	165
<i>Ferocactus viridescens</i>	-18	24	-15	17	19	28	8	119
<i>Hazardia squarrosa</i>	31	152	-2	73	29	24	27	36
<i>Hesperoyucca whipplei</i>	170	166	180	120	28	64	60	118
<i>Isocoma menziesii</i>	3	56	10	77	106	88	90	115
<i>Malosma laurina</i>	-95	-47	-71	-20	269	404	228	391
<i>Mimulus aurantiacus</i>	125	210	-22	76	102	304	86	458
<i>Mirabilis laevis</i> var. <i>crassifolia</i>	14	186	-23	154	143	277	119	305
<i>Opuntia littoralis</i>	-19	100	-30	46	96	294	91	310
<i>Ornithostaphylos oppositifolia</i>	-129	-129	-280	-244	401	401	379	412
<i>Ptelea aptera</i>	-59	-34	-40	-48	130	195	45	77
<i>Rhus integrifolia</i>	-5	31	-37	15	86	317	98	380
<i>Ribes speciosum</i>	-26	-30	-25	-21	110	165	97	201
<i>Rosa minutifolia</i>	-53	-34	-80	-85	91	96	109	164
<i>Salvia apiana</i>	389	174	300	213	53	308	39	226
<i>Salvia leucophylla</i>	122	243	189	276	28	12	47	28
<i>Salvia mellifera</i>	83	119	54	87	43	127	32	141
<i>Salvia munzii</i>	-11	49	-35	-2	83	93	62	139
<i>Xylococcus bicolor</i>	-80	-47	-111	-80	105	226	99	293

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CHAPTER 3

RELATIVE IMPACTS OF FUTURE LAND USE AND CLIMATE CHANGE ON A THREATENED ECOSYSTEM, CALIFORNIA SAGE SCRUB, IN A RAPIDLY EXPANDING URBAN AREA

ABSTRACT

The combined impacts of climate change and land use are projected to drive unprecedented rates of environmental change and biodiversity loss this century, particularly in highly diverse mediterranean-climate regions. Given the rapidly growing human populations in these systems; land use may pose a more immediate threat to biodiversity than climate change, however, few studies address the relative impacts of both drivers. Focusing on California sage scrub (CSS), a plant association of considerable diversity and threatened status in the mediterranean-climate California Floristic Province, we assess the extent to which habitat loss driven by future land use versus climate change will jeopardize key CSS species and alter CSS biodiversity patterns. To test whether the degree of threat posed by land use and climate change will vary temporally and spatially across CSS, we compare habitat loss and diversity impacts at two time intervals (mid- and late-century) in two ecoregions in California (Central Coast and South Coast). For individual CSS species, the degree of threat posed by climate change relative to land use will depend upon dispersal scenario with consistent patterns predicted for both mid and late century. We find land use and climate change pose similar threats under assumptions of no dispersal, but land use poses a significantly greater future threat under assumptions of

unlimited dispersal, where northern habitat expansion driven by climate change will offset some habitat losses from both drivers. Our models show impacts will vary spatially between Central and South Coast California Ecoregions. In the South Coast, we find notably high losses in habitat and diversity from both land use and climate change even under best-case, unlimited dispersal scenarios, whereas we find much of the Central Coast will experience gains in CSS habitat and diversity under unlimited dispersal scenarios. Furthermore, regions of the South Coast that are currently intact but projected to undergo future anthropogenic land use conversion will also have disproportionately high losses in CSS species richness driven by climate change. These findings highlight the potential for land use and climate change to have compounding negative impacts on CSS in southern California and emphasize the necessity to include analyses of both drivers in conservation and resource management planning.

INTRODUCTION

The combined impacts of climate change and land use are projected to drive unprecedented rates of environmental change and biodiversity loss this century. Mediterranean-climate regions are at particular risk, with land use followed by climate change predicted to cause among the highest biodiversity losses observed world-wide by 2100 (Sala et al. 2000). These global biodiversity hotspots (Myers et al. 2000) coincide with dense, rapidly growing human populations, which threaten the considerable diversity and endemism that characterize mediterranean-climate systems (Underwood et al. 2009). While many studies focus upon projected climate change impacts this century (Midgley et al. 2002, Fitzpatrick et al. 2008, Loarie et al. 2008, Yates et al. 2010, Farley et al. 2012), land use change may pose a more immediate threat to biodiversity than climate change, potentially driving greater short-term

impacts. Very few studies, however, address the relative impacts of both drivers (but see Dirnbock et al. 2003, Thuiller et al. 2006, Kulakowski et al. 2011, Barbet-Massin et al. 2012, Jongsomjit et al. 2012). Given the high rates of both projected land use and climate change in mediterranean regions, assessing the potential impacts of both drivers will be necessary for effective protection of biodiversity this century.

Focusing on California sage scrub (CSS), a plant association of considerable diversity, endemism, and threatened status in the mediterranean-climate California Floristic Province, we investigate the relative impacts of future land use and climate change on CSS habitat suitability and diversity. Worldwide, mediterranean scrub habitats, such as CSS, rank among the most heavily converted but least protected biomes (Hoekstra et al. 2005). The mediterranean-climate region in California has the greatest the urbanization and population growth of all five mediterranean regions (Underwood et al. 2009). California's current 37.5 million population is expected to grow to between 43.8 and 147.7 million by 2100 (Sanstad et al. 2011). Currently, nearly 25% of the state's > 6,500 native plant taxa have a rare, threatened, or endangered status on federal and/or state agency lists, primarily as a result of anthropogenic impacts including habitat degradation and destruction (CNPS 2012).

Within California, CSS coincides with areas of high human impact, occurring primarily in coastal and semiarid interior regions of southern California but also in scattered patches along the central California coast (Epling and Lewis 1942, Westman 1983, Rundel 2007). The coastal counties of southern California containing CSS (Ventura, Los Angeles, Orange, and San Diego counties) also house nearly half (45%) of the state's population, yet only account for seven percent of the state's total land area (CA-DOF 2011). Land development combined with habitat conversion to annual grasses driven by anthropogenic practices have caused widespread loss and

fragmentation of CSS, with as little as 10% of its original extent in the state currently intact (Westman 1981a, Minnich and Dezzani 1998, Taylor 2004, Rundel 2007, Talluto and Suding 2008). High land values and development pressure in the region continue to make the conservation of CSS challenging (Feldman and Jonas 2000). With rapidly expanding human population in southern California, future land use change poses an immediate threat to CSS (Syphard et al. 2007).

Climate change will likely drive additional habitat loss in CSS while exacerbating existing threats, including those from land use. Climate in California is expected shift substantially, with general circulation models (GCMs) predicting temperature increases of 1.35°C to 5.8°C statewide by the end of the century (Hayhoe et al. 2004). Dramatic range losses are predicted for as many as two-thirds of the endemic species of California, which make up over 25% of the state's flora (Loarie et al. 2008). Additionally, climate change is expected to drive the contraction and replacement of mediterranean-climate conditions with warmer and drier conditions along coastal areas of southern California and northwestern Baja California (Klausmeyer and Shaw 2009, Ackerly et al. 2010), areas of high CSS diversity and endemism (Epling and Lewis 1942, Westman 1981a, 1983, Rundel 2007). Climate change may cause considerable shifts in diversity patterns as individual species respond to the expansion, contraction, and replacement of mediterranean climates with novel climates (Williams et al. 2007a, Stralberg et al. 2009).

Given the potential threat future land use and climate change pose to CSS and its large number of associated threatened or sensitive species (O'Leary 1990, DeSimone 1995), successful CSS conservation will need to prioritize management efforts depending upon the relative impacts of both drivers. With high population growth and current anthropogenic conversion in coastal

southern California, land use may pose a more immediate threat to CSS than climate change. The spatial pattern of the magnitude of habitat loss projected under each driver may also vary geographically, which will influence patterns of CSS distribution and diversity, with implications for conservation and management. Species distribution models, which define a species range with respect to climate, land use, topography, and other predictive variables (Guisan and Zimmermann 2000, Guisan and Thuiller 2005), are valuable tools for predicting species and biodiversity impacts under environmental change (Pearson and Dawson 2003, Araujo et al. 2004, Thomas et al. 2004, Williams et al. 2007a). Such climate-based species distribution models have recently been shown to provide important information on habitat requirements of CSS species (Riordan and Rundel 2009).

Using a species distribution modeling framework, we investigate the relative threat of habitat loss from projected land use and climate change on CSS. We assess the extent to which habitat loss driven by future land use versus climate change will jeopardize key CSS shrub species and alter CSS biodiversity patterns. To test whether the degree of threat posed by land use and climate change will vary temporally and spatially across CSS, we compare habitat loss and diversity impacts at two time intervals (mid- and late-century) in two ecoregions in California (Central Coast and South Coast).

METHODS

Study system

California sage scrub is a unique plant association characterized by a diverse, herbaceous understory dominated by drought-deciduous species (e.g., *Salvia*) with a variable component of evergreen and succulent shrubs. California sage scrub is distributed in various community

compositions along the coast from Santa Barbara County in southern California, USA southwards to El Rosario at 30° N latitude in northwestern Baja California, Mexico, with scattered patches along the central California coast and the semi-arid interior of southern California (Shreve 1936, Epling and Lewis 1942, Westman 1983, Rundel 2007). The southern limit of CSS in Baja California marks the southern extent of mediterranean-type climate in North America and the transition to more arid, desert conditions (Shreve 1936). California sage scrub has high conservation priority, providing habitat for over 100 plant and animal species currently considered threatened, endangered, or of special conservation concern (O'Leary 1990, DeSimone 1995). We selected 20 dominant shrub species for analysis (Table 3.1) that collectively span the entire distributional range of CSS, from the San Francisco Bay Area in California to El Rosario in Baja California.

Current and future land cover-land use

We obtained current (2005) and projected future (2050 and 2080) land use-land cover scenarios for California from the LandCarbon Project of the United States Geological Survey (USGS) (http://www.usgs.gov/climate_landuse/land_carbon). The LandCarbon project has developed spatially explicit, high resolution (250 m) land use projections for 84 ecoregions across the conterminous United States that follow the future socio-economic scenarios outlined by the Special Report on Emission Scenarios (SRES) of the Intergovernmental Panel on Climate Change IPCC (Sleeter et al. 2012). We selected land use-land cover projections under the SRES A1B scenario, a future characterized by rapid economic growth, global population that peaks in mid-century and declines thereafter, rapid technological innovation, balanced energy sources, and active management of resources (Meehl et al. 2007). Under this scenario, projected urban

growth is high, particularly in coastal areas and near urban centers, and large increases in biofuel and food production drive large expansions in agricultural lands (Sleeter et al. 2012). This scenario represents just one possible storyline in a range of future demographic change, economic development, and technological change driving future emissions and subsequent climate change. The LandCarbon projections categorize land cover into 17 categories with five categories of human land use; developed, agriculture, mechanically disturbed (National Forest or private), mining, and hay/pasture; which we include as a single anthropogenic land use category in our study.

We focus our analysis of land use change patterns in two California ecoregions defined by Baldwin et al. (2012): the Central Coast Ecoregion (designated Central Western California region) and the South Coast Ecoregion (designated Southwestern California region) (Fig. 3.1). The Central Coast Ecoregion includes the San Francisco Bay Area at its northern limit, the central California coastline, the inner and other South Coast Ranges, and is bounded by the Santa Ynez Mountains in Santa Barbara County to the south where it borders the South Coast Ecoregion. The South Coast Ecoregion includes the southern California coastline from Point Conception to the U.S.-Mexico border, the Channel Islands, the Transverse Ranges, and the Peninsular Ranges.

Species distribution models

We modeled current and future climatically suitable habitat for CSS species from herbarium record occurrence and climate data using Maxent version 3.3.3 (Phillips et al. 2006), a maximum-entropy modeling algorithm. Maxent, which calculates probability distributions based on incomplete information, does not require absence data and has high performance with

spatially biased data, making it appropriate for modelling species distributions based on presence-only herbarium records (Elith et al. 2006, Phillips et al. 2006, Loiselle et al. 2008). In addition, Maxent is particularly useful for modeling CSS, where current fragmentation patterns may reflect anthropogenic absences rather than environmental limits.

