Modeling Suitable Habitat Under Climate Change for Chaparral Shrub Communities in the Santa Monica Mountains National Recreation Area, California

by

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ABSTRACT

Species distribution modeling is used to study changes in biodiversity and species range shifts, two currently well-known manifestations of climate change. The focus of this study is to explore how distributions of suitable habitat might shift under climate change for shrub communities within the Santa Monica Mountains National Recreation Area (SMMNRA), through a comparison of community level to individual species level distribution modeling. Species level modeling is more commonly utilized, in part because community level modeling requires detailed community composition data that are not always available. However, community level modeling may better detect patterns in biodiversity. To examine the projected impact on suitable habitat in the study area, I used the MaxEnt modeling algorithm to create and evaluate species distribution models with presence only data for two future climate models at community and individual species levels. I contrasted the outcomes as a method to describe uncertainty in projected models. To derive a range of sensitivity outcomes I extracted probability frequency distributions for suitable habitat from raster grids for communities modeled directly as species groups and contrasted those with communities assembled from intersected individual species models. The intersected species models were more sensitive to climate change relative to the grouped community models. Suitable habitat in SMMNRA's bounds was projected to decline from about 30-90% for the intersected models and about 20-80% for the grouped models from its current state. Models generally captured floristic distinction between community types as drought tolerance. Overall the impact on drought tolerant communities, growing in hotter, drier habitat such as Coastal Sage Scrub, was predicted to be less than on communities growing in cooler, moister more interior habitat, such as some chaparral types. Of the two future climate change models, the wetter model projected less impact for most communities. These results help define risk exposure for communities and species in this conservation area and could be used by managers to focus vegetation monitoring tasks to detect early response to climate change. Increasingly hot and dry conditions could motivate opportunistic restoration projects for Coastal Sage Scrub, a threatened vegetation type in Southern California.

TABLE OF CONTENTS

Page

APPENDIX

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Species distribution modeling (SDM) is used to study changes in biodiversity and species range shifts (Franklin, 2010; Guisan and Thuiller, 2005; Guisan and Zimmerman; 2000), two currently well-known manifestations of climate change (Chen et al. 2011; Thomas et al. 2010; Kelly and Goulden, 2008; Parmesan and Yohe, 2003; Shafer et al. 2001; Iverson and Prasad, 1998). The focus of this study is to explore how the distributions of suitable habitat might shift regionally under climate change for shrub communities within the Santa Monica Mountains National Recreation Area, through a comparison of community level to individual species level distribution modeling. SDM under climate change uses correlative models to project realized niches into potentially non-analogue climate space but the precision of such forecasts cannot be determined (Pearson & Dawson, 2003). A search for congruence in results through varying approaches is one way to explore and describe the uncertainty arising from these projections.

The central premise of species distribution modeling is that environmental requirements for a species can be derived from its observed distribution. In general, species distribution models (SDMs) statistically correlate biological survey data with environmental variables as predictors, and then map potentially suitable habitat in geographic space as a function of those environmental variables (Franklin, 2010; Pearson and Dawson, 2003), capturing the response to those variables that is inherent in a species' spatial distribution. Species level modeling is more commonly utilized, in part because community level modeling may require detailed community composition data that are not always available.

However, community level modeling can be used to derive patterns in community biodiversity that may not be possible through species level modeling (Ferrier and Guisan, 2006). Community models correlate a set of environmental variables to the observed distribution of all the community members simultaneously, rather than limiting this association to a single species, pooling the data from differing locations to detect shared patterns (Ferrier and Guisan, 2006). The advantage of the community approach is that response is embodied within a strong collective signal that might otherwise be missed if modeling at the individual species level (Elith et al. 2006), and it circumvents the need to combine individual species models (Mokany et al. 2011). Recent studies suggest that further exploration into community modeling is warranted (Chapman and Purse, 2011; Baselga and Araújo 2010; Riordan and Rundel, 2009; Wisz et al. 2008; Elith and Leathwick, 2007; Elith et al. 2006; Hernandez et al. 2006; Rehfeldt et al. 2006). Individual and community level approaches can be complementary because they differ in their limitations (Dubuis et al. 2011) and theoretical underpinnings (Guisan and Rahbek, 2011), making a comparison useful.

LITERATURE REVIEW

Climate Change As a Threat To Biodiversity

One of the greatest threats to Earth's biodiversity today is climate change (Thomas et al. 2004; Root et al. 2003; McCarty, 2001). Climate provides the physical template for plant distribution (Brown, 1995) and denotes a particular suite of influences that creates pattern in the spatial variation of vegetation (Box, 1996; Holdridge, 1947). It is expected that under climate change suitable habitat will shift (Thomas et al. 2004), and that plants will compensate by similarly shifting geographic distributions as the primary way to escape intolerable environmental changes (Huntley, 1991).

Climate change may affect not only the distribution of suitable habitat but also the composition of plant biodiversity as individual species shift their ranges, promoting reorganization in their communities (Walther, 2010). Landscape fragmentation is a compounding threat (Thuiller et al. 2005; Davis and Shaw, 2001; Shafer et al. 2001), and could impede community reorganization under climate change, where species may not enjoy the freedom of movement that historically enabled tracking of favorable climate through dispersal. Small-ranged species are vulnerable to extinction due to habitat loss, including habitat loss due to climate change (Pimm and Raven, 2000). This may particularly impact chaparral species in SMMNRA, where dispersal distances for many chaparral species is short (Keeley and Davis, 2007; Syphard et al. 2006).

Conservation Planning In a Nationally Significant Biodiversity Hotspot

The Santa Monica Mountains National Recreation Area (SMMNRA), an administrative unit of the National Park Service (NPS), is the world's largest urban park and comprises approximately 62,000 hectares within a Mediterranean-type ecosystem (MTE). The SMMNRA encompasses the largest expanse of mainland MTE in the national park system, extending 74 kilometers along an east-west direction, from Point Mugu in Ventura County to Griffith Park in Los Angeles County (NPS, FAQs). Its bounds lie entirely within the California Floristic Province (CFP) (Figure 1), an exceptionally diverse phytogeographic region of 29,380,400 hectares that covers most of California. Nearly 40% of the plant species found within the CFP are endemic (Stebbins and Major, 1965).

The CFP, and SMMNRA inclusively, is targeted for conservation priority as a Biodiversity Hotspot. Biodiversity Hotspots feature endemic species, possessing more than 1.5% of global plant diversity uniquely within their bounds, and have lost more than 70% of their original habitat (Myers et al. 2000). Occurring in one of the world's five regions comprising MTE, SMMNRA represents a vulnerable region of biodiversity, where more than 1,000 plant species provide habitat for approximately 500 mammal, bird, reptile, and amphibian species (NPS, n.d.).

Given that globally, MTEs are thought to be sensitive to all global climate change drivers (Sala et al. 2000), climate change is likely to impact both the extent and diversity of plant communities in SMMNRA. In California, climate change is projected to induce shifts in vegetation types, including shrublands (Lenihan et al. 2008; Kelly and Goulden 2008). Within mountainous MTEs, thermophilic and sclerophyllous species in particular (lower elevation species resistant to drought and heat) are projected to shift and increase in range (Ruiz-Labourdette et al. 2012). However, mountainous regions offer high topographic relief, providing microhabitat that can function as refugia habitat to facilitate species persistence (Franklin, et al. 2013), perhaps for species less drought tolerant. Comparing sensitivities between grouped community and intersected species models, as was done for this study, contrasts broader scaled bioclimatic effects of climate change with more topographic mediated climate change effects and may capture refugia habitat.

In addition to anticipated effects of climate change in California and for MTEs in general, the SMMNRA suffers from pressures related to urbanization (Underwood et al. 2009; Swenson and Franklin, 2000). Adjacent to Los Angeles, the second largest metropolitan area in the United States (NPS, 2005), nearly 70,000 people live within its borders in a patchwork of private and parkland property. As an administrative unit, the NPS is required by Congress to manage to preserve and enhance SMMNRA's recreational and scientific value, along with its scenic, natural and historic setting. Anticipating the potential impact of climate change in pragmatic and can help define risk exposure for communities and species in this conservation area.

Justification for Community Modeling

Community-level models are used less frequently than individual species-level models in SDM because paleoecological evidence suggests that species within a community will respond to climate change individually with differing rates and directions, forming new community associations rather than responding as a whole unit (Davis and Shaw, 2001; Huntley, 1991; Graham and Grimm 1990). However, this dichotomous view of plant response as either strictly individualistic or communal is likely oversimplified (Lortie, et al. 2004, Callaway, 1997; Brown, 1995). Shipley and Keddy (1987) demonstrated community assemblages are organized as neither individualistic nor as community units, concluding that plant community assemblage occurs along a spectrum of community to individualist organization. Plant communities buffer effects of environmental change drivers with plant–plant interactions through a variety of mechanisms and interactions (Wisz, et al, 2013; Gilman et al, 2010). Further, the relative effects of species interactions and environmental conditions on survival remains largely unknown (Brooker, 2006). California Mediterranean flora is strongly correlated with climate and geography (Ackerley, 2009), its inertial resistance unknown; here, existing community composition may stabilize selection for reassembly even under shifting climate (Ackerly, 2003).

RESEARCH OBJECTIVES

My overarching objective was to determine which communities are most vulnerable to climate change in SMMNRA. Projecting future changes can assist managers of protected areas anticipate the impacts of climate change on biodiversity. This study tested an application of community modeling; such models are presumably advantageous because managers of protected areas concerned with overall biodiversity may find a synthesized product more useful. Such a product can assist SMMNRA managers with climate change mitigation and contribute to the conservation of this flora.

To explore this objective, I created and evaluated species distribution models with the MaxEnt modeling algorithm at community and individual species levels, using a combination of frameworks described previously (Elith et al. 2010; Riordan and Rundel, 2009; Ferrier and Guisan, 2006). MaxEnt is a machine learning program that estimates the optimal probability distribution to assign continuous probabilities of the occurrence of the target response variable (species) to each pixel in a grid, indicating relative cell by cell probabilities of suitable habitat for the study area (Phillips et al. 2006). I used MaxEnt to generate probability grids in conjunction with a Geographical Information System (GIS) to overlay and compare the resulting predictive models for dominant species in SMMNRA. Future climate data was substituted for current climate data in the models to compare distributions of suitable habitat between levels of aggregation as an estimate of climate change response for each community.

RESEARCH QUESTIONS

1. What environmental drivers are important in the community models versus the species models?

To answer this question, I examined community and species level response curves (relating the probability of species occurrence to the value of each environmental predictor) and the relative importance of environmental variables generated within the modeling process. The importance of particular environmental drivers identified sensitivities to climatic change.

2. Will the extent of suitable habitat for communities currently protected by SMMNRA's administrative bounds remain so under climate change?

To answer this question, I used two complementary approaches:

i. To predict changes in suitable habitat for each community, I overlaid SMMNRA's boundary onto its modeled distribution under current and future climate ("climate change") and extracted the probabilities from cells across the area to derive a set of probability frequency distributions for comparison under each climate model.

ii. I did a similar comparison, but instead overlaid SMMNRA's boundary onto assembled models derived from the intersection of individual species models, and calculated the combined probability value at each intersected pixel to derive a comparative set of frequency distributions under each climate model.

Hypotheses

Question 1

I expected the community models would demonstrate sensitivity to broad-scale climatic variables, and the species models would be more sensitive to finer-scale substrate and topographic variables.

Question 2

I expected the community models would capture a wider range of ecological tolerances than the intersected species models. The response curves for communities should be smoothed relative to individual species with broad amplitude of response because a wider range of environmental tolerances are incorporated into the models. Therefore, the broad response amplitude in the community models will decrease apparent sensitivity to climate change relative to the intersected species models.

DATA AND METHODS

Study Area: The Santa Monica National Recreation Area (SMMNRA) Biogeographical Setting

SMMNRA as an administrative unit covers 62,360 hectares, and includes much of the Santa Monica Mountains, however, an additional 28,000 hectares beyond SMMNRA's bounds is required to define the entire Santa Monica Mountains Zone of about 89,000 hectares. The Santa Monica Mountains form the southernmost mountain chain in the Transverse Ranges of Southern California, with a mean elevation of 304 meters (NPS, 2005).