We obtained occurrence localities of 20 dominant CSS species (Figure 3.1, Table 3.1) occurring in both California and Baja California from the following herbarium databases: the Consortium of California Herbaria (CCH; <http://ucjeps.berkeley.edu/consortium>), the Southwest Environmental Information Network (SEINet; <http://swbiodiversity.org/seinet>), the Global Biodiversity Informatics Facility (GBIF; <http://www.gbif.org>), the San Diego Natural History Museum's Baja Flora (<http://www.sdnhm.org>), and the Red Mundial de Información sobre Biodiversidad (REMIB; http://www.conabio.gob.mx/remib/doctos/remib_esp.html). Prior to modeling, we mapped all records to identify and exclude cultivated plants, errors in georeferencing, obvious misidentifications, and duplicate collections. Only species collected from 1950 to present were retained for modeling, as earlier occurrence records may represent climates that do not reflect current climate conditions.

We obtained current (1950-2000) climate data from Worldclim (<http://www.worldclim.org>), a set of 19 bioclimatic variables derived from weather station monthly mean temperature and precipitation data (Hijmans et al. 2005). We selected seven bioclimatic variables minimizing correlations among variables, maximizing contribution to model predictions, and representing annual climate trends, seasonality and extremes: annual mean temperature, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation seasonality, precipitation of the warmest quarter, and precipitation of the coldest quarter.

We selected future climate scenarios to represent two possible trajectories of climate change in California under the SRES A1B storyline: (1) a warmer wetter future (CCCMA CGC 3.1) and (2) a warmer drier future (NCAR CCSM 3.0). We downloaded downscaled climate data from the climate change program of the International Center for Tropical Agriculture (CIAT; <http://www.ccafs-climate.org/data>), which has downscaled original global circulation model (GCM) output data from the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) (Meehl et al. 2007). We represent future climate at two time steps created each from 30 year averages, one mid-century (2050s: 2040-2069) and one late-century (2080s: 2070-2100). All climate data, current and future, were at 30-arcsec (ca. 1 km) spatial resolution.

We modeled the current climate-species relationships in Maxent using all herbarium records to train each species model, then projected these relationships onto future climate layers at two time periods, 2050s and 2080s. For each species model, the same set of 10,000 background pixels selected randomly over the study area were used as “pseudo absences,” the maximum set of iterations was 500, the convergence threshold was set to 10^{-5} , and regularization was set to “auto” allowing Maxent to set the amount of regularization automatically based on our locality and environmental data (Phillips et al. 2006). We used 10-fold cross-validation to replicate model runs and estimate evaluation statistics for each species. We measured overall model performance using the area under the receiving operator characteristics curve (AUC), which ranges from 0.5 (random prediction) to 1 (maximum prediction) and can be interpreted as the probability that a presence site is ranked above a random background site when using presence-only data (Phillips et al. 2006).

We created binary current and future habitat maps (0 = unsuitable, 1 = suitable) from

Maxent's logistic output using the maximum sensitivity plus specificity threshold (Liu et al. 2005). We assumed two different future dispersal scenarios, a best-case, unlimited dispersal scenario where species can colonize any future suitable habitat, and a worst-case, no dispersal scenario where species cannot disperse to future suitable habitat falling outside of modeled currently suitable habitat. We overlaid current and future habitat maps with current and projected land use data to estimate the percent of modeled current suitable habitat lost to anthropogenic land use and climate change separately, as well as combined. We assumed a complete loss of sage scrub species in all areas of anthropogenic land use (developed, mechanically disturbed, mining, agriculture, and hay/pasture). In order to estimate future changes in CSS diversity we overlaid individual modeled species habitat maps, assuming species presence in areas predicted as suitable, to create potential species richness maps under each climate change and dispersal scenario. We limited our analyses of habitat loss to California, where we have spatially explicit information for both current and projected future land use. All species models, however, are based upon the full range of location data (California and Baja California). All spatial analyses and model visualizations were performed in ArcMap 10 (ESRI, Redlands, CA, USA).

RESULTS

Land use-land cover change in coastal California

This century, anthropogenic land use in the Central and South Coast Ecoregions of California is predicted to increase considerably from currently high levels (Fig. 3.2). Current (2005) land use maps show anthropogenic surfaces already cover 16.25% of Central Coast and 25.25% of South Coast Ecoregions. The conversion of natural land covers to anthropogenic land

uses will increase this century at similar rates across the regions, just over a 1% yr⁻¹ conversion through 2050, slowing to 0.65% yr⁻¹ (Central Coast) and 0.44% yr⁻¹ (South Coast) from 2050 to 2080 (Table 3.2). By 2080, anthropogenic land use will cover an estimated 7,947 km² (28.71%) of the Central Coast and 13,190 km² (41.91%) of the South Coast Ecoregions. Land development and agriculture are the greatest drivers of projected anthropogenic land use change. In the Central Coast, developed areas will increase by 2,981 km² (118%) from 2005 to 2080, covering 16.73% of the region's land area and agriculture will increase by 927 km² (56.8%), covering 7.80% of the region's land area (Fig 3.3.). In the South Coast, developed areas will increase by 5,395 km² (87.02%) between 2005 and 2080, covering 36.83% of the region's land area. South Coast agriculture is projected to remain relatively constant, covering ~4% of the ecoregion's land area in 2005 and 2080, with agricultural increases offset by conversion to developed areas (Table 3.3). Projected conversion to hay and pasture will also contribute to anthropogenic land use change in both regions, but to a lesser extent (Table 3.3). Much of the projected anthropogenic land use change in the Central and South Coast will be at the expense of grassland, and more significantly to CSS, shrubland cover (Table 3.3, Appendix 3.1). Shrubland loss will be greatest in the South Coast with a projected decline of 3,750 km² (26.4% loss) by 2080, 2,131 km² of which will be converted to developed land, the greatest type of projected land cover/use change in the ecoregion (Table 3.3). While Central Coast shrublands are also projected to decline considerably, 847 km² (14% loss) from 2005 to 2080, their conversion to development, agriculture, and hay/pasture anthropogenic land uses are nearly equal (Table 3.3).

Current land use impact on CSS habitat

Overall, Maxent models performed well, having a median AUC score of 0.964 (range:

0.904–0.991) for the 20 species modeled in our study and indicating the importance of climate in determining CSS habitat suitability (Table 3.1). The current modeled habitat maps represent areas meeting the climatic requirements of each species and thus encompass a geographically larger area than the species present distributions. Currently, a median 34.56% (range = 20.62–47.70%) of climatically suitable habitat of CSS species has been converted to anthropogenic land covers (Table 3.4), with land development having the greatest contribution to current habitat loss (median 21.30% loss, range = 10.75–36.20%), followed by agriculture (median 7.45% loss, range = 5.53–12.14%), and hay/pasture (median 3.79% loss, range = 2.04–5.10%). Six species have already lost over 40% of their climatically suitable habitat in California to anthropogenic land uses: *Xylococcus bicolor*, *Rhus integrifolia*, *Encelia californica*, *Opuntia littoralis*, *Bahiopsis laciniata*, and *Cneoridium dumosum* which has the greatest percentage of converted suitable habitat (47.70%). These species are primarily distributed in coastal southern California and northwestern Baja California and are most impacted by land development, with > 30% of suitable habitat converted to developed lands. Widely distributed CSS species that range beyond strictly coastal habitats in central and southern California tend to have a lower degree of habitat conversion. These species include *Hesperoyucca whipplei*, *Mimulus aurantiacus*, *Eriogonum fasciculatum*, *Hazardia squarrosa*, and *Acmispon glaber* (*Lotus scoparius*); all with less than 28% habitat lost to anthropogenic land use and 15% or less of suitable habitat currently developed (Table 3.4).

Projected land use and climate change threats to CSS

3.1. Habitat loss

3.1.1. Land use only

Assuming a future scenario characterized by high economic growth, technological innovation, and land use-land cover change (SRES A1B), anthropogenic land use will pose a considerable future threat to CSS habitat in California. After accounting for current (2005) land use, we predict that anthropogenic land use alone (no climate change), will drive a median loss of 20.07% (range = 11.68–30.07%) of remaining climatically suitable habitat for dominant CSS species by 2050, increasing to 28.34% (17.3–41.6%) by 2080 (Table 3.5). Six of 20 species will lose an additional >25% of remaining unconverted suitable habitat 2050, doubling to 12 species by 2080 (Table 3.6a). When considering the cumulative pre-2005 land use, the median predicted habitat loss rises to 48.67% in 2050 and 54.18% in 2080 with 12 species showing over 50% cumulative habitat loss. These species include those that are currently most heavily impacted by human land use, *Xylococcus bicolor*, *Rhus integrifolia*, *Encelia californica*, *Opuntia littoralis*, *Bahiopsis laciniata*, and *Cneoridium dumosum*, with *Bahiopsis laciniata* and *Opuntia littoralis* having a projected >40% of current (2005) remaining suitable habitat converted to anthropogenic land uses by 2080.

3.1.2 Climate change only

Under climate change only future (SERS A1B) scenarios we predict considerable habitat losses assuming no species dispersal and net habitat gains assuming unlimited species dispersal (Table 3.5). These patterns are consistent across warmer wetter and warmer drier climate trajectories and across time periods (all $P > 0.143$; two-tailed, paired Wilcoxon Signed Rank test).

Assuming no dispersal, the geographic centroid of modeled species habitat will shift a median of 80 km (19–269 km) under a warmer wetter future and 73 km (20–228 km) under a warmer drier future. Assuming unlimited dispersal, the geographic centroid of modeled species habitat will shift a median of 166 km (12–404 km) under a warmer wetter future and 204 km (28–458 km) under a warmer drier future.

Under no dispersal scenarios, we predict median species habitat losses of 15.78% (0.12–48.8% loss; warmer wetter) and 14.25% (3.31–43.00% loss; warmer drier) by the 2050s after accounting for current (2005) land use. Losses will increase significantly from the 2050s to the 2080s (all $P < 0.0001$; one-tailed, paired Wilcoxon Signed Rank test), with predicted median habitat losses of 24.46% (0.21–81.48%; warmer wetter) and 31.84% (6.25–61.09%; warmer drier) by the 2080s. Under no dispersal scenarios, the predicted magnitude of habitat loss under climate change does not differ significantly than that predicted under projected land use only change (all $P > 0.40$), although climate change only scenarios have greater extreme losses. We predict four species will have >25% habitat loss under both future climate scenarios by the 2050s, increasing to eight species by the 2080s, three of which will have >50% habitat loss (coastal varieties of *Eriogonum fasciculatum*, *Salvia apiana*, and *Xylococcus bicolor*) (Table 3.6a, b). In contrast to the land use only future scenario, we predict large habitat losses in both widely distributed (e.g., *Eriogonum fasciculatum*) and more narrowly distributed south-coastal species (e.g., *Xylococcus bicolor*) assuming no dispersal.

Under unlimited dispersal climate change only scenarios, we predict habitat gains for many of the dominant CSS species, offsetting some of the considerable habitat losses under the worst-case no dispersal scenarios (Table 3.5). Under a warmer wetter future climate, we predict a median net habitat gain of 30.26% (-14.32% to 197.96%) by the 2050s and a median net

habitat gain of 36.77% (-23.52% to 229.45%) by the end of the century (2080s). Under a warmer drier future, we predict a median net habitat gain of 31.84% (-2.61% to 153.14%) by the 2050s and a median net habitat gain of 33.85% (-7.43% to 190.62%) by the 2080s. While the median net change in habitat for CSS species does not differ significantly from mid to late century (all $P > 0.15$; two-tailed, paired Wilcoxon Signed Rank test), both losses and gains are more extreme in the 2080s compared to the 2050s (Table 3.5). Three species show considerable net habitat gains of >90% by the 2080s consistent across climate scenarios, *Encelia californica*, *Rhus integrifolia*, and *Opuntia littoralis* (Table 3.6). Assuming scenarios of unlimited dispersal, land use alone will pose a significantly greater threat than climate change alone (all $P < 0.01$; two-tailed, paired Wilcoxon Signed Rank test).

3.1.3 Combined land use and climate change

We predict the greatest losses in CSS habitat under combined future land use and climate change with no dispersal. Under these worst-case scenarios, CSS species will lose a median of 32.25% (21.94–61.84%; warmer wetter) to 34.68% (24.53–48.81% warmer drier) of suitable habitat by the 2050s and 43.92% (29.16–87.66%; warmer wetter) to 50.04% (34.64–72.73%; warmer drier) by the 2080s (Table 3.5). We predict 18 of 20 species will have >25% habitat loss under both land use-climate change no dispersal scenarios by 2050, compared to six species under land use only and four species under climate change (no dispersal) only scenarios. By the 2080s, we predict seven species (*Xylococcus bicolor*, *Salvia apiana*, coastal varieties of *Eriogonum fasciculatum*, *Hazardia squarrosa*, *Bahiopsis laciniata*, *Mirabilis laevis* var. *crassifolia*, *Cneoridium dumosum*) will have >50% habitat loss.

Under unlimited dispersal scenarios of combined projected land use and climate change,

predicted habitat gains will offset much of the habitat losses from both climate change and land use. We predict a median net habitat gain of 12.53–19.56% by the 2050s and 8.51–8.59% by the 2080s (Table 3.5). Nearly half of the modeled species will have net gains under both future climate scenarios by the 2080s: *Acmispon glaber*, *Malosma laurina*, *Mimulus aurantiacus*, *Mirabilis laevis* var. *crassifolia*, *Salvia apiana*, *Artemisia californica*, *Encelia californica*, *Rhus integrifolia*, and *Opuntia littoralis* (Table 3.6a, b). A greater number of species, however, are predicted to have a net habitat loss by the 2080s than are predicted under the climate-change only unlimited dispersal scenarios.

3.2. Species richness

We predict similar patterns in species richness change across climate change trajectories: a loss in species richness in South Coastal areas (no dispersal and unlimited dispersal scenarios) driven by considerable southern habitat contraction for many CSS species (Fig. 3.4a, b), and an increase in species richness in the Central Coast (unlimited dispersal scenario) driven by a northern habitat expansion for many CSS species (Fig. 3.4b). Current modeled species richness is centered in the South Coast Ecoregion in lowland, coastal areas, with the ecoregion having a median modeled richness of 13 (0–20) species and a large proportion of land area having >15 species (Fig 3.5). Under projected climate change, however, we predict considerable declines in South Coast richness ranging from a median loss of four species (unlimited dispersal scenarios) to five species (warmer wetter, no dispersal scenario) (Table 3.7). Under unlimited dispersal scenarios, 23.16–28.65% of the land area in the ecoregion will experience net gains in richness by the 2080s, however the majority of the ecoregion (66.44–70.53%) will lose species, increasing to 75.71–78.12% of the land area under no dispersal scenarios (Table 3.8).

In the Central Coast Ecoregion, we predict a much different outcome: moderate diversity losses assuming no dispersal and considerable diversity gains assuming unlimited dispersal (Fig. 3.5, Table 3.7). Currently, the Central Coast has lower modeled richness (median 8 species; range: 0–20), although areas adjacent to the South Coast Ecoregion or in San Francisco Bay Area have relatively high modeled species richness. Under no dispersal scenarios, we predict a median loss of only one species across the ecoregion (warmer wetter: -9–0; warmer drier: -12–0) by the 2080s (Fig. 3.5), with 51.8–55.75% of the ecoregion’s land area experiencing a net loss in species richness (Table 3.8). In contrast, we predict a 3–4 species gain in median richness by the 2080s under unlimited dispersal scenarios, with only 12.92–21.86% of the ecoregion experiencing net losses in richness and >70% of the ecoregion experiencing net gains in richness (Table 3.8).

Incorporating land use change projections, we find that patterns of anthropogenic land use will likely compound losses in species richness predicted under climate change, particularly in the South Coast Ecoregion where we predict both high CSS richness losses and high anthropogenic conversion of CSS habitat. In this ecoregion, we find that both currently (2005) intact habitat with projected anthropogenic conversion and already converted habitats will experience a disproportionate loss in CSS species richness driven by projected climate change (Table 3.8, Fig. 3.6a,b). We predict higher median species richness losses in these land use categories compared to the ecoregion as a whole (Table 3.6); a pattern consistent across time periods, climate scenarios, and dispersal scenarios. We also predict a significantly greater proportion of land area in these regions will experience a net loss in species richness compared to regions without projected anthropogenic conversion (Table 3.8; all $P < 0.0001$ after Bonferroni correction for multiple comparisons; Pearson’s Chi-squared test). For example, assuming

unlimited dispersal and a warmer wetter future climate in 2050, we predict 36.3% of remaining intact (unconverted) land will experience a net loss in species richness, compared to net losses in species richness covering 81.47% of land area that is currently undeveloped with projected anthropogenic conversion and 87.57% of land area that is already converted. Similarly, we predict lands remaining unconverted under projected land use change will have a significantly greater proportion of land area with net gains in species richness (all $P < 0.0001$ after Bonferroni correction for multiple comparisons; Pearson's Chi-squared test).

In the Central Coast, we predict similar changes in median species richness across the three different projected land use categories (Table 3.7, Fig. 3.6a,b). Assuming unlimited dispersal, we predict the majority of land area in all three projected land use categories (>70%) will experience a net gain in species richness (Table 3.8). Mid-century (2050s), we predict slightly but significantly higher proportions of regions with current and projected anthropogenic conversion will have a net gain in species richness compared to areas without projected anthropogenic conversion (all $P < 0.0001$ after Bonferroni correction for multiple comparisons; Pearson's Chi-squared test). Only under a warmer wetter future climate in the 2080s (both dispersal scenarios), do we predict a greater proportion of land area in either anthropogenic conversion category will have net species losses compared to land without projected anthropogenic conversion (all $P < 0.0001$ after Bonferroni correction for multiple comparisons; Pearson's Chi-squared test).

DISCUSSION

Given the current unprecedented rate of environmental change, successful conservation of biodiversity this century must address the impacts of both projected land use and climate

change on species and systems. Our findings suggest that future land use and climate change will have considerable impacts on CSS habitat loss and diversity patterns, however the degree of threat posed by each driver will depend heavily upon dispersal scenario. For individual CSS species, we find land use and climate change pose similar threats under assumptions of no dispersal, but land use poses a significantly greater future threat under assumptions of unlimited dispersal, where northern habitat expansion driven by climate change will offset some habitat losses from both drivers. Our findings also highlight the potential for land use and climate change to have compounding negative impacts, particularly in southern California, where we predict disproportionately high losses in diversity driven by climate change in areas of projected anthropogenic conversion.

Interestingly, we predict similar patterns of CSS habitat change under both warmer wetter and warmer drier future climate scenarios: northern habitat expansion (unlimited dispersal) and southern habitat contraction (unlimited and no dispersal scenarios). However, this is likely due to the geographic pattern of projected precipitation under the warmer-wetter scenario, which has greatest increases in northern California and more moderate increases in the Central Coast with drier conditions projected for the South Coast. Unexpectedly, we do not find temporal differences in the relative threats of land use and climate change, which are consistent across mid- and late-century.

Projected land use will have a considerable impact across coastal areas of central and southern California. By late century, we find that over 40% of the land area of the South Coast Ecoregion will likely be converted to anthropogenic land uses, much of which will be at the expense of shrubland habitats. California sage scrub's occurrence along central and southern California coasts in lowland and relatively fertile areas with sizable human populations makes it

particularly vulnerable to current (O'Leary 1995) and future habitat conversion by both agriculture and land development. Indeed, we find that species distributed primarily in lowland coastal areas of southern California (*Cneoridium dumosum*, *Bahiopsis laciniata*, and *Opuntia littoralis*) will continue to be those most affected by projected land use change. In contrast, we predict that both coastally distributed (*Xylococcus bicolor*) and more broadly ranging species (*Eriogonum fasciculatum* and *Salvia apiana*) will be heavily affected by climate change with large habitat losses. Thus, while we predict land use and climate change will pose similar overall threats of habitat loss assuming no dispersal, their impacts will vary across individual species.

Although we predict climate change will drive widespread habitat loss and contraction for CSS species, it will also drive considerable habitat expansion for many species, offsetting some of the habitat losses projected under both land use and climate change. We find species with the greatest predicted habitat gains (*Encelia californica*, *Rhus integrifolia*, and *Opuntia littoralis*) tend to be those with current broad coastal distributions, typically spanning a notable gradient of increasing aridity from Los Angeles County in southern California to the southern limit of mediterranean-type climate in Baja California, south of El Rosario. Adaptation to drier conditions at the transition to desert may translate to greater tolerance to warmer and drier conditions predicted under climate change.

Our findings underscore the importance of dispersal in moderating habitat losses from both land use and climate. Although the broad dispersal capacities of species with small, wind dispersed seeds (e.g., *Artemisia californica*, *Encelia californica*, *Eriogonum fasciculatum*, *Mimulus aurantiacus*) (Wells 1962), may facilitate the northward expansion of CSS under climate change, species range expansions will also rely upon successful colonization and

establishment of newly suitable areas. A mosaic of chaparral, CSS, and grasslands dominate much of the central coast, and local patterns of CSS distribution are governed by a number of factors in addition to climate, such as topography, geological substrate, soil, disturbance and species interactions (Wells 1962, Harrison et al. 1971, Parsons and Moldenke 1975, Parsons 1976, Kirkpatrick and Hutchinson 1980, Westman 1981b, 1983, Zedler et al. 1983, Keeley and Keeley 1984, Malanson and Westman 1991, Callaway and Davis 1993, Franklin 1995, Meentemeyer et al. 2001).

Broad dispersal ability in many wind-dispersed CSS species enables CSS to invade areas of chaparral opened by disturbances such as fire (Keeley and Keeley 1984, Keeley et al. 2005, see review in Rundel 2007), however, short return intervals of fires or high levels of other anthropogenic disturbances facilitate type conversion of shrublands to exotic grasslands (Wells 1962, Minnich and Dezzani 1998, Stylinski and Allen 1999). Nitrogen deposition from pollution further reinforces this conversion (Padgett et al. 1999, Talluto and Suding 2008) and may impede the successful establishment of CSS in new, climatically suitable habitats under climate change. Dynamics of fire frequency and intensity will be influenced by both climate change (Westerling et al. 2011) and future urbanization (Syphard et al. 2007). Extensive land use, habitat fragmentation, and habitat degradation pose formidable barriers to species movement. Thus, the future dynamics of CSS expansion will likely be complex, governed by many factors and processes that are also influenced by anthropogenic change.

As individual species shift in distribution in response to climate change, we predict dramatically different patterns of change in CSS diversity across the region, with increasing species richness along the California Central Coast resulting from the northern habitat expansion of individual species, but considerable declines in species richness in the South Coast resulting

from the widespread southern habitat contraction of modeled species. We predict particularly large diversity declines in coastal San Diego County of southern California, a region of high CSS floristic diversity and endemism (Epling and Lewis 1942, Westman 1981a, 1983, Rundel 2007). Furthermore, we predict land use and climate change will have compounding negative impacts for coastal southern California, which will have disproportionately high losses in diversity driven by climate change in areas of projected anthropogenic conversion. Therefore, conservation efforts may need to prioritize the protection of sensitive species and communities in southern California at particular risk to future habitat loss. Coastal central California, in contrast, may increase considerably in CSS diversity if species are able to colonize expanding suitable habitat and may prove to be an important region of CSS restoration or possibly future species introductions.

Although excluded in our analyses due to a lack of spatially explicit information for future land use projections, we also predict considerable declines in CSS diversity in northwestern Baja California, a region of remarkably high floristic diversity and endemism, not just for CSS, but globally (Westman 1981a, Peinado et al. 1995, Riemann and Ezcurra 2005). While the degree of land conversion in northwestern Baja California has occurred more recently than in southern California, rapidly increasing agriculture, tourism, industry, and urban development in the region (Bullock 1999, Escofet and Espejel 1999, Riemann and Ezcurra 2005, Underwood et al. 2009) pose significant threats to CSS communities. There is minimal protection for the large number of endemic plants in northwestern Baja California (Riemann and Ezcurra 2005), many of which have restricted or local ranges and may be particularly vulnerable to both land use and climate change.

It is important to note that while our analyses of predicted future habitat loss and

subsequent diversity impacts is limited geographically to California, the species-climate relationship was modeled from data spanning the full range of each species. We made a concerted effort to obtain locality records at the southern limit of species ranges in Baja California and thereby minimize over-predictions of species habitat losses, which often arises when a restricted range of occurrence records (e.g., due to political boundaries) is used to model species distributions (Barbet-Massin et al. 2010). In addition, by using LandCarbon's land cover-land use projections based upon SRES future scenarios (Sleeter et al. 2012, Sohl et al. 2012), we are able to analyze the impacts of future land use and climate change on CSS under the same suite of assumptions and at a much larger spatial extent than has been previously possible (Syphard et al. 2007, Syphard et al. 2011). As our predictions are based upon the SRES A1B moderate-high emissions scenario with high rates of land use-land cover change, our findings should be interpreted as a possible scenario of future change in CSS.