The California Floristic Province (CFP) is composed of six second-tier regions defined by topographic, climatic and plant community variations. The Southwestern California (SW) second-tier region covers much of southern California, and is bounded by the transition to the desert regions on the east and the peaks of the Santa Ynez Mountains on the north. Within the SW region is the sub-region Transverse Ranges (TR), a third-tier geographical area characterized by its series of west to east-orientated mountain ranges, which collectively become increasingly higher, hotter and drier to the east. SMMNRA (Figure 1) lies within the lowest, coolest and wettest portion of the TR (Hickman, 1993).

Data

Individual species occurrence points and community assemblages. Georeferenced occurrence points from within the SW region were obtained for 23 chaparral shrub species from the Consortium of California Herbaria (CCH) (http://ucjeps.berkeley.edu/consortium/) and the California Department of Fish and Game's Natural Diversity Databases (http://www.dfg.ca.gov/whdab/html/cnddb.html). The data are compiled from a variety of sources, including herbarium records and ecological surveys taken from within the SW region between 1930 and 2004, by agencies such as The California Native Plant Society, The National Park Service and California State Parks. Because the data are derived from multiple sources and due to their arrangement in the databases, they are "presence only" (Graham et al. 2004) because absence is not necessarily known. Occurrence points from historical (1930's) surveys were excluded due to climate change that is thought to have occurred since then (Cayan et al. 2008). Species points total 13,849, with a minimum and maximum of 79 and 1,587, for an average of 717 points per species (Appendix A). The occurrence points extracted from the database for this study are for common shrub or sub-shrub dominants of chaparral shrub communities in SMMNRA and additionally include less common species in SMMNRA, yet are still diagnostic or 'indicator' species (Jennings, et al. 2009) for plant communities.

Presence points in the models. The community models were based on all occurrences for the community indicator species as a group. In other words, duplicate occurrence locations were permitted to accommodate records indicating multiple species occurring in a single location in addition to unique occurrences. The resulting group assembly models give the distribution of suitable habitat for each community in terms of its component species.

In contrast, the individual indicator species models did not contain locational duplicates because ultimately the individual models were assembled into communities by the intersection of overlapping pixels. The intersected models give the distribution of suitable habitat for each community in terms of the overlapping distributions of component species.

After applying models to future climate data and obtaining the probability grids at both levels of data aggregation, I delimited the modeled area encompassed by SMMNRA's bounds to explore the range of outcomes for the management unit.

Basis for species assemblages. To establish baseline and spatial assessments of vegetative communities for conservation planning and inventory purposes, the NPS undertook an extensive vegetation classification and mapping project beginning in 2001; this effort was in accordance with a then-recent mandate to develop and improve vegetative mapping on federal lands. The objective was to develop a classification that met both NPS and US National Vegetation Classification System standards (Keeler-Wolf et al, 2007; Keeler-Wolf and Evens, 2006).

The US National Vegetation Classification System defines vegetation types hierarchically (Jennings et al. 2008), and this study focused on two levels in that hierarchy, the Alliance and Association. A vegetation alliance is defined based on the dominant (or diagnostic) species of a vegetation stand. The presence of one or more dominant species are a reflection of regional to sub-regional climate, substrate, hydrology, moisture, nutrients and disturbance regimes, while an association is more narrowly defined by a recurring species composition as a response to all the above but additionally to topo-edaphic factors (Jennings et al. 2008). For the NPS Vegetation Classification, these groups were refined to the association level by factors such as elevation, slope, aspect, soil texture and geology, and were used in part to develop and map broad “ecological zones” defined by maritime, upland-continental, hot and dry or moist and shady conditions within SMMNRA (Keeler-Wolf et al. 2007).

I used combinations of these associations to create the eight species assemblages as a basis for modeling. To generalize the range of tolerance outside SMMNRA for the community assemblages and to improve model calibration, I combined associations within alliances if their distributions within SMMNRA’s ecological zones more or less overlapped to create assemblages composed of species that will similarly respond to environmental variations over the SW region (Listed in Appendices B and C).

I could not group Coastal Sage Scrub (CSS) assemblages similarly because most associations contained less widespread species (e.g. *Eriogonum cinereum*) or were associated with a variety of “phases”, an association sub-category, or disturbance (Keeler-Wolf and Evens, 2006). To generate species assemblages incorporating similar environmental responses for CSS, I combined species sharing broad response to temperature and moisture gradients as above (Keeler-Wolf, et al. 2007), then refined by comparing to updated classifications (Davis et al. 1994) previously classified by Axelrod (1978) and then Westman (1981). The mapped distributions for the CSS communities are given in Figure 2, South West Ecoregion Modeled Distributions for CSS.

In the study region, the range of recurring species composition creates a mosaic of vegetation that makes organization even at the alliance level difficult (Keeley and Davis, 2007). To represent the vegetation realistically, I shared (overlapped) species between assemblages. To construct the eight assemblages, I used the 13,849 occurrence points for a total of 22,955 points within the assemblages, where 9,106 of those points were used more than once, or about 40% of the points.

Climate models. Models were developed using the PRISM (Parameter-elevation Regressions on Independent Slopes Model) current climate dataset, comprising monthly climate averages for the period of 1971-2000 (www.prism.oregonstate.edu). This model was interpolated utilizing local regression techniques to account for spatially varying elevation relationships and terrain induced climate transitions, suitable for California's high topographic relief (Daly, 2006).

To encompass a range of outcomes for comparison, models trained on current climate were projected onto two future climate models for one emissions scenario averaged for years 2071–2100 to generate two modeled outcomes for each community or species. I used the National Center for Atmospheric Research and Department of Energy group's Parallel Climate Model (PCM1) and the National Oceanic Atmospheric Administration Geophysical Fluid Dynamics Laboratory (GFDL) group's CM2.1 General Circulation Models (GCMs), under the Intergovernmental Panel on Climate Change A2 emission scenario (Cayan et al. 2008). These climate models were used because they accurately reflect California's historical (late nineteenth and entire-twentieth century) precipitation and temperature regime, in addition to its spatial structure (Cayan et al. 2008). In general, the GFDL GCM projects a warmer and drier future, with warmer temperatures and less precipitation relative to PCM 1model projections.

I used the less conservative (A2) of the two available emission scenarios used to force the models because it is estimated that actual C02 concentrations have already exceeded this projected threshold (Sitch, et al. 2005). I refer to these models as PCM A2 and GDFL A2. According to both models, California will generally experience more warming in summer than in winter (but with relatively less warming for PCM A2), with the majority of precipitation continuing to occur in winter. However, the PCM A2 model projects a wetter future and change in the precipitation regime, with an extrinsic fall season peak for southern California where precipitation currently occurs nearly exclusively in winter (Cayan et al. 2008).

Environmental variables. I used a set of 11 eco-physiologically appropriate bioclimatic and terrain variables (Appendix D) previously used for modeling plant species' distributions in this region (Franklin et al. 2013; Franklin, 1998; Franklin, 1995). A combination of terrain and bioclimatic temperature and moisture-related variable is necessary, at least for individual species models, to model the realized niche (Gioia and Pigott, 2001). Terrain variables such as slope and potential summer solstice solar insolation were derived from the U.S. Geological Survey's 30-m resolution digital elevation model. Soil depth, available water capacity and pH were obtained from the State Soil Geographic Data Base (STATSGO; details in Appendix D). The remaining bioclimatic variables were selected and derived as described in Franklin et al. (2013). The PCM A2 and GDFL A2 models were spatially downscaled to 90-m resolution to accommodate California's topographic variability (Flint and Flint, 2012). I have resampled the environmental data, including the climate data, to 100-m (1 hectare) resolution.

Species Distribution Models

MaxEnt. The MaxEnt modeling algorithm is one of the most accurate and effective machine learning algorithms used to develop predictive models utilizing presence only data (Elith et al. 2010; Elith et al. 2006; Graham et al. 2008). In general, generative or inductive machine learning methods are appropriate for large and complex datasets. MaxEnt has been shown to accurately capture known response curves with simulated data (Elith and Graham, 2009) and is particularly suited for regional modeling (Elith et al. 2006). MaxEnt has successfully been used to model Coastal Sage Scrub communities in this region (Riordan and Rundel, 2009).

MaxEnt's algorithm estimates the probability distribution of maximum entropy, as derived from patterns found within the data. It estimates the optimal probability distribution from which it is assumed that the presence data are drawn (Phillips et al. 2009). The best model output (as a set of probabilities) is that which creates the most uniform distribution, or where the distribution is closest to the average observed distribution based on habitat occurrence likelihoods over the entire dataset. It yields the conditional probability of presence, given a particular set of environmental conditions, where the response variable is the probability of a site being suitable. The output is a grid of probabilities that refer to the likelihood of suitable habitat being found in that pixel (Phillips and Dudik, 2008).

Current climate SDMs.

Settings. Community models for current climate were run using MaxEnt software, version 3.3.3k (Phillips, et al. 2006, http://www.cs.princeton.edu/~schapire/ MaxEnt/). I did not use the default settings for MaxEnt, but instead followed best practices for reliability and projection to novel conditions as recommended in Elith et al. 2010, varying the regularization parameter to 2.5 (to “enforce smooth responses”) and using “hinge only” features (Phillips and Dudik, 2008) to build a more generalized and GAM-like model (Elith et al. 2011). Additionally, I “jackknife sampled” my data into train and test partitions (Fielding and Bell, 1997) of 60/40 ratio respectively, using the subsample and random seed settings to divide training and test data into ten random partitions. Ten replicates were run for each community model to derive the average behavior of the models (Phillips et al. 2006). Individual species’ models for current climate were run using the same settings.

To compensate for spatial and environmental bias in occurrence locations, I used the “samples with data” (SWD) format to implement a restriction on background points (Phillips, 2011). Spatial bias may be distinct from environmental bias, if spatially biased localities successfully capture the relevant range of environmental conditions (Elith et al. 2011). In contrast, environmental bias violates the assumption that localities in environmental space are random, such that the biased representation of environmental conditions is disproportionate to the true conditions (Phillips et al. 2006; Phillips et al. 2009).

The data points I used are spatially biased, with 86% located within SMMNRA’s boundary (Table 1; Figure 3). A first run of the community models predicted high probabilities within SMMNRA for all communities and low probabilities elsewhere over the SW region, without much differentiation between communities. This suggested environmental bias. I determined that my data were environmentally biased using a null model procedure to compare the real SDMs built with the environmental conditions associated with actual occurrence points to models run using the same number but randomly drawn points taken from a representative environmental grid covering the entire SW region (Raes and ter Steege, 2007) (Figure 4).

To correct for environmental bias, essentially factoring it out (Dudik et al. 2006), I used a Target Group Background (Phillips et al. 2009; Phillips Dudik, 2008), rather than allowing MaxEnt to draw background points randomly over the entire SW region. In this case, MaxEnt restricts the background data it draws from to the locations of presence points for all the species, so that both presence points and background points used to construct the model share the same sampling bias. In addition, restricting the background focuses differentiation between occupied and unoccupied sites to the local area and may refine the model (e.g. Figures 5 and 6) (Bystriakova et al. 2012; Elith et al. 2011; Phillips et al. 2009).

Calibration/Validation. To improve accuracy and calibration for current climate relative to known distributions, models were developed for the entire SW region to encompass the core of the ranges for most of the constituent species of the SMMNRA communities. To assess which models might be less trustworthy for future climate prediction, all calibration/validation analyses were conducted on both the community and single species models before projecting. The collection of performance metrics described below allowed me to gauge which models might project more successfully than others.

Visual assessment: Correspondence between areas of high predicted probability and occurrence points can indicate the model is fitted well. I overlaid occurrence points onto modeled results to assess the fit to current climate. Additionally, MaxEnt generates a series of plots, or “response curves”, depicting the probability of species presence as a function of each of the predictor variables. I used these plots along with the modeled distributions to evaluate their plausibility based on known environmental tolerances for the community or species.

Quantitative Assessment. MaxEnt output generates a number of performance metrics: the fractional predicted area, the extrinsic omission error rate, test gain and the AUC (Phillips, 2011). The fractional predicted area and extrinsic omission rate are related and are useful indicators of model performance. The extrinsic omission rate provides a measure of model over-fitting. A model with a high omission error rate predicts to an area that is too small, is overly specific, and incorrectly excludes true positives from the predicted area (because the fractional predicted area in the model is small). Low omission error rates indicate that false negatives are low (so true positives are higher), increasing the certainty that the species would actually be found where the model predicts (Fielding and Bell, 1997).