Finally, our models may underestimate habitat loss from land use and overestimate habitat loss from climate change. Previous papers estimate anthropogenic activities have driven losses of up to 90% of CSS's original extent (Westman 1981a, Minnich and Dezzani 1998, Taylor 2004, Rundel 2007), considerably higher than our median estimate of 35% habitat loss for individual shrub species. Our habitat models are based upon climatic requirements only and encompass geographically larger and more continuous areas than CSS's typically fragmented and mosaic-like distributions. Thus, our results likely underestimate the degree of current and future habitat conversion for individual species.

Conversely, the 1 km spatial resolution of our analyses may overestimate CSS habitat losses driven by climate change. Fine scale environmental heterogeneity, such as variability in topoclimate (Ackerly et al. 2010), may buffer ecological impacts of climate change by

facilitating migration across the landscape (thus, alleviating dispersal limitation) and by providing a greater pool of diversity, both in numbers of species and genetic diversity within a species, for adaptation to climate change. For example, a species may be able to track suitable climate by moving relatively short distances from a north to a south facing slope, rather than 50 to 100 km along the coast. Additionally, our models do not incorporate dynamic processes that may buffer climate change, such as the capacity of a species for acclimation or adaptation to new environmental conditions. Nevertheless, our findings provide important insight and hypotheses into how both projected land use and climate change may impact CSS species and diversity. The presence-only modeling approach used in our study is particularly useful in modeling potential suitable CSS habitat (Riordan and Rundel 2009), where current fragmentation patterns may reflect anthropogenic absences rather than environmental limits.

In conclusion, our findings emphasize the necessity to include analyses of both projected land use and climate change in conservation and resource management planning. We predict high levels of habitat conversion in CSS under projected land use change along with considerable habitat losses and shifts in diversity patterns under projected climate change. Our models underscore the importance of dispersal in moderating CSS habitat losses as well as in shaping future patterns of diversity. The future persistence and extent of CSS will likely hinge upon the protection of remaining critical habitat in southern California as well as the successful dispersal and establishment of species along the coastal central California. We also illustrate the potential for land use and climate change to have compounding negative impacts on CSS, particularly in southern California. Thus, conservation efforts should focus on prioritizing protection of critical species and habitat in southern California and promoting species movements (e.g., protection of strategic migration corridors) in coastal central California.

Table 3.1. List of California sage scrub species with number of herbarium records used in models (N) and overall model performance measured as the mean test area under the receiver operating characteristic curve (AUC) score (range: min–max). Taxonomy follows Baldwin et al. (2012).

Taxon name	Family	Growth Form	N	Test AUC (range)
<i>Acmispon glaber</i> (<i>Lotus scoparius</i>)	Fabaceae	Drought-deciduous subshrub	603	0.9265 (0.9053–0.942)
<i>Artemisia californica</i>	Asteraceae	Drought-deciduous shrub	242	0.9573 (0.9343–0.9755)
<i>Bahiopsis laciniata</i>	Asteraceae	Drought-deciduous shrub	176	0.9675 (0.9248–0.9825)
<i>Cneoridium dumosum</i>	Rutaceae	Evergreen shrub	117	0.97375 (0.957–0.9893)
<i>Encelia californica</i>	Asteraceae	Drought-deciduous shrub	204	0.9693 (0.9551–0.979)
<i>Ericameria ericoides</i>	Asteraceae	Evergreen shrub	85	0.9911 (0.985–0.995)
<i>Eriogonum fasciculatum</i> (coastal vars.)	Polygonaceae	Evergreen shrub	665	0.92315 (0.9132–0.9447)
<i>Hazardia squarrosa</i>	Asteraceae	Evergreen shrub	223	0.96045 (0.9231–0.9673)
<i>Hesperoyucca whipplei</i>	Agavaceae	Evergreen shrub (rosette)	226	0.93305 (0.8803–0.9521)
<i>Isocoma menziesii</i>	Asteraceae	Evergreen shrub	313	0.95805 (0.9484–0.9621)
<i>Malosma laurina</i>	Anacardiaceae	Evergreen shrub	218	0.96435 (0.9485–0.975)
<i>Mimulus aurantiacus</i>	Phrymaceae	Drought-deciduous shrub	793	0.90365 (0.8896–0.922)
<i>Mirabilis laevis</i> var. <i>crassifolia</i>	Nyctaginaceae	Drought-deciduous subshrub	289	0.9439 (0.9222–0.9518)
<i>Opuntia littoralis</i>	Cactaceae	Succulent shrub	79	0.97815 (0.9341–0.9858)
<i>Rhus integrifolia</i>	Anacardiaceae	Evergreen shrub	196	0.97745 (0.9707–0.9813)
<i>Ribes speciosum</i>	Grossulariaceae	Drought-deciduous shrub	138	0.9772 (0.9681–0.9843)
<i>Salvia apiana</i>	Lamiaceae	Drought-deciduous shrub	305	0.94845 (0.9389–0.9666)
<i>Salvia leucophylla</i>	Lamiaceae	Drought-deciduous shrub	60	0.9818 (0.9228–0.993)
<i>Salvia mellifera</i>	Lamiaceae	Drought-deciduous shrub	325	0.9646 (0.9463–0.9722)
<i>Xylococcus bicolor</i>	Ericaceae	Evergreen shrub	189	0.97695 (0.9628–0.9859)

Table 3.2. Current (2005) and projected (2050, 2080) land cover and annual rate of land cover change (percent yr⁻¹) by California ecoregion. Total ecoregion land area is shown in parentheses. The total anthropogenic land use category includes developed, agriculture, hay/pasture, mining, and mechanically disturbed land uses. The natural land use category includes all other terrestrial land covers. Land cover/use data is from the USGS Land Carbon project (Sleeter et al. 2012).

Land cover	2005		2050		2080		Rate of change	
	km ²	%	km ²	%	km ²	%	2005-2050	2050-2080
Central Coast	32803							
Grassland	12389	37.77	10426	31.78	9282	28.29	-0.35	-0.37
Shrubland	5855	17.85	5389	16.43	5014	15.28	-0.18	-0.23
Evergreen forest	5593	17.05	5495	16.75	5486	16.72	-0.04	-0.01
Mixed forest	1960	5.97	1955	5.96	1952	5.95	-0.01	0.00
Deciduous forest	848	2.59	844	2.57	843	2.57	-0.01	-0.01
Barren	790	2.41	789	2.41	789	2.41	0.00	0.00
Wetland	38	0.12	25	0.08	23	0.07	-0.78	-0.22
Developed	2507	7.64	4662	14.21	5488	16.73	1.91	0.59
Agriculture	1632	4.98	1985	6.05	2559	7.80	0.48	0.96
Hay/pasture	1118	3.41	1144	3.49	1296	3.95	0.05	0.44
Mining	38	0.12	33	0.10	29	0.09	-0.32	-0.35
Mechanically disturbed	35	0.11	62	0.19	50	0.15	1.76	-0.67
Total natural	27473	83.75	24923	75.97	23389	71.29	-0.21	-0.21
Total anthropogenic	5365	16.25	7947	24.03	9471	28.71	1.06	0.65
South Coast	31458							
Grassland	3491	11.10	2418	7.68	2143	6.81	-0.68	-0.38
Shrubland	14194	45.12	11645	37.01	10444	33.19	-0.40	-0.34
Evergreen forest	4079	12.97	4023	12.79	3991	12.68	-0.03	-0.03
Mixed forest	864	2.75	844	2.68	834	2.65	-0.05	-0.04
Deciduous forest	303	0.96	297	0.94	294	0.93	-0.04	-0.04
Barren	548	1.74	548	1.74	548	1.74	0.00	0.00
Wetland	35	0.11	27	0.09	27	0.09	-0.49	-0.08
Developed	6195	19.69	10186	32.37	11590	36.83	1.43	0.46
Agriculture	1239	3.94	1109	3.52	1262	4.01	-0.23	0.46
Hay/pasture	481	1.53	356	1.13	326	1.04	-0.58	-0.28
Mining	12	0.04	9	0.03	8	0.02	-0.58	-0.44
Mechanically disturbed	17	0.05	1	0.00	2	0.01	-2.07	2.78
Total natural	23514	74.75	19804	62.94	18281	58.09	-0.35	-0.26
Total anthropogenic	7960	25.25	11662	37.06	13190	41.91	1.04	0.44

Table 3.3. Primary projected changes in land cover-land use for the Central Coast and South Coast California Ecoregions. The change in land cover-land use is shown as an area (km²) and as the percent of total land area in each ecoregion.

Land cover change	2005 to 2050		2005 to 2080	
	Area (km ²)	% Ecoregion	Area (km ²)	% Ecoregion
Central Coast				
Grassland to developed	1268	3.87	1758	5.36
Grassland to agriculture	516	1.57	1026	3.13
Agriculture to developed	393	1.20	525	1.60
Grassland to hay/pasture	184	0.56	324	0.99
Hay/pasture to developed	237	0.72	317	0.97
Shrubland to agriculture	159	0.48	298	0.91
Shrubland to hay/pasture	156	0.48	289	0.88
Shrubland to developed	169	0.52	267	0.82
South Coast				
Shrubland to developed	2131	6.77	3079	9.79
Grassland to developed	1017	3.23	1251	3.98
Agriculture to developed	531	1.69	666	2.12
Shrubland to agriculture	356	1.13	598	1.90
Hay/pasture to developed	225	0.71	272	0.86
Shrubland to hay/pasture	87	0.28	93	0.30
Grassland to agriculture	46	0.15	81	0.26
Evergreen forest to developed	51	0.16	73	0.23

Table 3.4. Current (2005) land use of current modeled climatically suitable habitat for CSS species in California.

Species	Modeled habitat (km ²)		Percent land cover					
	Total	Unconverted	Total Anthropogenic	Developed	Disturbed	Mining	Agriculture	Hay/Pasture
<i>Acmispon glaber</i> (<i>Lotus scoparius</i>)	66737	48103	27.92	15.09	0.05	0.12	8.37	4.30
<i>Artemisia californica</i>	35996	24045	33.20	24.05	0.03	0.12	6.03	2.98
<i>Bahiopsis laciniata</i>	22120	12211	44.80	32.72	0.01	0.07	8.25	3.74
<i>Cneoridium dumosum</i>	15305	8004	47.70	36.20	0.01	0.06	7.76	3.67
<i>Encelia californica</i>	25778	14870	42.32	31.03	0.02	0.09	7.65	3.53
<i>Ericameria ericoides</i>	13549	8515	37.15	24.91	0.14	0.16	7.12	4.83
<i>Eriogonum fasciculatum</i> (coastal vars.)	69040	51585	25.28	13.96	0.11	0.08	7.14	3.99
<i>Hazardia squarrosa</i>	64381	46843	27.24	14.29	0.05	0.09	8.72	4.09
<i>Hesperoyucca whipplei</i>	61771	49032	20.62	10.85	0.17	0.08	5.83	3.69
<i>Isocoma menziesii</i>	40151	25236	37.15	21.36	0.02	0.10	10.73	4.94
<i>Malosma laurina</i>	29228	18025	38.33	28.19	0.02	0.09	6.73	3.30
<i>Mimulus aurantiacus</i>	99458	76907	22.67	10.75	0.44	0.10	7.32	4.07
<i>Mirabilis laevis</i> var. <i>crassifolia</i>	51324	32793	36.11	19.33	0.02	0.10	11.55	5.10
<i>Opuntia littoralis</i>	21203	11999	43.41	33.00	0.01	0.09	7.59	2.72
<i>Rhus integrifolia</i>	21744	12664	41.76	33.97	0.01	0.11	5.53	2.14
<i>Ribes speciosum</i>	42305	30144	28.75	18.73	0.09	0.12	5.80	4.01
<i>Salvia apiana</i>	29965	21143	29.44	21.24	0.04	0.07	6.05	2.04
<i>Salvia leucophylla</i>	74857	52591	29.74	12.71	0.05	0.10	12.14	4.74
<i>Salvia mellifera</i>	50238	34268	31.79	19.12	0.03	0.11	8.70	3.83
<i>Xylococcus bicolor</i>	19787	11635	41.20	32.46	0.02	0.08	5.67	2.98

Table 3.5. Predicted change in habitat area for CSS species under future land use and climate change scenarios for 2050 and 2080. Values are the median percent loss or gain (range: min to max) of modeled current habitat that was unconverted in 2005. The climate change only scenario takes into account 2005 land use in future habitat area.

Scenario	Climate change	Dispersal	Year	Median	Range (min to max)
Land use only	None	–	2050	-20.07	(-30.7 to -11.68)
		–	2080	-28.34	(-41.61 to -17.3)
Climate change only	Warmer wetter	No	2050	-15.78	(-48.8 to -0.21)
		No	2080	-24.46	(-81.48 to -0.51)
		Yes	2050	30.26	(-14.32 to 197.96)
		Yes	2080	36.77	(-23.52 to 229.45)
	Warmer drier	No	2050	-14.25	(-43.00 to -3.31)
		No	2080	-24.31	(-61.09 to -6.25)
		Yes	2050	31.84	(-2.61 to 153.14)
		Yes	2080	33.85	(-7.43 to 190.62)
Land use & climate change	Warmer wetter	No	2050	-32.25	(-61.84 to -21.94)
		No	2080	-43.92	(-87.66 to -29.16)
		Yes	2050	19.57	(-39.06 to 169.57)
		Yes	2080	8.51	(-59.13 to 184.91)
	Warmer drier	No	2050	-34.68	(-48.81 to -24.53)
		No	2080	-50.04	(-72.73 to -34.64)
		Yes	2050	12.53	(-23.53 to 125.4)
		Yes	2080	8.59	(-41.59 to 145.94)

Table 3.6a. Predicted change in habitat area for CSS species under future land use and warmer wetter (CCCMA CGC 3.1) climate change scenarios for 2050 and 2080. Values are the median percent loss or gain of modeled current habitat that was unconverted in 2005. The climate change only scenario takes into account 2005 land use in future habitat area.

Species	Land use only		Climate change only				Land use and climate change			
			No dispersal		Unlimited dispersal		No dispersal		Unlimited dispersal	
	2050	2008	2050	2080	2050	2080	2050	2080	2050	2080
<i>Acmispon glaber</i> (<i>Lotus scoparius</i>)	-15.75	-22.75	-7.26	-8.59	28.61	41.84	-21.94	-29.16	19.55	27.60
<i>Artemisia californica</i>	-23.05	-31.68	-4.11	-9.30	53.14	65.64	-26.20	-37.71	44.85	51.52
<i>Bahiopsis laciniata</i>	-30.70	-41.61	-18.79	-40.17	59.04	33.90	-43.36	-63.74	34.80	-2.37
<i>Cneoridium dumosum</i>	-28.84	-38.62	-30.44	-43.70	-14.32	-23.52	-49.66	-63.44	-39.06	-53.37
<i>Encelia californica</i>	-29.43	-39.76	-6.98	-8.52	90.88	91.66	-33.63	-43.99	74.06	70.47
<i>Ericameria ericoides</i>	-18.45	-26.80	-12.20	-20.33	1.84	-11.46	-27.34	-41.06	-7.91	-27.00
<i>Eriogonum fasciculatum</i> (coastal vars.)	-13.67	-19.83	-28.12	-50.27	6.55	2.91	-37.44	-58.08	-18.24	-36.96
<i>Hazardia squarrosa</i>	-14.61	-21.27	-24.33	-40.87	-5.33	-8.83	-34.36	-51.11	-25.22	-38.91
<i>Hesperoyucca whipplei</i>	-11.73	-17.30	-20.87	-34.09	18.65	9.42	-29.20	-43.25	-1.46	-19.52
<i>Isocoma menziesii</i>	-22.22	-31.77	-10.42	-16.23	-5.26	-14.48	-30.87	-43.86	-15.51	-29.04
<i>Malosma laurina</i>	-26.08	-35.55	-12.77	-21.56	42.38	53.84	-35.58	-49.12	25.91	28.21
<i>Mimulus aurantiacus</i>	-11.68	-17.51	-29.84	-39.08	45.39	61.89	-36.44	-45.71	19.58	30.09
<i>Mirabilis laevis</i> var. <i>crassifolia</i>	-21.08	-29.88	-21.96	-43.05	48.73	66.79	-37.65	-57.20	27.21	31.62
<i>Opuntia littoralis</i>	-30.52	-41.04	-0.21	-0.51	197.96	229.45	-30.67	-41.36	169.57	184.91
<i>Rhus integrifolia</i>	-28.29	-37.87	-2.80	-10.28	101.48	144.83	-29.87	-42.25	82.45	111.47
<i>Ribes speciosum</i>	-17.07	-24.10	-11.91	-21.58	-3.65	-4.53	-26.51	-38.10	-13.55	-20.43
<i>Salvia apiana</i>	-17.49	-24.32	-39.85	-62.42	106.53	85.60	-44.87	-66.05	68.03	32.00
<i>Salvia leucophylla</i>	-14.86	-21.77	-18.91	-26.64	20.10	19.98	-29.18	-40.19	4.04	-1.59
<i>Salvia mellifera</i>	-19.05	-26.73	-10.49	-22.28	31.90	39.64	-26.79	-42.14	21.20	18.60
<i>Xylococcus bicolor</i>	-27.48	-37.24	-48.80	-81.48	7.90	-3.27	-61.84	-87.66	-32.36	-59.13

Table 3.6b. Predicted change in habitat area for CSS species under future land use and warmer drier (NCAR CCSM 3.0) climate change scenarios for 2050 and 2080. Values are the median percent loss or gain of modeled current habitat that was unconverted in 2005. The climate change only scenario takes into account 2005 land use in future habitat area.

Species	Land use only		Climate change only				Land use and climate change			
			No dispersal		Unlimited dispersal		No dispersal		Unlimited dispersal	
	2050	2008	2050	2080	2050	2080	2050	2080	2050	2080
<i>Acmispon glaber</i> (<i>Lotus scoparius</i>)	15.75	22.75	11.82	16.83	23.01	24.23	25.68	34.64	11.02	7.35
<i>Artemisia californica</i>	23.05	31.68	9.57	15.41	25.75	43.37	31.47	43.78	13.78	23.68
<i>Bahiopsis laciniata</i>	30.70	41.61	11.32	23.20	80.64	90.38	38.03	54.37	59.29	56.68
<i>Cneoridium dumosum</i>	28.84	38.62	14.88	23.09	37.92	24.33	38.26	50.75	16.86	-3.57
<i>Encelia californica</i>	29.43	39.76	8.64	10.33	98.97	127.24	34.70	45.61	80.54	102.31
<i>Ericameria ericoides</i>	18.45	26.80	8.71	12.94	19.65	18.76	24.53	34.98	11.28	6.64
<i>Eriogonum fasciculatum</i> (coastal vars.)	13.67	19.83	26.28	50.88	7.67	3.30	36.30	59.31	-16.38	-38.80
<i>Hazardia squarrosa</i>	14.61	21.27	23.73	43.88	-2.61	-7.43	34.55	54.75	-22.95	-41.59
<i>Hesperoyucca whipplei</i>	11.73	17.30	32.35	49.15	13.97	7.49	39.83	56.89	-15.98	-34.88
<i>Isocoma menziesii</i>	22.22	31.77	7.87	10.39	11.64	11.91	28.89	39.87	1.99	-1.93
<i>Malosma laurina</i>	26.08	35.55	9.62	16.08	55.56	72.50	33.18	45.62	41.22	50.15
<i>Mimulus aurantiacus</i>	11.68	17.51	43.00	61.09	44.29	64.62	48.81	66.51	5.66	10.85
<i>Mirabilis laevis</i> var. <i>crassifolia</i>	21.08	29.88	20.01	35.41	76.04	81.95	37.10	53.73	53.84	49.80
<i>Opuntia littoralis</i>	30.52	41.04	3.31	6.25	153.14	190.62	32.53	44.10	125.40	145.94
<i>Rhus integrifolia</i>	28.29	37.87	10.01	21.28	120.56	169.64	34.66	49.32	96.19	129.65
<i>Ribes speciosum</i>	17.07	24.10	16.96	30.60	1.85	-1.19	31.08	45.03	-12.15	-22.88
<i>Salvia apiana</i>	17.49	24.32	34.21	55.87	69.69	55.49	41.19	61.70	38.07	9.84
<i>Salvia leucophylla</i>	14.86	21.77	33.27	52.98	3.36	-0.24	41.31	60.40	-23.53	-39.76
<i>Salvia mellifera</i>	19.05	26.73	13.62	25.41	19.59	18.60	29.52	44.87	6.40	-4.29
<i>Xylococcus bicolor</i>	27.48	37.24	31.41	58.63	61.64	74.48	48.74	72.73	28.36	23.21

Table 3.7. Predicted change in modeled future CSS species richness under land use and climate change by ecoregion. Values are the median change in richness (range: max–min), reported for three different land use change categories: ‘natural’ corresponding to areas with natural land cover that will remain unconverted in the future, ‘natural to anthropogenic’ corresponding to areas of current natural land cover projected to undergo conversion to anthropogenic land uses, and ‘anthropogenic’ corresponding to areas with anthropogenic land uses that will remain converted in the future.

Region	Future climate scenario		Dispersal	Ecoregion	Natural	Natural to anthropogenic	Anthropogenic
Central Coast	Warmer wetter	2050	Yes	4 (-3–18)	5 (-3–8)	4 (-2–17)	4 (-2–12)
			No	0 (-6–0)	0 (-6–0)	0 (-5–0)	0 (-4–0)
	Warmer wetter	2080	Yes	4 (-8–18)	5 (-8–18)	3 (-8–18)	3 (-7–12)
			No	-1 (-9–0)	0 (-9–0)	-1 (-8–0)	-1 (-8–0)
	Warmer drier	2050	Yes	4 (-8–19)	4 (-8–19)	4 (-4–19)	4 (-7–13)
			No	0 (-8–0)	0 (-8–0)	0 (-6–0)	0 (-7–0)
Warmer drier	2080	Yes	3 (-10–18)	4 (-10–18)	2 (-9–18)	2 (-8–14)	
		No	-1 (-12–0)	-1 (-12–0)	-1 (-10–0)	-1 (-10–0)	
South Coast	Warmer wetter	2050	Yes	-1 (-12–11)	1 (-12–11)	-4 (-11–10)	-5 (-11–8)
			No	-2 (-12–0)	0 (-12–0)	-4 (-11–0)	-5 (-11–0)
	Warmer wetter	2080	Yes	-4 (-17–11)	0 (-17–11)	-7 (-16–10)	-9 (-17–7)
			No	-5 (-17–0)	-2 (-17–0)	-7 (-16–0)	-9 (-17–0)
	Warmer drier	2050	Yes	-1 (-12–12)	0 (-11–12)	-3 (-11–11)	-4 (-12–9)
			No	-2 (-12–0)	0 (-11–0)	-4 (-11–0)	-4 (-12–0)
	Warmer drier	2080	Yes	-4 (-14–16)	-1 (-16–14)	-6 (-15–13)	-8 (-15–9)
			No	-4 (-16–0)	-2 (-16–0)	-6 (-15–0)	-8 (-15–0)

Table 3.8. Percent of land area with predicted change in modeled future CSS species richness by land cover-land use category. Total area covered by each land use category is reported as Land Area (km²). Values in parentheses correspond to no dispersal scenarios, all other values correspond to unlimited dispersal scenarios. Land cover-land use categories: ‘natural’ corresponding to areas with natural land cover that will remain unconverted in the future, ‘natural to anthropogenic’ corresponding to areas of current natural land cover projected to undergo conversion to anthropogenic land uses, and ‘anthropogenic’ corresponding to areas with anthropogenic land uses that will remain converted in the future.

Ecoregion	Climate scenario	Land use	Land Area (km ²)		Loss		Gain	
			2050	2080	2050	2080	2050	2080
Central Coast	Warmer wetter	Natural	24998	23492	1.87 (37.77)	11.3 (47.6)	93.19	82.05
		Natural to Anthropogenic	2627	4124	0.5 (36.89)	15.13 (60.29)	95.96	76.01
		Anthropogenic	5177	5186	0.28 (31.59)	18.5 (64.08)	96.28	71.09
		<i>Total</i>	<i>32803</i>	<i>32803</i>	<i>1.51 (36.72)</i>	<i>12.92 (51.8)</i>	<i>93.9</i>	<i>79.56</i>
	Warmer drier	Natural	24998	23492	12.95 (42.9)	21.97 (54.08)	80.04	71.97
		Natural to Anthropogenic	2627	4124	4.11 (33.6)	22.14 (59.7)	91.5	69.63
		Anthropogenic	5177	5186	2.33 (33.42)	21.13 (60.14)	93.4	71.52
		<i>Total</i>	<i>32803</i>	<i>32803</i>	<i>10.57 (40.66)</i>	<i>21.86 (55.75)</i>	<i>83.06</i>	<i>71.61</i>
South Coast	Warmer wetter	Natural	19932	18379	36.3 (48.46)	47.58 (60.69)	53.39	45.35
		Natural to Anthropogenic	3688	5238	81.47 (86.31)	88.05 (95.17)	13.21	8.6
		Anthropogenic	7838	7841	87.57 (90.87)	96.2 (97.92)	6.68	2.89
		<i>Total</i>	<i>31458</i>	<i>31458</i>	<i>54.37 (63.46)</i>	<i>66.44 (75.71)</i>	<i>37.04</i>	<i>28.65</i>
	Warmer drier	Natural	19932	18379	41.71 (53.82)	54.49 (65.53)	44.24	36.19
		Natural to Anthropogenic	3688	5238	79.58 (83.23)	89.04 (93.06)	13.13	7.56
		Anthropogenic	7838	7841	87.42 (89.61)	95.77 (97.63)	7.97	3.05
		<i>Total</i>	<i>31458</i>	<i>31458</i>	<i>57.54 (66.19)</i>	<i>70.53 (78.12)</i>	<i>31.56</i>	<i>23.16</i>

Figure 3.1. Study area and herbarium record locations for the 22 modeled CSS shrub species. Central Coast and South Coast California Ecoregions are shown in gray. Species distribution models were created from all herbarium localities, while habitat loss and land use analyses were restricted to within California.