However, for presence only data models, low omission error rates are a better measure of over-prediction than for over-fitting because the omission rate is estimated as presence distinguished from random (as background data) rather than from true absence because absence is not known. The lack of true absence data could cause model over-prediction due to decreased characterization of unfavorable sites (Pearson et al. 2006). An over-predicted model predicts an area that is too large and is overly general or sensitized because it incorporates too many false positives. A model that reduces over-prediction reduces the number of false positives and so predicts to a smaller area. A good fitting model balances over-prediction and over-fitting, predicting to the smallest predicted fractional area with the lowest extrinsic omission error (Anderson et al. 2003).

As a metric of model fit, MaxEnt calculates the fractional area predicted to be suitable if the logistic probabilities were converted to binary data over a range of threshold values. MaxEnt then uses the fractional area predicted to calculate the extrinsic omission error rate for test data falling outside the predicted area. The extrinsic omission error rate is the fraction of the test localities that fall into pixels not predicted as suitable by the model. A 10% extrinsic omission error rate corresponds to a threshold where the model is neither over-fitted nor over-predicted (Anderson et al. 2003). I used MaxEnt's Cumulative 10% Omission rate to assess model predictive power without actually converting to binary values.

Test gain is a measure of goodness-of-fit, and indicates how closely the model is concentrated around the presence samples. In MaxEnt, the value given to the gain for the model is the exponent on e indicating the average likelihood of the presence samples relative to a random background pixel; the greater the gain the better the model fit (Phillips 2011).

The area under the curve (AUC) uses test data to calculate model performance over all fitted thresholds. The AUC refers to the area under the curve relative to a receiver operating characteristic (ROC) curve and quantifies the ability of the model to discriminate observed presences from observed absences (Fielding and Bell, 1997). For presence only data this definition is again modified, where AUC scores represent the ability of the model to distinguish presence data from background data, rather than distinguishing presence from absence. For presence only data, the AUC characterizes the probability that a classifier will assign a randomly chosen positive instance more often than a randomly chosen negative (or background) instance (Phillips, et al. 2006).

AUC measures relative ranking of predictions and can be used to compare relative model performance but does not assess the model's fit (Lobo et al. 2008). However, the AUC has been previously utilized to assess MaxEnt performance in this region (e.g., Riordan and Rundel 2009; Saatchi et al. 2008), and so I provide AUC values for comparison.

Finally, MaxEnt calculates a one-tailed binomial test on the significance of its predictions, assessing the ability of the model to correctly classify the test data points as presences within the predicted area as compared to random background points, given the same predicted area (Phillips, et al. 2006). I used this to verify that the models are valid.

Future climate SDMs. For each community and modeling approach, I re-estimated a model based on current climate using the same settings described above but did not divide my data into train and test partitions because using the complete data set will on average build the best model for projection (Fielding and Bell, 1997). I then projected each model onto each future climate scenario by using each set of future climate grids as projection layers in MaxEnt. Additionally, to allow for conservative prediction I "clamped" the models.

MESS maps and clamping. When projecting a model onto another climate, MaxEnt generates a file representing "novel" environmental conditions as part of the multivariate environmental similarity surface (MESS) analysis. It calculates a measure of similarity of the training and prediction environments to quantify the extent of extrapolation between the current climate and the projected model. It is species independent and is a measure of the differences between climates. MaxEnt uses the "novel" file to generate its "clamping" layer, showing values for which the model would be required to fit outside the training range of the variables. These are treated as if they exceed the tolerances of the species, zeroing out the species response where this occurs. Clamping the model means that it is not required to extrapolate beyond the range for which it was calibrated (Thuiller et al. 2004), reducing uncertainty. I applied the "clamping" option to the future climate projected models, so that the response is constant where values for projected environmental variables exceed those found under current climate (Phillips, 2011).

Methods to Answer Question 1. What environmental drivers are important in the community models versus the species models?

Most important variables. MaxEnt determines variable importance by a jackknife procedure and importance is measured by a decrease in AUC based on training gain (Phillips, 2011). The variable with the lowest gain (and hence the largest change in gain when the variable is dropped in the jackknifing procedure) is the most important variable (Elith et al. 2010). The drop in AUC is displayed as a percentage in a table as "permutation importance". To identify the most influential community predictors, I used this table to identify variables with an importance value greater than or equal to 10 percent

Explain Tool. Additionally, for projected models, MaxEnt calculates a multivariate environmental similarity surface (MESS) with an "explain tool" that produces a clickable map allowing the user to view the fitted response functions of the model at any point. Because I used the SWD format in my models, I was able to utilize this tool under current climate because I am "projecting" onto current climate. To create images and maps for distribution models trained using the SWD format, a raster environmental layer must be used for the projection (Phillips, 2011). "Projecting" the model onto current climate allowed me to use this tool to examine areas of high or low prediction accuracy in terms of response curves at specific locations to aid in ecological interpretation and comparison between models.

Methods to Answer Question 2. Will the extent of suitable habitat for communities currently protected by SMMNRA's administrative bounds remain so under climate change?

Probability frequency distributions. MaxEnt provides a logistically scaled (Phillips and Dudik, 2008) probability surface ranging from 0 to 1 that can be imported as a raster into a GIS for analysis on a pixel by pixel basis. I applied a GIS overlay of SMMNRA bounds onto the probability grids to obtain frequency distributions of the probabilities for community and individual species models under both current and future climate models.

I extracted the probabilities directly from the community models to obtain their frequency distributions. To obtain probability frequency distributions from the individual species models as representatives of my defined communities, I intersected their probability grids. At each pixel intersection, pixels were averaged as a geometric rather than an arithmetic mean to ensure intersected grids combined all component species yet did not exclude those with very small values. I extracted the combined pixels to derive the frequency distribution for the probabilities within the area for the assembled communities.

I compared the set of frequency distributions from current climate models for each community and intersected species models to those for future climates to obtain a summary of projected change in habitat suitability within SMMNRA.

Significance testing on probability frequency distributions. Two non-parametric tests measured significance of climate change response. A two-tailed Wilcoxon Matched Pairs Signed Ranks T Test compared changes in median values as response to climate change by organizational level. The expectation was that if community models are less sensitive to climate change, differences in median values for the community models would be non- or less significant than for the intersected models. A Wilcoxon-Mann-Whitney test compared inter-community differences for changes in median values as response to climate change for both intersected and modeled communities separately.

Marginal response curves smoothness: *Standard deviation.* As a measure of response curve shape, the standard deviation on the y axis for marginal response curve plots was calculated for each model for all environmental variables concomitantly important for communities and their component species. Smaller values were thought to indicate less variability on the amplitude and spread of the range on y for the response variable, resulting in a flatter curve. I used this measure to determine if the community models more often exhibited a generalized, or less variable, response as hypothesized in Question 2.

Marginal response curves smoothness: Gower's General Coefficient of Similarity. As a more comprehensive measure of response curve shape, I used Gower's General Coefficient of Similarity (Gower, 1971) to calculate a matrix of similarities for measurements derived from response curve plots for variables commonly important for species and the community. The calculation compared the minimum, maximum and standard deviation for y and the area under the curve for all pairs (note that this area under the curve of the response plots is different from the AUC of the ROC plot that was used as a measure of model performance). I used this measure to compare relative similarity in response curve shape for species and communities as another method to evaluate community model generalization.

RESULTS

Current Climate

Model fit. The best fitting models had the highest values for test gain with the lowest predicted area (Appendix E). The *Ceanothus cuneatus* and the Venturan CSS communities had the best fitting models. The *Ceanothus cuneatus* community had the highest value for test gain (0.281), with the second lowest value for predicted area (0.736), while the The Venturan CSS community had the second highest value for test gain (0.223), with the lowest value for predicted area (0.709) The *Ceanothus megacarpus* community was the worst fitting model and had the lowest value for test gain (0.085) with the highest predicted area (0.792). The test AUCs ranged high to low for the same communities, 0.701, 0.686 and 0.559 respectively. All model omission rates were significant according to MaxEnt's calculated one-tailed binomial test, indicating all the models correctly classified the test data points as presences at a statistically significant level (not shown) relative to background samples.

The species models had higher test gain and AUC values, with lower predicted area values and omission rates (Appendix E). Riordan and Rundel (2009) found group models were likely to over-predict the distribution specific to individual species, and similarly, the community models in this study were fitted less well. For both species and community models, there was a tendency for the rarest species (defined by low number of presence points) to have better fitting models, as has been previously noted (Syphard and Franklin, 2010; Hernandez et al. 2006; Brotons et al. 2004). Overall, the values for test gain are low, particularly for the community models (Appendix E) but are not necessarily less accurate. Because the data points used in this study were spatially and environmentally biased, (Data and Methods: Species Distribution Models, page 14) I used Target Group Background (Data and Methods: Species Distribution Models, pages 14-15). The models were created using a set of background points restricted to the occurrences for all the species which may or may not include presences. This decreases the likelihood that a test data point will be distinguished from a randomly selected background pixel, thus decreasing the values for both the test AUC and test gain. Moreover, due to the way presence only data models are constructed, the AUC > 0.7 "good model" standard does not apply, and models with low AUCs may not reflect decreased model accuracy but rather a broad niche amplitude or habitat generalism (Raes and ter Steege, 2007, Lobo et al. 2008). Values for test AUC and test gain can nevertheless be used to compare relative accuracy between models within this study, or between studies. For example, AUCs and test gain values are similar in relative rank for six species I have modeled in common with Riordan and Rundel (2009).

Intersected species models versus modeled communities. As expected, the community models captured a wider range of ecological tolerances. Variable selection between species and community models differed. Topographic and substrate level variables were important in the species models only, confirming the hypothesis for Research Question 1, that species models would demonstrate sensitivity to topographic variables more often than the community models. The difference helps to substantiate the model set and confirms the models represent a range of ecological tolerance. The community models represented the union of environmental tolerances for component species, because suitable habitat requirements were pooled and incorporated into the model. In contrast, the intersected species models, calculated as the geometric mean of stacked individual models, were more restrictive because low to zero values within a pixel for one species lowers or eliminates suitability for the other species. Therefore, the intersected community models were less inclusive, while the modeled community models were more inclusive.

Community models appeared more diffused and predicted to a larger area because the less inclusive intersected species models incorporated a larger proportion of small pixel values. Medians for pixel value distributions for intersected models were consistently lower in all cases for both current and future climate, with exceptions for the *Ceanothus megacarpus* and Diegan CSS communities, where both were about equivalent. The contrast between intersecting and modeling communities directly is illustrated in Figure 7 for the *Ceanothus cuneatus* community within the study area. In Figure 8, boxplots show the distribution of suitable habitat probabilities within SMMNRA for all pixel values from the modeled grids corresponding to Figure 7.

Environmental drivers: Community models. With the exception of Soil pH for Scrub Oak, all important environmental drivers for community models were climatic at the ≥ 10 percent permutated importance threshold. Overall, the variables chosen by MaxEnt as most important for these models fit expectations, indicating that collectively modeling dominants captures bioclimatic trends influencing distribution.

Precipitation of Warmest Quarter (BIO18), a measure of summer rain, was the most frequently important in the community models, and was important for all of them (Figure 9; Appendix F). Response curves indicated that probabilities for suitable habitat varied similarly among communities, increasing sharply at the lowest values (< 20 mm) before leveling off. Exceptions were for coastal Diegan and Venturan CSS, where response curves dipped sharply rather than leveling off at >20 mm.

The Aridity Index, or Annual Precipitation/Potential Evaporation (BIO24) was the second most frequent important variable, for 7 of 8 communities. Riversidean Scrub, Diegan and Venturan CSS responded negatively to decreasing Aridity (values > 50), along with the *Ceanothus megacarpus* and *Ceanothus crassifolius* communities, while the more mesic Scrub Oak and Northern Mixed communities responded positively (values > 100). The *Ceanothus cuneatus* community responded similarly (though BIO24 not ≥ 10 percent important).

Temperature Seasonality (BIO4), a proxy for coastal proximity, was important for 5 of the 8 communities: all 3 CSS, *Ceanothus megacarpus* and the *Ceanothus cuneatus* communities. The response curve for Venturan CSS was highest at the lowest values for Temperature Seasonality, i.e. coastal, very low elevation habitat. Riversidean Sage Scrub response was low at both low and high values, peaking at mid-range. Diegan CSS and *Ceanothus megacarpus* were intermediate to Venturan and Riversidean Scrub, while *Ceanothus cuneatus* favored the highest values, or least coastal, high elevation habitat.

Temperature of Warmest Month (BIO5), a measure of summer temperature intensity, was important for 4 or the 8 communities. Of these, the most heat tolerant was Riversidean Sage Scrub, followed by the *Ceanothus crassifolius* community, with Diegan CSS and *Ceanothus megacarpus* communities being about equivalent.

Cumulative Growing Degree Days above 5 C degrees (BIO20), a measure of growing season length, was important for 2 communities, Venturan CSS and *Ceanothus crassifolius*, both preferring high values. Soil pH was important for Scrub Oak, the only topographic variable important in any of the community models. Annual Precipitation (BIO12) was ≤ 10 percent important for all modeled communities, suggesting the importance of precipitation seasonality rather than its annual amount.

Environmental drivers: **Species models**. Temperature Seasonality (BIO4) was the most frequently important variable in the species models. Of 32 species models, Temperature Seasonality was important for 23 of them. Nearly all the CSS-type species models favored low values (coastal, temperature modulated habitat). The exceptions were *Salvia apiana*, favoring higher values for Temperature Seasonality (and belonging to the “interior” CSS community, Riversidean Sage Scrub), and *Artemesia californica* and *Rhus ovata*, responding neutrally (variable ≤ 10% important). Other non-CSS type examples for species favoring high values (interior habitat more likely to experience freezing temperatures) were *Ceanothus cuneatus* and *C. leucophylla*.

Precipitation of Warmest Quarter (BIO18) ranked a close second in frequency of importance, and of 32 species models it was important for 22 of them. Species favoring low values (little summer rain) were generally coastal. Soil pH (PH) was important for 7 species models, Available Water Capacity (AWC) and Potential Summer Solstice Solar Insolation (SUMRAD) were each important for 4 models. Appendix Table F gives a full account of variables with ≥ 10 percent permutated importance for both species and community models. Table 2, Community and Species Model Variable Selection Comparison gives a more succinct view summarizing the contrast between variables selected as important in the community models with those in the species models. Figure 9, Frequency of Variable Importance ≥ 10 Percent Permutated Value gives the frequencies for variables selected as important in all the models.

Marginal Response Curves Smoothness.

Standard deviation. For Research Question 2, I hypothesized that the community response curves would appear smoothed, or generalized relative to the species response curves, but calculating the standard deviation on the Y axis as a measure of model generalization did not confirm this expectation. I expected that for the species models, the standard deviation on the y axis for response curve plots would be greater more frequently than for the community models, though it was more often lower, with greater values occurring in only 38% of cases for equivalent variables (Appendix G, Standard Deviation on Y Axis for Marginal Response Curve Plots).

***Gower Similarity Coefficient Matrices*.** **Si**milarity coefficients indicated that response curves for the community models are generalized, confirming in part the hypothesis for Research Question 2. If community response curves represent a collective average of component species' curves, similarity should be greater among species relative to the community curves (down column one for each matrix) than among species (the remaining comparisons within each matrix). The rate for dissimilarity between species and communities in column one was consistently less than the rate for dissimilarity between species, indicating that species curves were more often similar to their collective average for the community. Coefficient values exceeding 0.5 were considered dissimilar; the rate of dissimilarity between values in column one exceeded or was equivalent to that for the remaining values within the matrix in only two cases (Appendix H; rate calculations not shown).

Figure 10, Response Curves for Temperature Seasonality (BIO4) for Modeled Scrub Oak Community gives an example illustrating how, by visual inspection, community curve shapes seemed an aggregate of the more variable shapes for the component species, appearing to represent their collective average.

Future Climate

Summary community response to climate change. Across the SMMNRA study area, suitable habitat is predicted to decrease for most communities under both climate change GCMs for either modeling approach, with exceptions for community modeled Riversidean Sage Scrub and Diegan CSS. The intersected species modeling approach predicts a relatively greater percentage decrease in summed probabilities for suitable habitat (30-90%) than the community modeling approach (20-80%), with the exception of the *Ceanothus megacarpus* community under the PCM A2 climate model. Generally, the greater percentage decrease in suitable habitat predicted by the intersected approach occurred when using the GFDL A2 climate model, the warmer and drier of the two climate models (Figure 11; also Appendix I, 1-8, Box Plot Graphs by

Community). Numerical values for the summed probabilities as extracted from modeled grids for all models are given in Table 3. Less impact under the PCM A2 model is supported by an earlier simulated model study projecting that an increase in precipitation as a result of climate change could mean less stressful conditions for shrubland species here (Malanson and O'leary, 1995), and their ability to facultatively respond to increased summer rain (Minnich, 1985).

Differences in community median habitat suitability between current and averaged future climates models was significant ($\alpha = 0.05$) based on a two-tailed Wilcoxon Matched Pairs Signed Ranks T Test ($p = 0.02344$ for community models; $p = 0.007813$ for intersected models, confidence level 0.95). Both modeling approaches predict a significant decline in habitat suitability for these communities in response to climate change, but the p value for the community models was less significant than for the intersected models. Significance indicates that median differences between pairs of samples (before and after climate change across communities) are not random. This result confirms the hypothesis for Research Question 2, that the increased range of environmental tolerances present in the community models will decrease their apparent sensitivity to climate change relative to the intersected models.

***Prominent Trends*.**

Community models. All non-CSS community responses were highly statistically significant (Table 4). The decrease in suitable habitat for the community models was generally attributable to GFDL A2, except for the three CSS/Scrub communities, for which habitat suitability either increased or was less affected. Group level community models indicated that suitable habitat for all three CSS communities will decrease less for climate change conditions (Figure 11, Community Response to Climate Change as Percent Change in SMMNRA Suitable Habitat Probability Sums). Suitable habitat for Riversidean Sage Scrub increased under the GFDL A2 GCM, and for Diegan CSS, it increased for both GDFL A2 and PCM A2 climate models. Venturan CSS was less affected using GFDL A2 than PCM A2. A Wilcoxon-Mann-Whitney test indicated that differences in median probability values between communities for averaged climate change response were less significant for the Riversidean Scrub and Venturan CSS modeled communities (Table 4). Significance indicates the samples (as probabilities sampled from each community for current and averaged climate change) do not come from populations with identical distributions and are distinct from one another. Diegan CSS was not differentiated along with the other two CSS communities as less significant because the test was two tailed, so significance was detected in either direction. Consequently, the change in suitable habitat for Diegan CSS was similar in magnitude for significance for non-CSS communities, though in the positive direction to indicate habitat gain. In contrast, for non-CSS communities predicted habitat decline was greater. Of these communities, Northern Mixed and Scrub Oak shared the largest negative response to climate change (Figure 11).

Intersected models. The response to climate change differed somewhat when species were intersected to form communities. CSS and non-CSS communities were not statistically distinguishable. Rather, statistical significance between communities for response to averaged climate change was indicated for all the communities, except for the *Ceanothus megacarpus* community (Table 4). As an intersected model *Ceanothus megacarpus* community habitat was predicted to decrease much less under the PCM A2 climate model compared to all other communities. This was an exception in the intersected models. Like the modeled communities, the percentage decrease in probability sums for GFDL A2 was greater than for PCM A2, but decreases for PCM A2 were comparable to GFDL A2 (or relatively greater) and therefore more pronounced in the intersected models.

Consistency across modeling approach and climate models. The chaparral models were consistent across modeling approaches. The predicted decline in habitat for chaparral models differed in magnitude somewhat but retained their relative relationships between GCMs. Generally all chaparral habitat will be worse off if climate change presents as the GFDL A2 GCM (hotter and drier), especially for the Northern Mixed, Scrub Oak and *Ceanothus cuneatus* communities. Of the chaparral models, the *Ceanothus megacarpus* community was particularly consistent and nearly identical across modeling approaches. The *Ceanothus megacarpus* community was predicted to be the least impacted for any chaparral community, but this nonetheless corresponds to a decline of about 40% for suitable habitat. Habitat for this community was predicted to decrease minimally (2-3%) if climate change presents as the PCM A2 GCM (Figure 11).

The CSS models were less consistent across modeling approaches. The intersected models differed in magnitude and varied in their response and sensitivity to GCMs (Figure 11). For Riversidean Sage Scrub and Diegan CSS, positive response in the modeled communities to GFDL A2 became negative when species were intersected, with a larger net decrease for Diegan CSS. Venturan CSS decreased markedly when intersected (Figure 11; Appendix I, Box Plot Graphs by Community: Figures I-3 for Diegan CSS and I-8 for Venturan CSS). For Riversidean Coastal Sage Scrub, the predicted small increase in suitable habitat for GFDL A2 reversed when the species models were intersected because habitat for *Salvia apiana* and *Rhus ovata* decline more than for *Eriogonum fasciculatum*. Diegan CSS habitat is predicted to increase when species are modeled as a group for both GCMs but decreased when individual responses were intersected due to *Encelia californica* sensitivity to both GCMs, *Artemesia californica* to the wetter PCM A2 climate, and the sensitivity of *Salvia melifera* to the GFDL A2 GCM. The large decline projected for suitable habitat for the intersected Venturan CSS models is primarily due to an extreme response for one of the four species, *Salvia leucophylla*, for both GCMs.

DISCUSSION

Ecological Implications for Modeled Trends

At the regional scale, vegetation in southern California has been significantly shaped by temperature and precipitation gradients (Ackerly, 2009). Given species in a group respond similarly to these gradients, group models can adequately describe habitat requirements and suitability for the whole assemblage. Riordan and Rundel (2009) successfully modeled suitable habitat for CSS and found their three floristic groups (spatially defined as coastal, interior and widely distributed) were also distinguished by response to temperature and precipitation.

Such climatic controls have contributed to the biogeographic and physiognomic separation of CSS and chaparral. Coastal Sage Scrub is the more drought tolerant vegetation type and generally grows near the coast where precipitation is lower, while chaparral is found further inland at higher, moister elevations (Harrison et al, 1971). Environmental drivers designated by MaxEnt as most important in both the community and species models supports these long standing observations. For example, the importance of summer rain in both the community (ranking as most frequently important) and species models (second most frequent) reflects the long established Mediterranean climate, characterized in part by the absence of summer rain (Axelrod, 1978).

In this study, the Impact of climate change is predicted to be less overall for drier, lower elevation habitat. Two trends were evident across modeling approaches, though more consistent in the modeled communities. One was that the CSS communities (Riversidean Sage Scrub, Diegan and Venturan CSS) were less responsive to climate change than the chaparral communities. The other was that of the five chaparral communities, three (Northern Mixed, Scrub Oak and *Ceanothus cuneatus*) were more responsive to climate change. The remaining two chaparral communities (*Ceanothus megacarpus* and *C. crassifolius*) were relatively less responsive, similarly ranking with CCS (Table 5, Sorting By Increasing Response To Averaged Climate Change Between Mesic And Non-Mesic Communities). I refer to the separation between communities as mesic or non-mesic as an approximation of their relative drought tolerance.

Differentiation between mesic or non-mesic communities in the chaparral models might be explained by taxonomic division within the Ceanothus genus, which is divided into two subgenera: *Ceanothus* and *Cerastes*. Members of these subgenera have diversified to adapt to particular temperature and precipitation gradients even though they live in close proximity (Burge et al, 2011). Members of the subgenus *Cerastes* (*Ceanothus megacarpus, C. crassifolius* and *C. cuneatus*) tolerate water stress better than *Ceanothus* subgenus species (*C. spinosus, C. oliganthus* and *C. leucophylla*) (Davis et al, 1999; Davis et al, 2007). The high-elevation Northern Mixed community contains all three less drought tolerant *Ceanothus* subgenus species and Scrub Oak contains one of them, C.*spinosus*. While *C. cuneatus* is a more drought tolerant *Cerastes* species, it may experience the most water stress of the Cerastes group at high elevation (compare Ewers et al, 2003 with Davis et al, 1999) and may be why it was consequently grouped with the mesic communities in the models for this study.

Climate change risk exposure and model uncertainty. The goal of this study was to contrast grouped species with intersected species models in the context of conservation interest. This approach was to explore a range of climate change projections for shrub communities in SMMNRA as a method to evaluate uncertainty.

Evaluating consistency across modeling approaches and between GCMs can describe uncertainty. Uncertainty is reduced if a model is both ecologically plausible and consistent across modeling approaches. The most consistent responses are those that retain their relative relationships between GCMs without extreme differences in magnitude when intersected. Such changes in the intersected model indicate that when modeled alone, one or more species' response to climate change diverges from the group. This suggests experimental error, or may indicate species deserving enhanced observation.