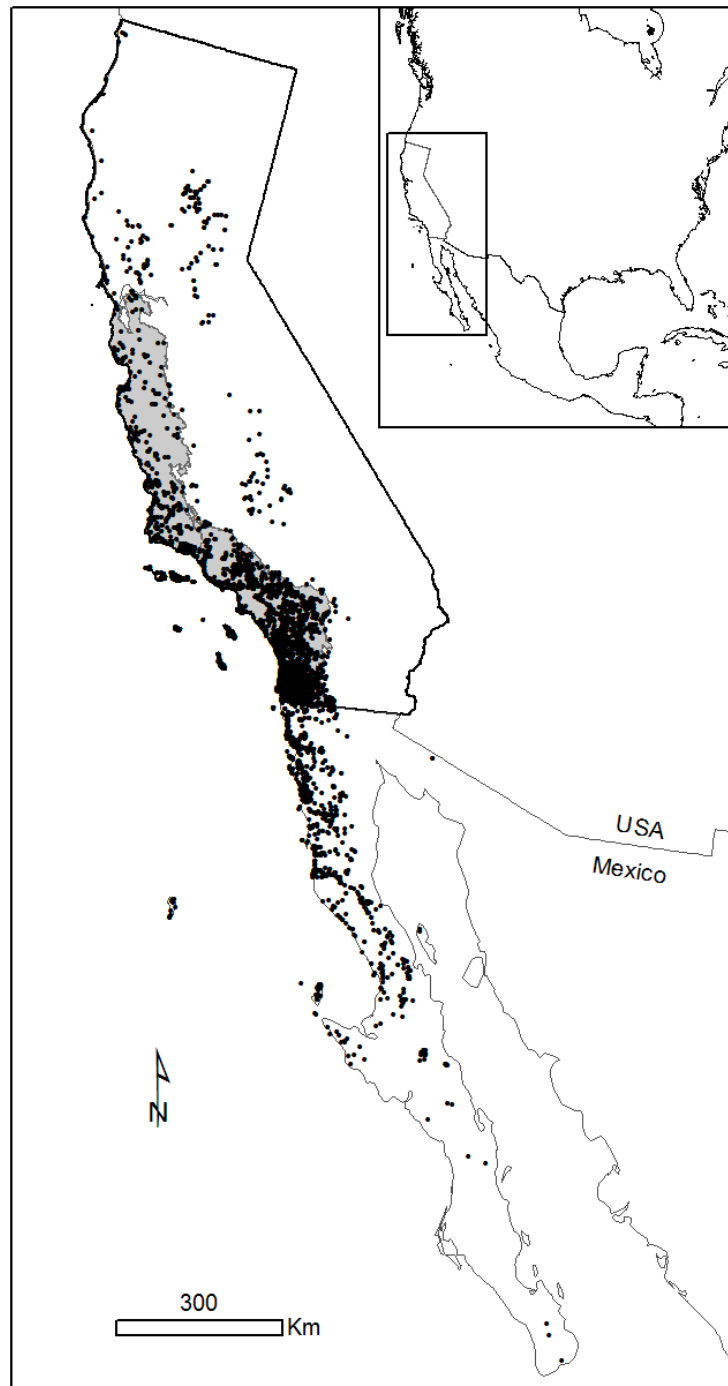


Figure 3.2. Projected land cover in coastal California. Central and South Coast Ecoregions are shown in black outlines over historical (2005) and projected future (2050, 2080) land cover-land use maps.

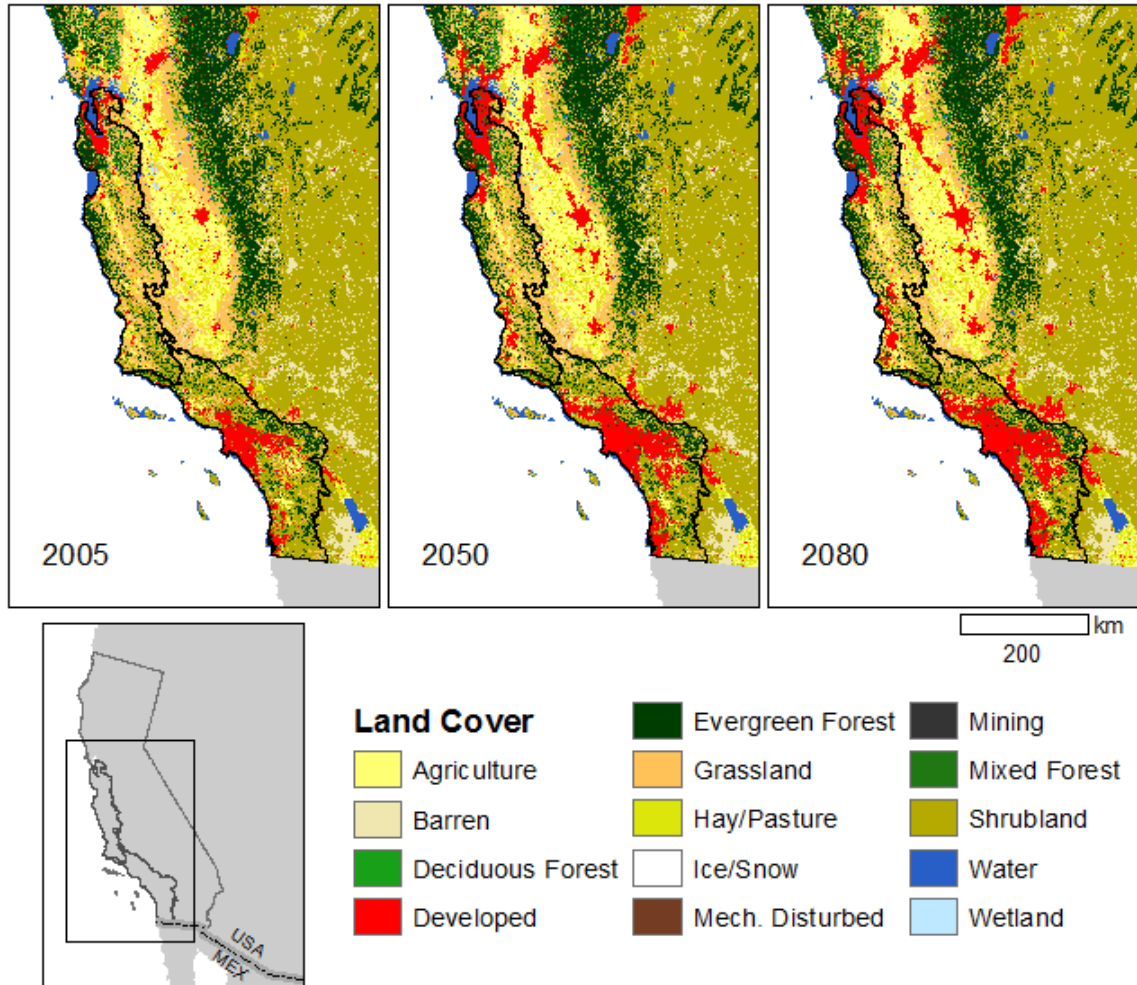


Figure 3.3. Percent change in projected land cover/use from 2005 to 2050 (white bars) and from 2005 to 2080 (gray bars) by ecoregion: Central Coast (A) and South Coast (B) California. Anthropogenic land use includes developed, mining, mechanically disturbed, agriculture, and hay/pasture categories. Total natural land cover includes all other land cover.

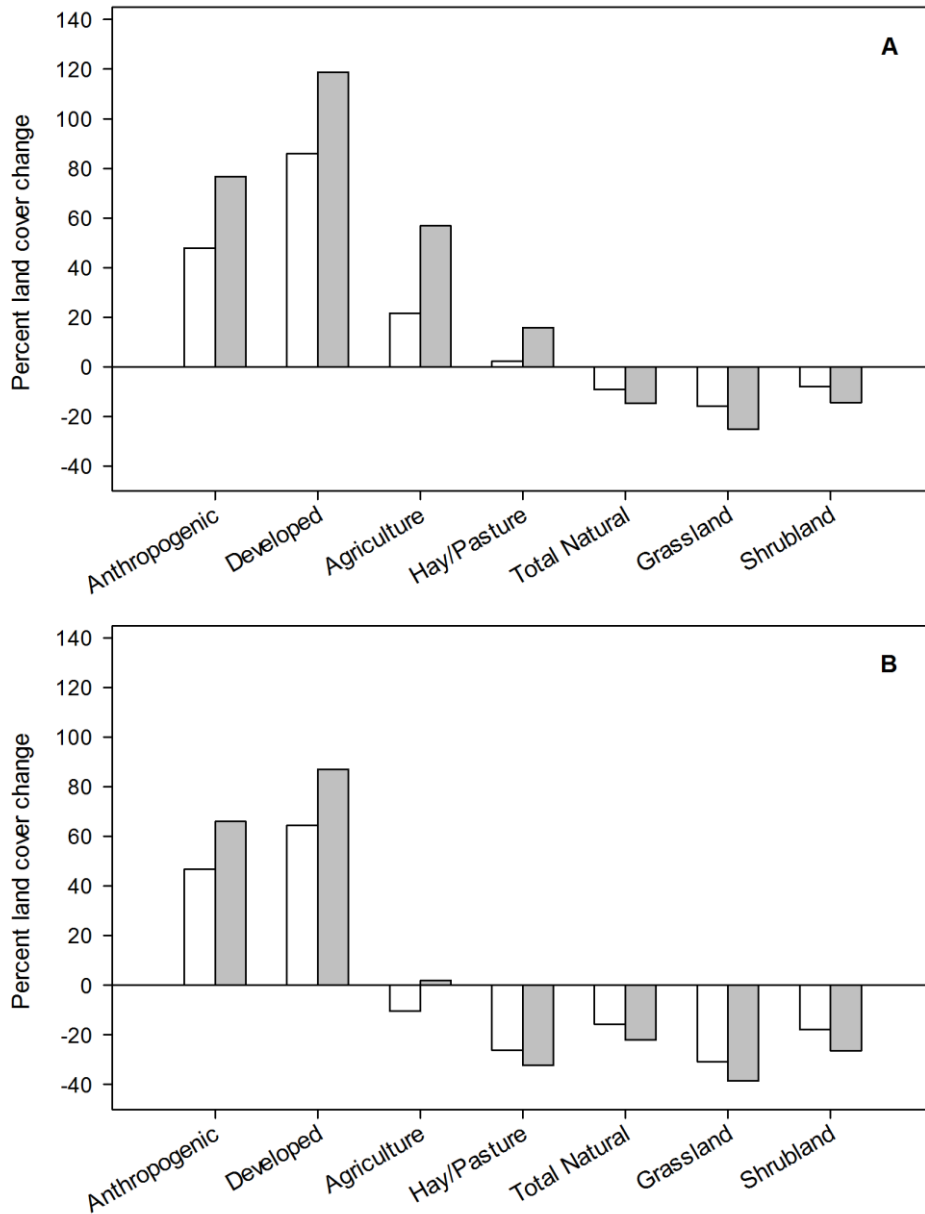


Figure 3.4a. Projected mid-century (2050s) and late-century (2080s) change in species richness under no dispersal with projected anthropogenic land cover-land use. Climate scenarios: warmer wetter (CCCMA CGC 3.1), warmer drier (NCAR CCSM 3.0). Anthropogenic land use includes developed, mining, mechanically disturbed, agriculture, and hay/pasture.