The *Ceanothus megacarpus* community was most consistent. Composite species for this community have been found to be particularly drought tolerant (*Ceanothus megacarpus* and *Salvia melifera:* Kolb and Davis,1994; and for *Malsosma laurina* in Westman, 1981), but *Salvia melifera* has also been reported to tolerate mesic conditions (e.g. Westman, 1981). Despite their reported drought tolerance, previous simulations for climate change have predicted increasing dominance for *Ceanothus megacarpus* and *Salvia melifera* for increased temperature and precipitation (Malanson and O'Leary, 1995). Additionally, *Malosma laurina* has been placed into a large number of vegetation associations (Keeler-Wolf et al. 2007), suggesting its niche amplitude is wide. AUC values for the community model and the component species are among the lowest, another indicator for broad niche amplitude. Within this community model, broad niche amplitude may increase overlap between component species responses, smoothing the response range across modeling approaches to improve consistency.

The overall consistency in the chaparral models may reflect niche partitioning among species in the *Ceanothus* subgenera Ceanothus and Cerastes. Distributions for these subgenera have been observed to separate along environmental gradients such as elevation and irradiation (Nicholson, 1993), and are differentiated by species' tolerance to water stress (Pratt et al, 2007; Meentemeyer and Moody, 2002), and freeze injury (Ewers et al, 2003; Davis et al, 2007). Freeze injury and drought stress tolerance are related and work together to influence chaparral distribution (Davis, et al, 2007; Langan, et al. 1997). Accordingly, indices for precipitation, aridity and coastal proximity (or temperature modulation) were selected as the three most frequently important variables across species and community levels, suggesting distinctions among these species were resolved and helped to improve coherence across modeling approaches.

The CSS models were less consistent across modeling approaches, varying when intersected. Diegan CSS was particularly variable and was the least consistent. CSS as a vegetation type has been difficult to classify floristically; species comprising CSS are pioneering (Axelrod, 1978) growing in a variety of combinations in variable habitats (Rundel, 2007). It may be that CSS habitat was better characterized by the more generalized community models that intrinsically encompass local variety in CSS. Despite inconsistencies in the CSS models, overall, the predicted impact upon habitat for CSS communities was less than for chaparral.

Such projections may be viewed as an early response to climate change outlining risk exposure to better inform policy. Though validation is not possible when projecting into the future, I have used best practice techniques to minimize error and reduce uncertainty (Elith et al. 2010; Hijmans and Graham, 2006), and strove to balance generalization against utility. To generalize projections without sacrificing their utility, I summed pixel probabilities to avoid introducing error by “thresholding”’ the data (converting pixel probabilities to presence or absence) (Nenzen and Araujo, 2011), and to avoid associating habitat probabilities with particular locations within SMMNRA. Nevertheless, the projections do not account for fire or disturbance, propagule dispersal, biotic interaction or individualistic genetic responses, to name just a few dynamic influences these models ignore (see Wiens et al. 2009; Pearson and Dawson, 2003). Shifts in probability distributions for suitable habitat portrayed by these models characterize relative shifts given a species’ or community’s requirements are stable. The models assume environmental requirements will not change over the modeled period for both species and communities.

Implications For Management

Recommendations. To accommodate anticipated or observed changes for vegetation within the Park, I recommend managers implement policy based on principles of adaptive management. Adaptive management is an approach used to incorporate uncertainty and responsive flexibility in policy decision making (Walters and Holling, 1990). The response rate to climate change is unpredictable and may be slow (Ordonez, 2013), and species’ adaptive capacity is unknown. Many species in this region appear to be habitat generalists (except for members of Ceanothus and Arctostaphylos genera), because past climatic fluctuations may have been too rapid to allow for strict habitat specialization (Zedler, 1994).

Management objectives should be both habitat and species oriented. A conservative expectation is that relatively mesic habitat will decrease and drier, more exposed habitat will increase. Existing habitat within the SMMNRA should be monitored to detect general changes for dominant species across types in differing locations (e.g., CSS versus non-CSS habitats). Trends in species sensitivity indicators (e.g., changes in cover, fecundity, seedling survival or branch dieback) may indicate early response to climate change for dominant species comprising particular habitat types. Shifting community character may occur at the upper elevation bound for CSS, since much of what has already been lost or impacted is at lower or intermediate elevation (Malanson and Oleary, 1995). The SMMNRA vegetation map can help determine these locations and can be used to expand or modify the already existing Inventory and Monitoring (I&M) in Parks program (NPS, n.d.). Management response motivated by ongoing monitoring will depend on the sensitivities detected and their coherence across locations, and whether those trends indicate changing habitat.

The model projections may be considered conservation opportunities (Schwartz 2012), requiring flexible thinking to manage for change (Sax et al. 2013; Jackson and Hobbs, 2009). Nearly twenty years ago, Southern California CSS was ranked 9th of 21 most endangered ecosystems in the United States (Noss and Peters, 1995). The situation has not improved since (Riordan and Rundel, 2014; Taylor, 2004). Management policy could be developed to take advantage of favorable conditions for CSS restoration. Many CSS species are easily established (Bozzolo and Lipson, 2013) even when rainfall is unpredictable (DeSimone and Zedler, 2001). Restoration could be implemented with a particular context in mind (very broadly, high or low elevation habitat) on land currently under Park management or as cooperative interagency projects, and designed to reflect the local character of CSS habitat. Where private ownership fragments public ownership, an effort can be made to acquire new landholdings, or landowner incentive programs (e.g., Cox and Underwood, 2011) could be adopted to increase the connectivity of managed area. Contiguity of managed land, or at least cooperation from private landowners within SMMNRA's larger bounds may become important to facilitate migration into changing habitat, especially at CSS-chaparral interfaces. For example, this may be critical for *Salvia leucophylla*, the species primarily driving the relatively extreme response to climate change (as decreasing habitat) for the Venturan CSS community. Davis and others (1994) recommended priority management consideration for *S. leucophylla* because the majority of its habitat in the Western transverse ranges occurred on private lands.

Regional Context. The community models were based on combined vegetation associations, sub-regional variations that are a particular expression of vegetation alliances existing both within and beyond SMMNRA (Keeler-Wolf et al 2007). While some associations have been found only in SMMNRA, the community models in this study were calibrated regionally and were formed by grouping associations, and therefore may apply more generally to Southern

California. Within the Southern California region, more land mass could increase opportunities for refugia habitat and may warrant future expansion of protected areas.

Two of the shrub species I have included in my study, *Ceanothus megacarpus* and *Ceanothus spinosus,* have their center of world distribution in the Santa Monica Mountains (Keeler-Wolf and Evens, 2006) and while abundant in SMMNRA they are rare elsewhere. Loarie and others (2008) projected that in general, species will recede from the center of the state, pursuing habitat southward to cluster about the coastal mountains of southern California, in part, toward SMMNRA. As a result, SMMNRA could become a refuge for species in the CFP while displacing species already there.

Riordan and Rundel (2014) developed maps based on models combining the effects of land use and climate change, projecting increasing development on lands surrounding SMMNRA by 2080 (Supplementary Figure S1).   Potentially, this restriction could hinder species' ability to emigrate, or alternatively, immigrate inward to SMMNRA to track favorable habitat.

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APPENDIX A

SPECIES AND ASSEMBLY POINT COUNTS

Species Assembly	Species Frequency	Common Name	Points per Species	Total Assembly Points
Ceanothus crassifolius				
Ceanothus crassifolius	*1*	Hoaryleaf Ceanothus	221	
Malosma laurina	*3*	Laurel Sumac	1587	
Rhus ovata	*3*	Sugar Bush	771	**2579**
Ceanothus megacarpus				
Ceanothus megacarpus	*1*	Bigpod Ceanothus	1170	
Malosma laurina	*3*	Laurel Sumac	1587	
Salvia mellifera	*2*	Black Sage	1169	**3926**
Ceanothus cuneatus				
Ceanothus cuneatus	*1*	Buckbrush	160	
Cercocarpus betuloides	*2*	Mountain Mahogany	837	
Quercus berberidifolia	*2*	Scrub Oak	732	
Rhus ovata	*3*	Sugar Bush	771	**2500**
Northern Mixed				
Arctostaphylos glandulosa	*1*	Eastwood's Manzanita	123	
Arctostaphylos glauca	*1*	Big Berry Manzanita	100	
Ceanothus leucodermis	*1*	Chaparral Whitethorn	79	
Ceanothus oliganthus	*1*	Hairy Ceanothus	153	
Ceanothus spinosus	*2*	Greenbark Ceanothus	556	
Cercocarpus betuloides	*2*	Mountain Mahogany	732	
Heteromeles arbutifolia	*2*	Toyon	1096	
Prunus illicifolia	*1*	Hollyleaf Cherry	251	**3090**
Scrub Oak				
Ceanothus spinosus	*2*	Greenbark Ceanothus	556	
Heteromeles arbutifolia	*2*	Toyon	1096	
Quercus berberidifolia	*2*	Scrub Oak	837	**2489**
Diegan CSS				
Artemisia californica	*1*	California Sagebrush	1294	
Encelia californica	*1*	California Encelia	556	
Malosma laurina	*3*	Laurel Sumac	1587	
Salvia mellifera	*2*	Black Sage	1169	**4606**
Riversidean Sage Scrub				
Eriogonum fasciculatum	*1*	California Buckwheat	926	
Rhus ovata	*3*	Sugar Bush	771	
Salvia apiana	1	White Sage	123	**1820**
Venturan CSS				
Opuntia littoralis	*1*	Western Prickly Pear	118	
Rhus integrifolia	*1*	Lemonade Berry	346	
Salvia leucophylla	*1*	Purple Sage	646	
Yucca whipplei	*1*	Our Lord's Candle	835	**1945**

APPENDIX B

COMBINATIONS OF ASSOCIATIONS UNDER ALLIANCES FOR CHAPARRAL ASSEMBLAGES

Assembly	USDA Code†	Alliance	Association
Ceanothus cuneatus		CECU	
Ceanothus cuneatus	CECU		CECU/QUBE
Quercus berberidifolia	QUBE5		
Cercocarpus betuloides	CEBE3		
Rhus ovata	RHOV		
Ceanothus megacarpus		CEME	
Ceanothus megacarpus	CEME		CEME
Malosma laurina	MALA6		CEME/MALA
Salvia mellifera	SAME3		
Ceanothus crassifolius		CECR	
Ceanothus crassifolius	CECR		CECR
Malosma laurina	MALA6		CECR/MALA
Rhus ovate	RHOV		
Northern Mixed		ARGL3	
Arctostaphylos glandulosa	ARGL3	CEBE	ARGL3
Arctostaphylos glauca	ARGL4	CEOL	CEOL
Ceanothus leucodermis	CELE2	CESP	CESP
Ceanothus oliganthus	CEOL	PRIL	CEBE
Ceanothus spinosus	CESP		CEBE/CESP
Cercocarpus betuloides	CEBE3		PRIL/HEAR
Heteromeles arbutifolia	HEAR5		
Prunus illicifolia	PRIL		
Scrub Oak		QUBE	
Ceanothus spinosus	CESP		QUBE/CESP
Heteromeles arbutifolia	HEAR5		
Quercus berberidifolia	QUBE5		QUBE
Diegan CSS		ENCA	
Artemisia californica	ARCA11		ENCA/ARCA11
Encelia californica	ENCA		ENCA
Malosma laurina	MALA6		ENCA/MALA/SAME
Salvia mellifera	SAME3		
Riversidean Sage Scrub		ERFA/SAAP	
Eriogonum fasciculatum	ERFA2		
Rhus ovata	RHOV		
Salvia apiana	SAAP2		
Venturan CSS			
Opuntia littoralis	OPLI3		