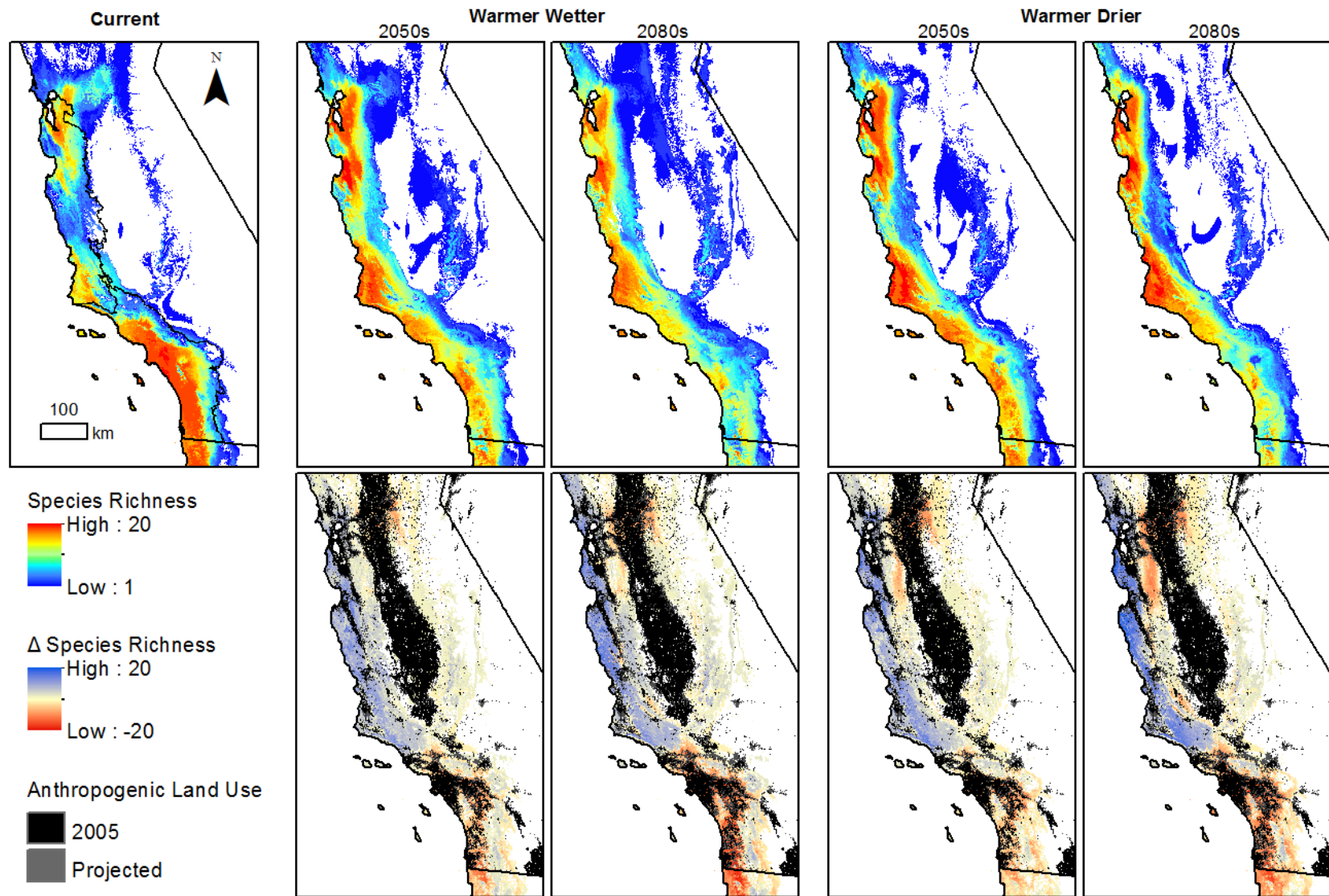


Figure 3.4b. Projected mid-century (2050s) and late-century (2080s) change in species richness under unlimited dispersal with projected anthropogenic land cover-land use. Climate scenarios: warmer wetter (CCCMA CGC 3.1), warmer drier (NCAR CCSM 3.0). Anthropogenic land use includes developed, mining, mechanically disturbed, agriculture, and hay/pasture.

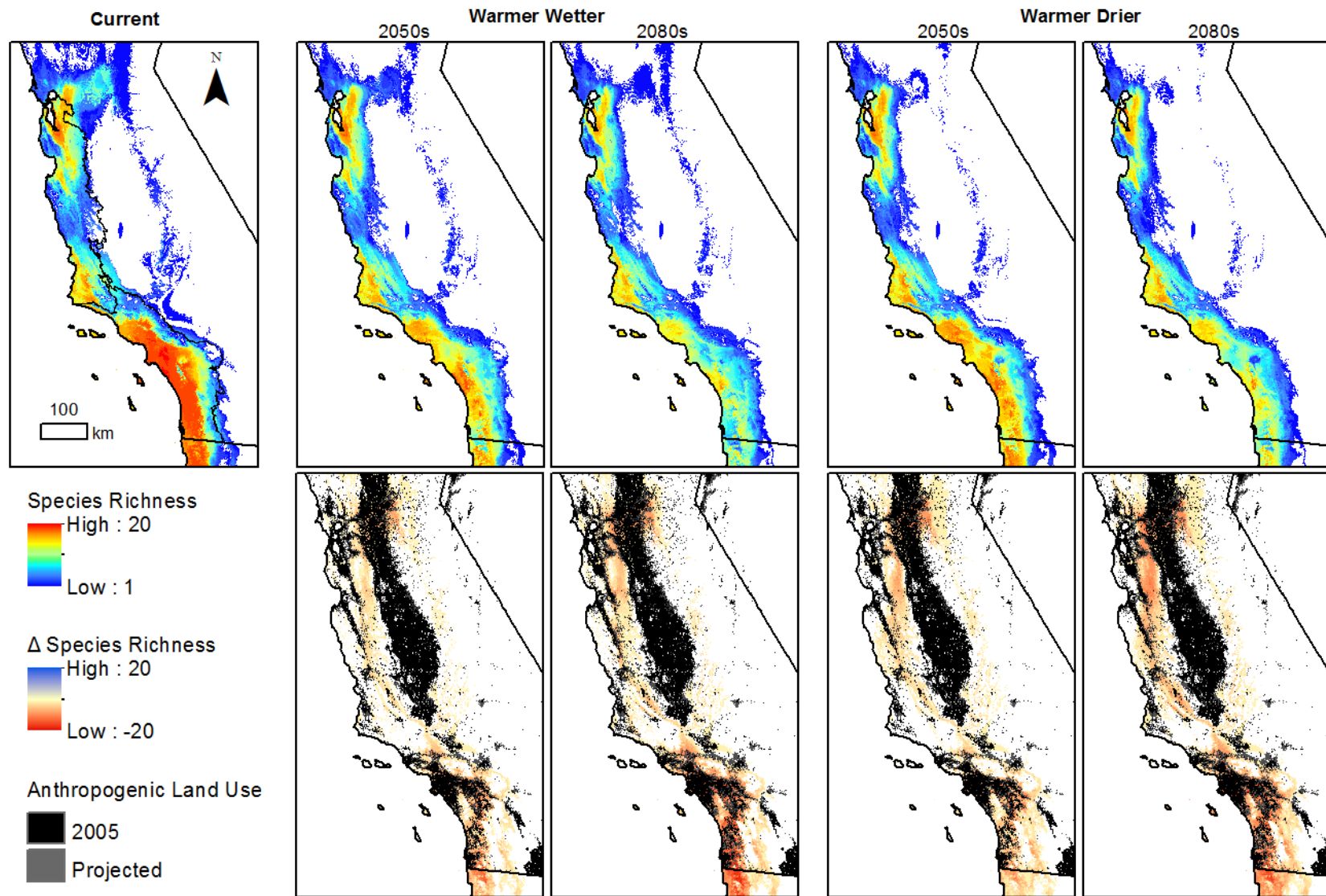


Figure 3.5. Histograms of current and future modeled CSS species richness by percent ecoregion land area. Modeled richness under unlimited dispersal scenarios is shown by a solid line, no dispersal scenarios by a dotted line.

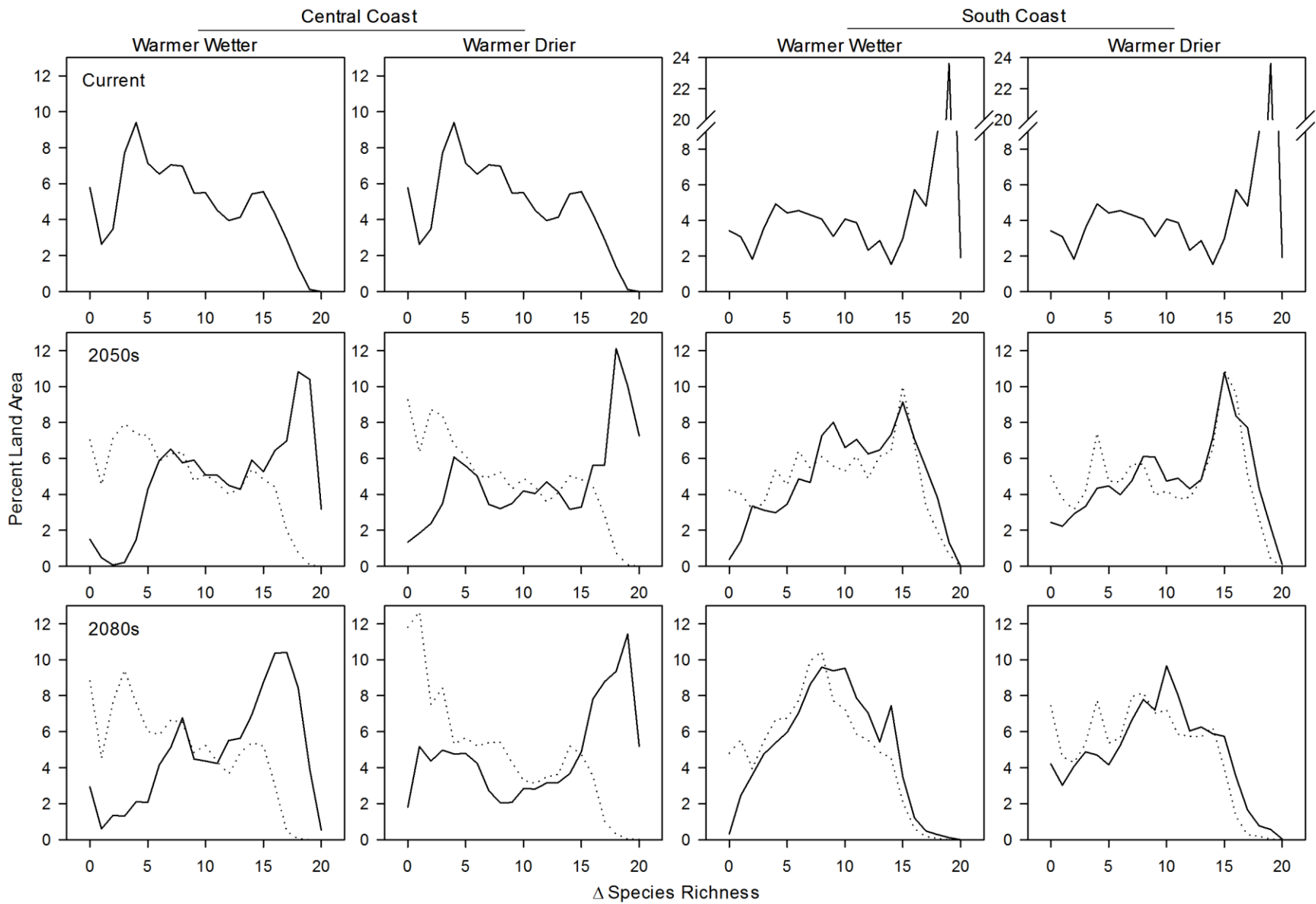


Figure 3.6a. Histograms of current and future modeled CSS species richness assuming unlimited dispersal by percent ecoregion land area for three different projected land use categories: 'natural' designating areas that will remain unconverted under projected land use scenarios, 'natural to anthropogenic' designating areas that are currently unconverted but will undergo conversion to anthropogenic land uses, and 'anthropogenic' designating areas currently converted to anthropogenic land uses that will remain converted in the future. Anthropogenic land uses includes developed, mining, mechanically disturbed, agriculture, and hay/pasture land cover categories; natural includes all other land cover categories. Black lines represent mid-century (2050s) modeled species richness and red lines represent late century (2080s) modeled species richness.