Rhus integrifolia	RHIN2		
Salvia leucophylla	SALE3		
Yucca whipplei	YUWH		

† http://plants.usda.gov

APPENDIX C

COMMON ECOLOGICAL TOLERANCES FOR ASSOCIATIONS AND ALLIANCES

Assembly	**General Tolerances for Associations/Alliance**			
Ceanothus cuneatus	**Aspect**	**Elevation (meters)**	**Slope**	**Frequent co-species**
Ceanothus cuneatus	NE - SE	Low 226-408 m	Steep	QUBE/CEBE3/RHOV
Quercus berberidifolia				
Cercocarpus betuloides				
Rhus ovata				
Ceanothus megacarpus				
Ceanothus megacarpus	Variable	Low - Mid 53-730 m	Moderate - Steep	MALA6 /SAME3
Malosma laurina	Variable	Low - Mid 42-780 m	Gentle - Steep	
Salvia mellifera				
Ceanothus crassifolius				
Ceanothus crassifolius		Low 312 - 640 m	Moderate - Steep	MALA6/HEAR5
Malosma laurina	Variable	Low 337 - 675 m	Moderate - Steep	RHOV
Rhus ovate				
Northern Mixed				
Arctostaphylos glandulosa	NW	Mid - High 557 - 878 m	Steep - Steep	HEAR5/ (ADFA)*/ARGL4
Arctostaphylos glauca	Variable	Low - Mid 498 - 847 m	Gentle - Steep	HEAR5
Ceanothus leucodermis	NE - NW	Low 0 - 692 m	Steep -Very Steep	HEAR5 / mesophytic
Ceanothus oliganthus	NE - NW	Low 10 - 661 m	Steep - Steep	HEAR5
Ceanothus spinosus	NW	Low 64 - 526 m		PRIL
Cercocarpus betuloides	NE - NW	Low 281 - 687 m	Steep - Steep	
Heteromeles arbutifolia				
Prunus illicifolia				
Scrub Oak				
Ceanothus spinosus	Variable	Low 230 - 563 m	Steep - Steep	HEAR5
Heteromeles arbutifolia				
Quercus berberidifolia	NE - NW	Low - Mid 119 - 783 m	Gentle - Very Steep	HEAR5
Diegan CSS				
Artemisia californica	SW - SE	Low 3 - 423 m	Gentle - Steep	MALA6/SAME3
Encelia californica	SW - SE	Low 2- 496 m	Gentle - Steep	ARCA11/MALA6
Malosma laurina	SW - SE	Low 5 - 457 m	Gentle - Steep	
Salvia mellifera				
Riversidean Sage Scrub	SW - SE	Low 202 - 262 m	Steep - Very Steep	YUWH / (ADFA)*
Eriogonum fasciculatum				
Rhus ovata				
Salvia apiana				

Venturan CSS				
Opuntia littoralis				
Rhus integrifolia				
Salvia leucophylla				
Yucca whipplei				

* ADFA: *Adenostoma fasciculatum*-species not selected for study

APPENDIX D

BIOCLIMATIC AND TERRAIN VARIABLES

Bioclimatic Variables		Units	PRISM Range	PCM A2 Range	GFDL A2 Range
BIO4	Temperature Seasonality	standard deviation x100	6-42	5-70	15-55
BIO5	Max Temperature of Warmest Month	degrees C x10	235-350	284-391	300-407
BIO12	Annual Precipitation	mm	125-1347	190-1473	112-999
BIO18	Precipitation of Warmest Quarter	mm	6-29	8-25	5-24
BIO20**	Growing Degree Days above 5 C	cumulative degrees C	3308-5107	4510-6221	4734-6649
BIO24**	Aridity index (AnnPrec/Potential Evap)	X100	28-256	29-237	12-94
Terrain Variables		**Units**	**Range**		
dep	Soil Depth*	meter	0.133-1.778	No Change	No Change
awc	Soil Available Water Capacity*	cm/cm	0.022-0.156		
ph	Soil pH*		1.785-8.353		
slope	Slope Angle †	degrees	0-71		
sumrad	Potential Summer Solstice Solar Insolation †	watt hour/m2	3762-8099		

*Obtained from State Soil Geographic (STATSGO) data base for California, U.S. Department of Agriculture Natural Resources Conservation Service (http://soils.usda.gov/survey/geography/statsgo/).

**Conventional bioclimatic variables are BIO1-BIO19 (Hijmans et al, 2005). BIO20and BIO24 derived as described in Franklin et al, 2013.

†Solar insolation variables calculated from DEM (http://rockyweb.cr.usgs.gov/elevation/dpi_dem.html).

APPENDIX E

COMMUNITY AND SPECIES MODELS BY PREDICTED AREA, OMISSION RATE, TEST AUC AND TEST GAIN

Predicted Area is the proportional predicted area or the fraction of all pixels that are predicted as suitable at a fixed 10% omission rate. **Cumulative 10% Test Omission** is the fraction of the test localities that fall into pixels not predicted as suitable for the species at a 10% omission threshold. **Test AUC** is the probability that a test presence site will be ranked above a random background site. Its value ranges from 0 to 1, with 0.5 corresponding to random prediction. **Test Gain** is the average log probability of the test samples used to test the model and is the average likelihood that a test sample is higher than that of a random background pixel.

Community	Predicted Area	Cumulative 10% Test Omission	Test AUC	Test Gain	Presence Point Count for Assembly
Ceanothus cuneatus	0.736	0.085	0.701	0.281	2500
Venturan CSS	0.709	0.097	0.686	0.223	1945
Scrub Oak	0.761	0.085	0.661	0.160	2489
Riversidean Scrub	0.754	0.091	0.648	0.149	1820
Northern Mixed	0.765	0.088	0.648	0.135	3090
Diegan CSS	0.779	0.097	0.607	0.099	4606
Ceanothus crassifolius	0.791	0.078	0.598	0.086	2579
Ceanothus megacarpus	0.792	0.086	0.599	0.085	3926

Species	Predicted Area	Cumulative 10% Test Omission	Test AUC	Test Gain	Presence Point Count
Ceanothus leucodermis	0.206	0.058	0.952	2.003	79
Ceanothus cuneatus	0.499	0.044	0.880	1.190	160
Arctostaphylos glandulosa	0.360	0.071	0.874	1.058	123
Arctostaphylos glauca	0.492	0.040	0.854	1.037	100
Salvia apiana	0.543	0.049	0.850	1.000	123
Ceanothus oliganthus	0.439	0.072	0.866	0.991	153
Opuntia littoralis	0.418	0.061	0.858	0.918	118
Quercus berberidifolia	0.525	0.088	0.826	0.854	837
Ceanothus crassifolius	0.470	0.093	0.843	0.846	221
Rhus integrifolia	0.411	0.057	0.840	0.828	346
Salvia leucophylla	0.581	0.057	0.783	0.530	646
Ceanothus spinosus	0.563	0.054	0.758	0.456	556
Prunus illicifolia	0.682	0.049	0.753	0.387	251
Encelia californica	0.620	0.096	0.737	0.373	556
Cercocarpus betuloides	0.734	0.083	0.720	0.348	732
Artemisia californica	0.708	0.087	0.667	0.183	1294
Rhus ovata	0.730	0.077	0.652	0.151	771
Eriogonum fasciculatum	0.782	0.076	0.643	0.143	926
Heteromeles arbutifolia	0.775	0.092	0.637	0.126	1096
Malosma laurina	0.784	0.059	0.631	0.125	1587

Ceanothus megacarpus	0.745	0.091	0.619	0.123	1170
Yucca whipplei	0.784	0.092	0.636	0.123	835
Salvia mellifera	0.807	0.087	0.586	0.072	1169

APPENDIX F

ENVIRONMENTAL VARIABLES EXCEEDING A 10 PERCENT IMPORTANCE THRESHOLD FOR COMMUNITIES AND SPECIES

Numerical values are importance assigned as a percentage by MaxEnt. Bolded numerical values are the variables with the highest percentage importance for that community. Italicized numerical values are the variables with the highest percentage importance for that species. Bioclimatic variables are shaded in grey; topographic variables are shaded in green. Unshaded variables were important for species but not for the community to which they belong. Environmental Variables in the headings are followed by their WorldClim name in parentheses: Summer Rain or Precipitation of Warmest Quarter (**BIO18)**; Aridity or Aridity Index (**BIO24)**; Temp Season or Temperature of Seasonality (coefficient of variation for mean monthly temperatures) (**BIO4**); Maximum Temperature of Warmest Period (**BIO5**); Growing Season or Growing Degree Days > 5 Celsius (**BIO20)**; Annual Precipitation (**BIO12)**; Soil pH; Soil Depth; Water Capacity; Slope Angle; Solar Insolation.

	Bioclimatic						**Topographic**				
Community / *component species*	**Summer Rain**	**Aridity**	**Temp Season**	**Max Temp**	**Growing Season**	**Annual Precip**	**pH**	**Soil Depth**	**Water Capacity**	**Slope Angle**	**Solar Insolation**
Ceanothus crassifolius	**43**	12		14	15						
Ceanothus crassifolius				37		14			24		
Malosma laurina	32	10	10	29							
Rhus ovata	*46*				38						
Ceanothus cuneatus	**52**		19								
Ceanothus cuneatus			10		22	13	17	16			
Quercus berberidifolia	14		*55*				10				
Cercocarpus betuloides	33		11	30			11				
Rhus ovata	46				38						
Ceanothus megacarpus	**38**	14	24	11							
Ceanothus megacarpus	23		*58*	11							
Malosma laurina	32	10	10	29							
Salvia mellifera	25	30	26								
Northern Mixed	**59**	22									
Arctostaphylos glandulosa		29				44					
Arctostaphylos glauca	39			51							
Ceanothus leucodermis			*79*								
Ceanothus oliganthus			30	17	10				26		
Ceanothus spinosus	29	14	26				17				
Cercocarpus betuloides	33		11	30			11				
Heteromeles arbutifolia	38	13				12					13
Prunus illicifolia	45				25						16
Scruboak	**54**	24					12				
Ceanothus spinosus	29	14	26				17				
Heteromeles arbutifolia	38	13	12								13
Quercus berberidifolia	14		*55*				10				

	Bioclimatic						Topographic				
Community / component species	**Summer Rain**	**Aridity**	**Temp Season**	**Max Temp**	**Growing Season**	**Annual Precip**	**pH**	**Soil Depth**	**Water Capacity**	**Slope**	**Solar Insolation**
Diegan CSS	14	**41**	11	11							
Artemisia californica	10					*55*			11		14
Encelia californica		52	43								
Malosma laurina	32	10	10	29							
Salvia mellifera	25	30	26								
Riversidean Scrub	**43**	16	10	15							
Eriogonum fasciculatum	28	15	11	35							
Rhus ovata	*46*				38						
Salvia apiana		19	31	32		10					
Venturan CSS	13	11	**33**		24						
Opuntia littoralis			44	10					25		
Rhus integrifolia			*49*	21	12						
Salvia leucophylla			27		15	26					
Yucca whipplei	14	41	17		26						

APPENDIX G

STANDARD DEVIATION ON Y AXIS FOR MARGINAL RESPONSE CURVE PLOTS

In the left column and within each group, the community is in the top row followed by species for that community. The standard deviation values are in the right column and are listed by environmental variable. Note that the important environmental variables are not the same across communities (down columns). Bolded values for species' standard deviation are those that are greater than for the community for that variable.