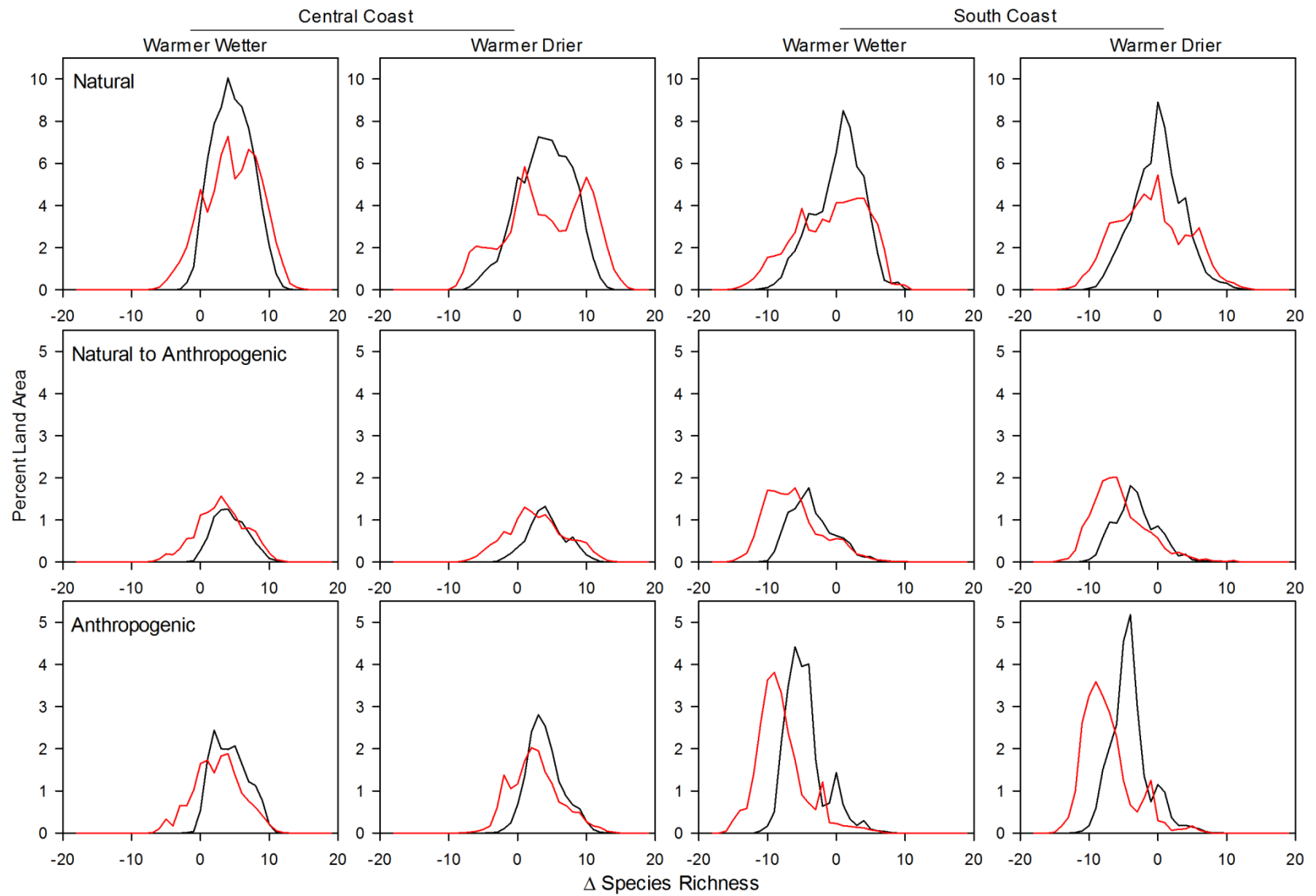
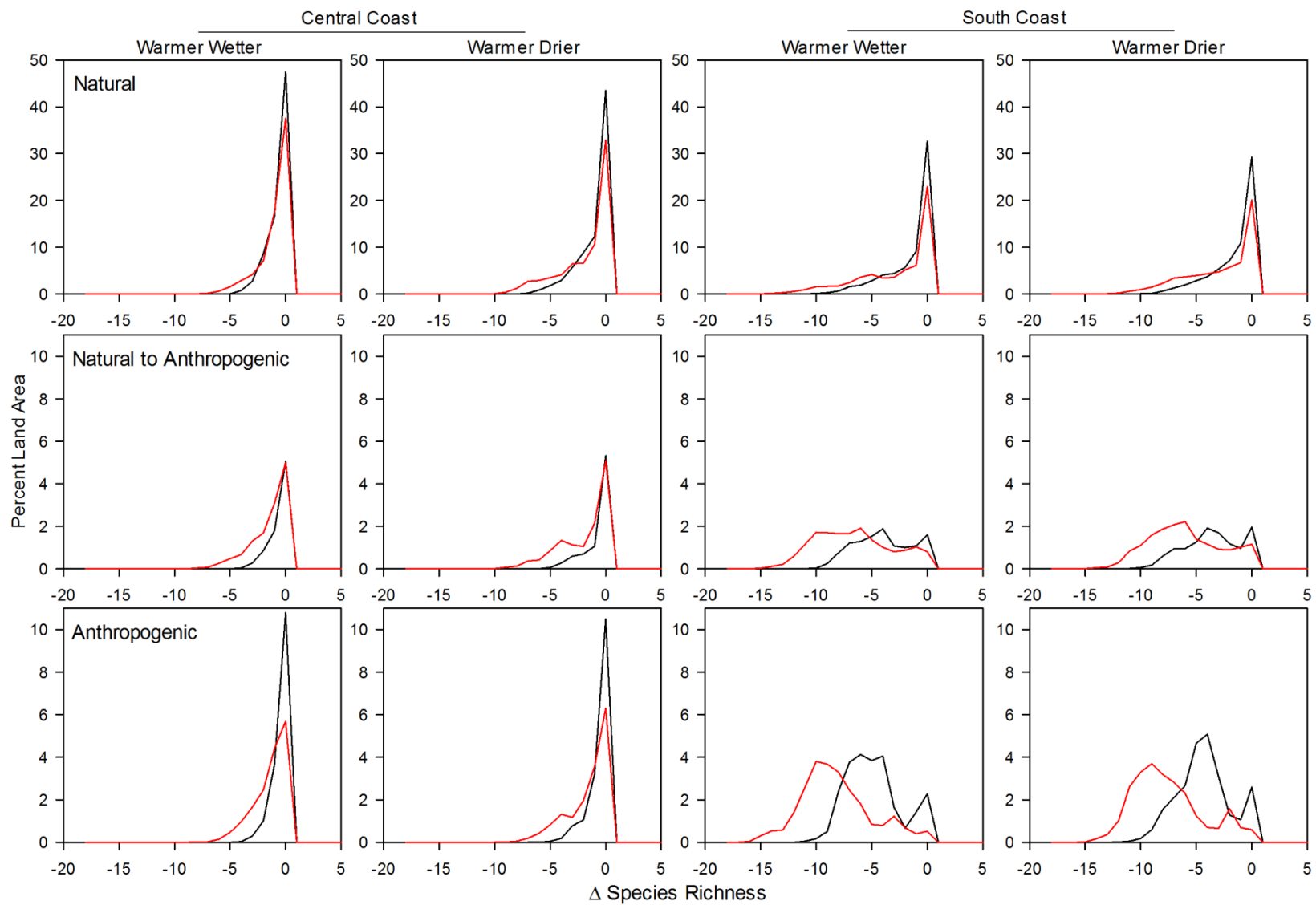


Figure 3.6b. Histograms of current and future modeled CSS species richness assuming no dispersal by percent ecoregion land area for three different projected land use categories: 'natural' designating areas that will remain unconverted under projected land use scenarios, 'natural to anthropogenic' designating areas that are currently unconverted but will undergo conversion to anthropogenic land uses, and 'anthropogenic' designating areas currently converted to anthropogenic land uses that will remain converted in the future. Anthropogenic land uses includes developed, mining, mechanically disturbed, agriculture, and hay/pasture land cover categories; natural includes all other land cover categories. Black lines represent mid-century (2050s) modeled species richness and red lines represent late century (2080s) modeled species richness.



Appendix 3.1. Projected land cover change matrices (2005 to 2050 and 2005 to 2080) for the Central Coast and South Coast California Ecoregions. Change is measured as percent of ecoregion land area. Gray boxes indicate percent of area that is constant between times steps for each land cover category. DE = developed, MD = mechanically disturbed, MI = mining, BA = barren, DF = deciduous forest, EF = evergreen forest, MF = mixed forest, GL = grassland, SL = shrubland, AG = agriculture, HP = hay/pasture, WE = wetland.

2005	2050											
Central Coast	DE	MD	MI	BA	DF	EF	MF	GL	SL	AG	HP	WE
Developed	7.59											
Mechanically disturbed	< 0.01	0.00			< 0.01	0.08	0.02					
Mining	0.02		0.08			< 0.01		< 0.01	0.01			< 0.01
Barren				2.39				< 0.01	< 0.01			
Deciduous forest	0.01	< 0.01			2.55					< 0.01	< 0.01	
Evergreen forest	0.17	0.18	0.01			16.53	< 0.01	< 0.01		0.02	0.01	
Mixed forest	0.02	0.01					5.89			0.01	< 0.01	
Grassland	3.84		0.01			0.01	< 0.01	31.51	< 0.01	1.56	0.56	< 0.01
Shrubland	0.51		0.01			0.01	< 0.01	< 0.01	16.23	0.48	0.47	
Agriculture	1.19					< 0.01	< 0.01	0.01	0.02	3.66	0.06	
Hay/pasture	0.72					< 0.01		0.02	0.03	0.26	2.35	
Wetland	0.04											0.07
South Coast	DE	MD	MI	BA	DF	EF	MF	GL	SL	AG	HP	WE
Developed	19.59											
Mechanically disturbed	< 0.01	0.00			< 0.01	0.04	< 0.01					
Mining	0.01		0.02					< 0.01	0.01			
Barren				1.73								
Deciduous forest	0.02	< 0.01			0.94					< 0.01	< 0.01	
Evergreen forest	0.16	< 0.01	< 0.01			12.67				0.03	0.03	
Mixed forest	0.06	< 0.01					2.66			0.01	< 0.01	
Grassland	3.21		< 0.01					7.64	< 0.01	0.15	0.03	
Shrubland	6.74		0.01			0.01		< 0.01	36.72	1.13	0.28	
Agriculture	1.68								0.07	2.17	< 0.01	
Hay/pasture	0.71								0.02	0.02	0.77	
Wetland	0.02											0.09

2005	2080											
Central Coast	DE	MD	MI	BA	DF	EF	MF	GL	SL	AG	HP	WE
Developed	7.59											
Mechanically disturbed	< 0.01	< 0.01	< 0.01		< 0.01	0.08	0.02					
Mining	0.03	< 0.01	0.06			< 0.01		0.01	0.02	< 0.01		
Barren	< 0.01			2.39				< 0.01	< 0.01			
Deciduous forest	0.01	< 0.01			2.55					< 0.01	< 0.01	
Evergreen forest	0.23	0.14	0.01			16.49	< 0.01	< 0.01		0.04	0.02	
Mixed forest	0.03	0.01				< 0.01	5.88			0.01	< 0.01	
Grassland	5.32		0.01			0.01	< 0.01	28.05	< 0.01	3.10	0.98	< 0.01
Shrubland	0.81		0.01		0.00	0.01	< 0.01	< 0.01	15.10	0.90	0.87	< 0.01
Agriculture	1.59					< 0.01	< 0.01	0.01	0.02	3.27	0.05	
Hay/pasture	0.96					< 0.01	< 0.01	0.01	0.03	0.40	1.98	
Wetland	0.05											0.07
South Coast	DE	MD	MI	BA	DF	EF	MF	GL	SL	AG	HP	WE
Developed	19.59											
Mechanically disturbed	< 0.01				< 0.01	0.04	< 0.01					< 0.01
Mining	0.02		0.01					< 0.01	0.01			
Barren				1.73								
Deciduous forest	0.02	< 0.01			0.93					< 0.01	< 0.01	
Evergreen forest	0.23	0.01	< 0.01			12.56				0.04	0.05	
Mixed forest	0.08	< 0.01					2.63			0.01	0.01	
Grassland	3.96		< 0.01					6.77	< 0.01	0.26	0.05	
Shrubland	9.74		0.01			0.01		< 0.01	32.93	1.89	0.29	
Agriculture	2.11								0.06	1.75	< 0.01	
Hay/pasture	0.86								0.01	0.02	0.62	
Wetland	0.03											0.08

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