Community/Species		**Standard Deviation on Y Axis**			
		Environmental Variable ≥ 10% Importance			
		bio 4	bio 18		
Community	*Ceanothus cuneatus*	0.123	0.115		
Species	*Cercocarpus betuloides*	0.111	**0.126**		
Species	*Ceanothus cuneatus*	**0.209**	0.036		
Species	*Quercus berberidifolia*	**0.208**	0.070		
Species	*Rhus ovata*	0.053	**0.157**		
		bio 18	bio 24		
Community	Northern Mixed	0.129	0.089		
Species	*Arctostaphylos glandulosa*	0.067	**0.206**		
Species	*Arctostaphylos glauca*	**0.204**	0.002		
Species	*Cercocarpus betuloides*	0.126	0.050		
Species	*Ceanothus leucodermis*	0.063	0.000		
Species	*Ceanothus oliganthus*	0.088	**0.140**		
Species	*Ceanothus spinosus*	**0.179**	**0.106**		
Species	*Heteromeles arbutifolia*	0.063	0.046		
Species	*Prunus illicifolia*	**0.163**	0.048		
		bio 18	bio 24	ph1	
Community	Scrub Oak	0.099	0.071	0.110	
Species	*Ceanothus spinosus*	**0.179**	**0.106**	**0.210**	
Species	*Heteromeles arbutifolia*	0.063	0.046	0.080	
Species	*Quercus berberidifolia*	0.070	0.041	**0.123**	
		bio 5	bio 18	bio 20	bio 24
Community	*Ceanothus crassifolius*	0.072	0.111	0.210	0.129
Species	*Ceanothus crassifolius*	**0.240**	0.105	0.117	0.000
Species	*Malosma laurina*	**0.079**	0.097	0.160	**0.150**
Species	*Rhus ovata*	0.003	**0.157**	0.205	0.050
		bio 4	bio 5	bio 18	bio 24
Community	*Ceanothus megacarpus*	0.204	0.034	0.123	0.113
Species	*Ceanothus megacarpus*	**0.217**	**0.099**	**0.124**	0.002
Species	*Malosma laurina*	**0.210**	**0.079**	0.097	**0.150**
Species	*Salvia mellifera*	0.154	0.005	0.112	**0.146**

		bio 4	bio 5	bio 18	bio 24
Community	Diegan CSS	0.113	0.030	0.090	0.166
Species	*Artemisia californica*	0.031	0.010	**0.106**	0.052
Species	*Encelia californica*	**0.226**	**0.031**	0.069	**0.209**
Species	*Malosma laurina*	**0.210**	**0.079**	**0.097**	0.150
Species	*Salvia mellifera*	**0.154**	0.005	**0.112**	0.146
		bio 4	bio 5	bio 18	bio 24
Community	Riversidean Sage Scrub	0.202	0.078	0.134	0.095
Species	*Eriogonum fasciculatum*	0.194	**0.100**	0.093	**0.140**
Species	*Rhus ovata*	0.053	0.003	**0.157**	0.050
Species	*Salvia apiana*	0.145	**0.161**	0.001	**0.210**
		bio 4	bio 18	bio 20	bio 24
Community	Venturan CSS	0.206	0.048	0.086	0.183
Species	*Opuntia littoralis*	0.203	0.027	**0.094**	0.118
Species	*Rhus integrifolia*	**0.237**	**0.059**	**0.127**	0.010
Species	*Salvia leucophylla*	**0.288**	**0.126**	**0.237**	0.111
Species	*Yucca whipplei*	0.200	**0.147**	**0.110**	**0.196**

APPENDIX H

GOWER SIMILARITY COEFFICIENT MATRICES

Coefficient values range from 0.0 (completely similar) to 1.0 (completely dissimilar).

Each matrix compares pairwise combinations for the minimum, maximum and standard deviation for y, and the area under the curve derived from the response curve plots for each environmental variable between communities and their component species. Similarity coefficients for community versus their species are listed across rows in column 1 under each variable. The coefficients for species versus other species are listed as all other values, across remaining rows and columns. Dissimilar values (values >0.5) are bolded. See Appendix B for community/species lists and definitions of four-letter species codes. Comparison matrices were developed for environmental variables ≥ 10% important for each community.

Community *Ceanothus cuneatus*

BIO4					BIO18				
	ceacun	cebe	cecu	qube		ceacun	cebe	cecu	qube
cebe	0.20				cebe	0.09			
cecu	0.50	**0.63**			cecu	0.49	0.58		
qube	0.47	**0.67**	0.21		qube	**0.55**	0.52	0.58	
rhov	0.43	0.49	**0.77**	**0.71**	rhov	0.48	0.40	**0.80**	0.44

Community *Ceanothus megacarpus*

BIO4				BIO5				BIO18				BIO24			
	ceameg	ceme	mala		ceameg	ceme	mala		ceameg	ceme	mala		ceameg	ceme	mala
ceme	0.40			ceme	**0.60**			ceme	0.33			ceme	0.47		
mala	0.12	0.35		mala	0.37	0.34		mala	**0.56**	**0.69**		mala	0.40	**0.76**	
same	**0.77**	**0.83**	**0.73**	same	0.35	**0.95**	**0.71**	same	**0.52**	0.45	**0.69**	same	0.32	**0.73**	**0.52**

Community Diegan CSS

BIO4					BIO5					BIO18					BIO24				
	dieg css	arca	enca	mala		dieg css	arca	enca	mala		dieg css	arca	enca	mala		dieg css	arca	enca	mala
arca	0.40				arca	0.34				arca	0.36				arca	**0.60**			
enca	**0.67**	**0.93**			enca	0.05	0.39			enca	0.45	**0.78**			enca	0.35	**0.88**		
mala	0.40	**0.69**	0.27		mala	**0.61**	**0.91**	**0.57**		mala	0.44	0.24	**0.64**		mala	0.36	0.41	**0.64**	
same	0.24	**0.51**	0.42	0.25	same	0.35	0.13	0.40	**0.96**	same	**0.60**	**0.56**	**0.62**	0.43	same	0.17	0.50	0.39	0.27

Community Riversidean Sage Scrub

BIO4				BIO5				IBO18				BIO24			
	riv scrub	erfa	rhov		riv scrub	erfa	rhov		riv scrub	erfa	rhov		riv scrub	erfa	rhov
erfa	0.07			erfa	0.29			erfa	0.23			erfa	0.37		
rhov	**0.91**	**0.94**		rhov	0.41	**0.71**		rhov	0.49	**0.60**		rhov	0.28	**0.61**	
saap	0.45	0.48	**0.54**	saap	0.37	**0.51**	**0.79**	saap	**0.55**	0.47	**0.82**	saap	**0.70**	0.41	**0.99**

Community *Ceanothus crassifolius*

BIO5				BIO18				BIO20				BIO24			
	ceacrass	cecr	mala		ceacrass	cecr	mala		ceacrass	cecr	mala		ceacrass	cecr	mala
cecr	**0.79**			cecr	0.40			cecr	**0.96**			cecr	**0.92**		
mala	0.08	**0.71**		mala	0.25	0.25		mala	0.41	**0.55**		mala	0.09	**0.99**	
rhov	0.35	**0.87**	0.31	rhov	**0.85**	**0.64**	**0.90**	rhov	0.13	**0.91**	0.49	rhov	0.49	0.43	**0.57**

Community Venturan CSS

BIO4					BIO18					BIO20					BIO24				
	vent css	opli	rhin	sale		vent css	opli	rhin	sale		vent css	opli	rhin	sale		vent css	opli	rhin	sale
opli	0.38				opli	0.37				opli	0.05				opli	**0.63**			
rhin	0.40	**0.55**			rhin	0.37	0.38			rhin	**0.55**	**0.57**			rhin	**0.82**	**0.51**		
sale	**0.63**	**0.64**	0.41		sale	**0.53**	**0.71**	**0.66**		sale	0.49	0.47	**0.86**		sale	**0.57**	0.31	0.32	
yuwh	0.15	0.41	**0.55**	**0.77**	yuwh	**0.58**	**0.72**	**0.50**	0.30	yuwh	0.20	0.16	**0.67**	0.39	yuwh	0.34	0.32	**0.80**	0.50

Community Northern Mixed

BIO8

	nmixed	argland	arglauc	cebe	cele	ceol	cesp	hear
argland	**0.60**							
arglauc	**0.70**	**0.60**						
cebe	0.05	**0.55**	**0.66**					
cele	**0.55**	0.07	**0.64**	0.50				
ceol	0.20	0.43	**0.68**	0.20	0.38			
cesp	0.36	0.49	0.40	0.34	0.46	0.48		
hear	0.45	0.17	**0.70**	0.40	0.10	0.28	**0.52**	
pril	0.23	**0.52**	**0.50**	0.21	0.47	0.35	0.13	0.42

BIO24

	nmixed	argland	arglauc	cebe	cele	ceol	cesp	hear
argland	0.46							
arglauc	0.49	**0.69**						
cebe	0.17	**0.63**	0.49					
cele	0.39	**0.67**	0.11	0.38				
ceol	0.36	0.25	0.46	**0.53**	0.45			
cesp	0.22	0.33	0.36	0.39	0.34	0.14		
hear	0.25	**0.71**	**0.58**	0.10	0.48	**0.61**	0.47	
pril	0.15	**0.53**	0.36	0.13	0.26	0.43	0.29	0.23

Community Scrub Oak

BIO18

	scrub oak	cesp	hear
cesp	**0.80**		
hear	0.27	**0.87**	
qube	**0.62**	**0.55**	0.39

BIO24

	scrub oak	cesp	hear
cesp	**0.59**		
hear	0.25	**0.82**	
qube	**0.69**	0.62	0.55

PH1

	scrub oak	cesp	hear
cesp	**0.72**		
hear	0.28	**1.00**	
qube	0.33	**0.66**	0.34

APPENDIX I

BOX PLOT GRAPHS DEPICTING RESPONSE TO CLIMATE CHANGE BY MODELING APPROACH FIGURES 1 - 8

FIGURE I-1

In each figure, from left to right graphs 1-3 represent probability distributions extracted from the group models for the PRISM (current climate), PCM A2 (warmer and wetter) and GFDL A2 GCMs (warmer and drier) . Graphs 4-6 are for the same community as intersected species models. The y-axis is the probability value for suitable habitat extracted from the models. Median values for the probability distributions for each graph is given in the pink boxes at the top. Appendix figure I-2 (*Ceanothus cuneatus*) was shown in Figure 8, but is included again for completeness. The communities are displayed in alphabetical order.

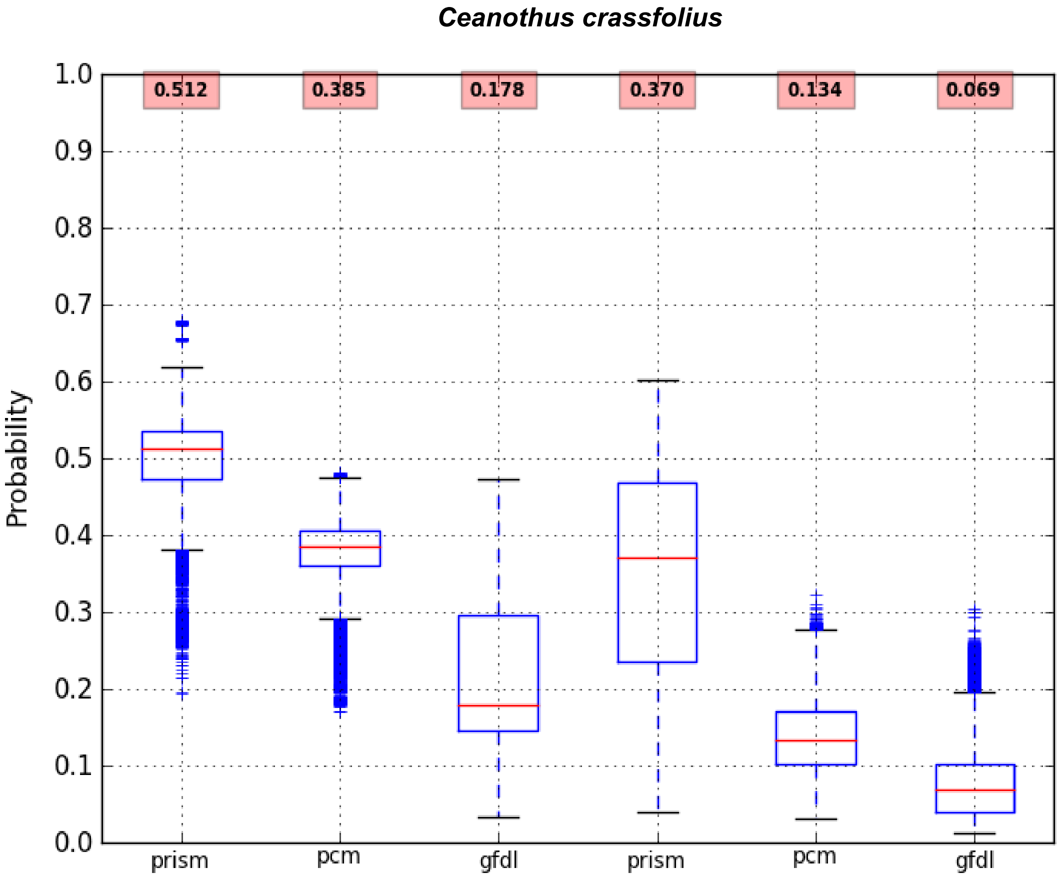


FIGURE I-2

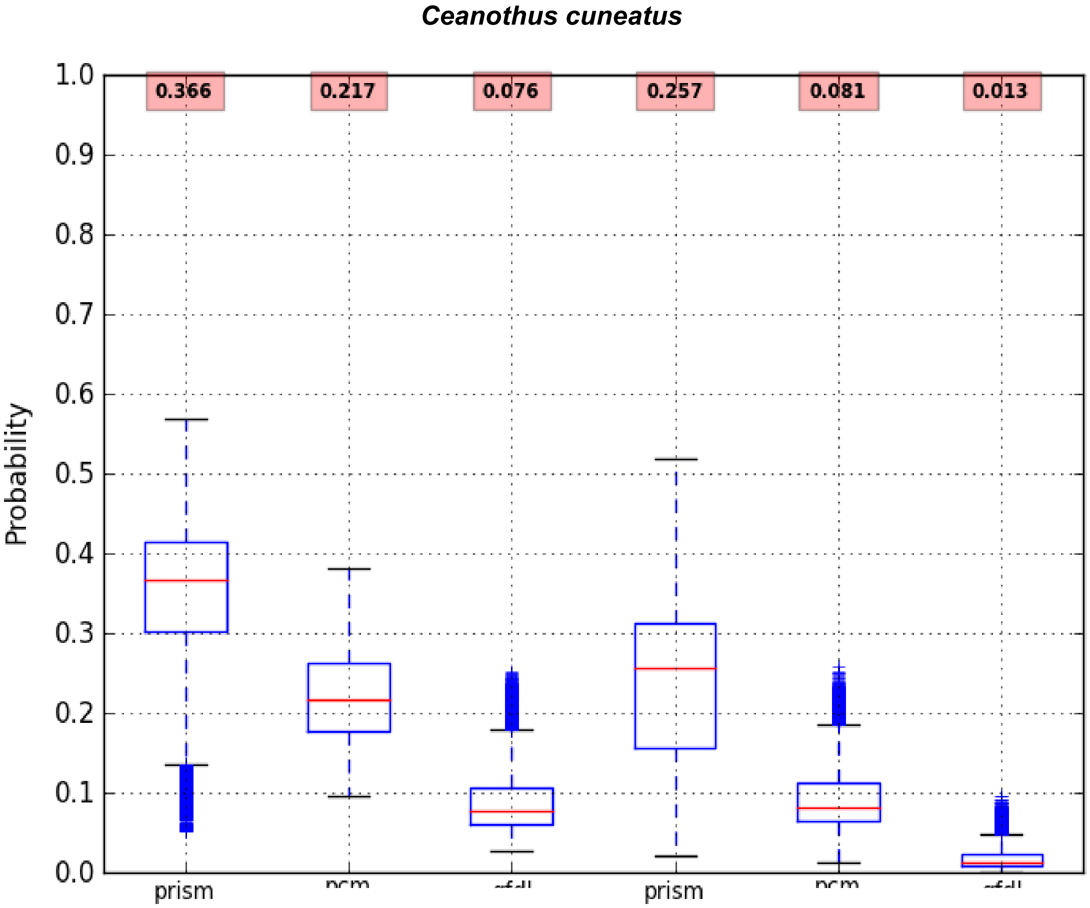

Ceanothus cuneatus

FIGURE I-3

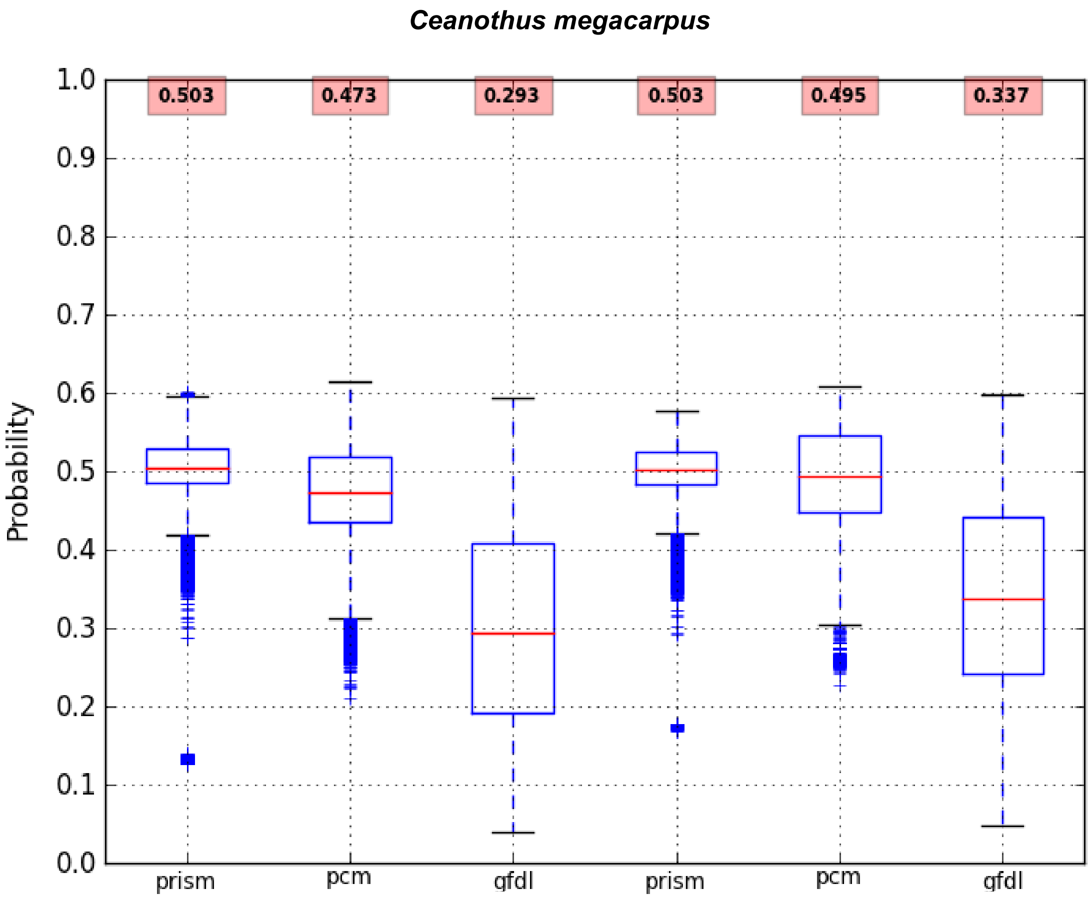
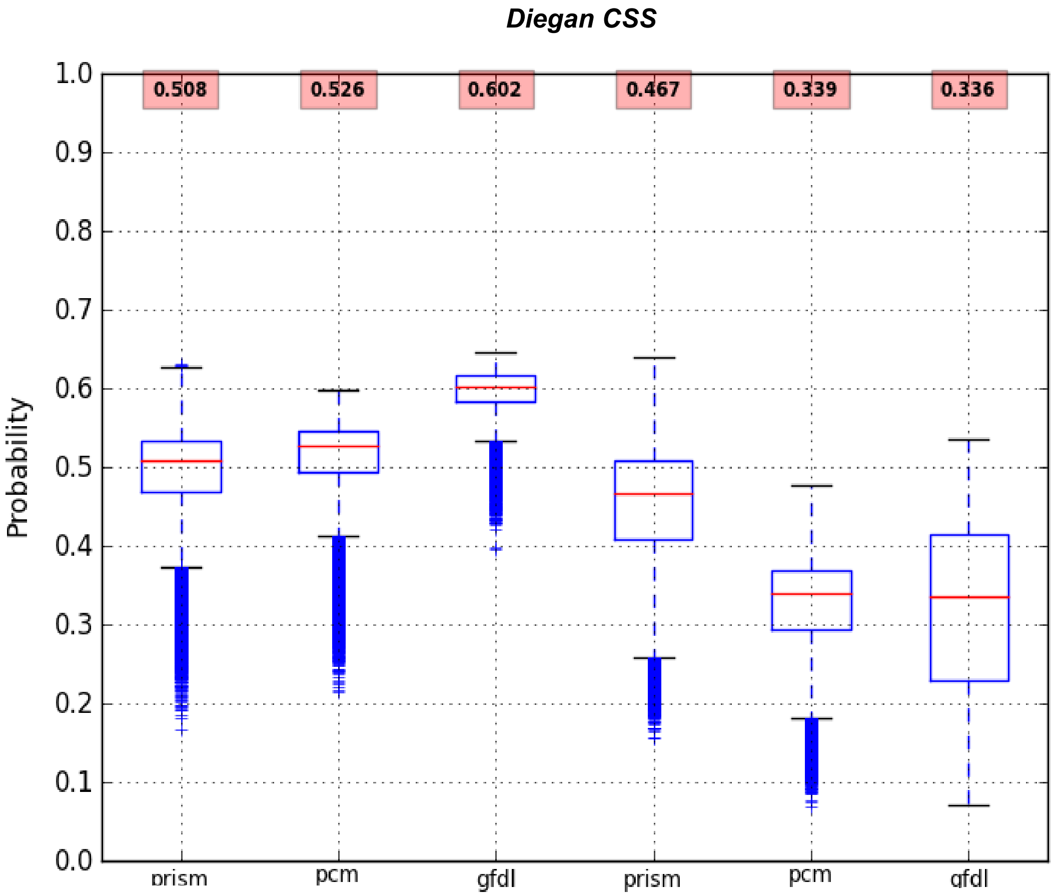

Ceanothus megacarpus
0.503
0.473
0.293
0.503
0.495
0.337
Probability
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
prism
pcm
gfdl
prism
pcm
gfdl

FIGURE I-4



Diegan CSS
Probability
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.508
0.526
0.602
0.467
0.339
0.336
prism
pcm
gfdl
prism
pcm
gfdl

FIGURE I-5

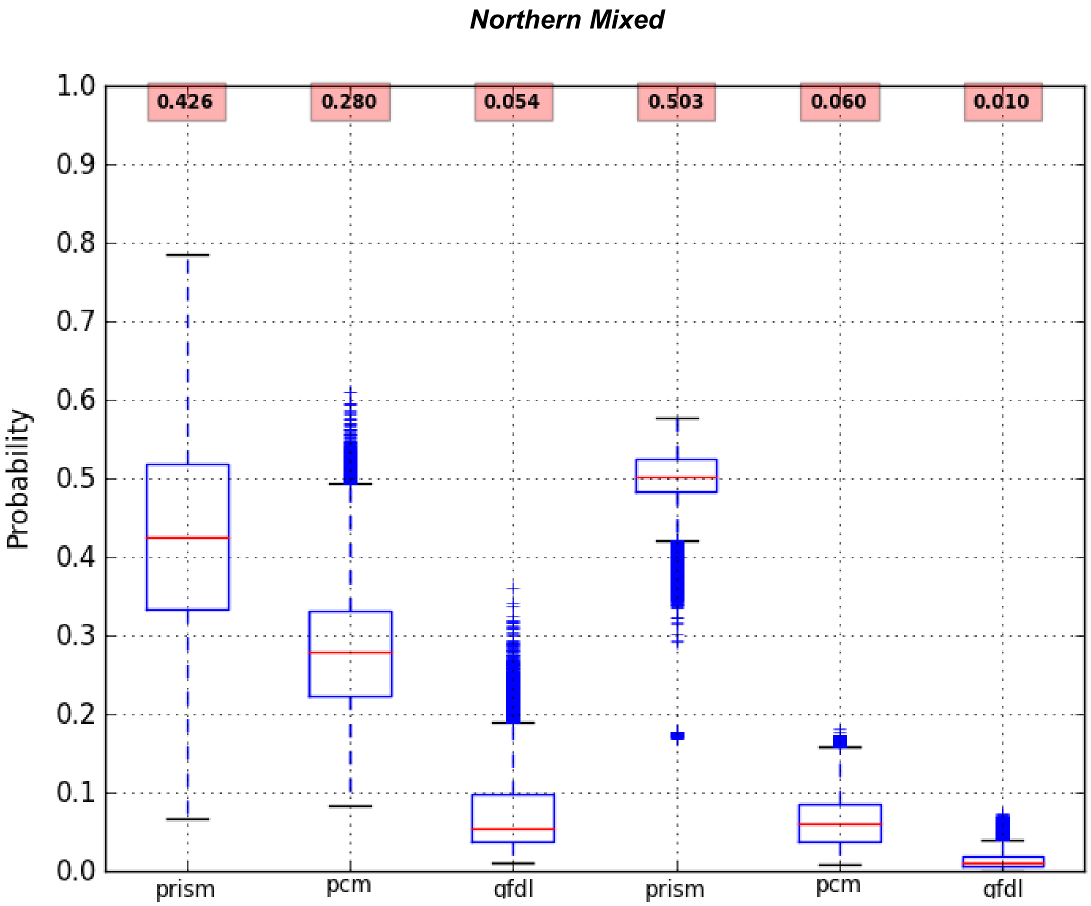

Northern Mixed
Probability
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.426
0.280
0.054
0.503
0.060
0.010
prism
pcm
gfdl
prism
pcm
gfdl

FIGURE I-6

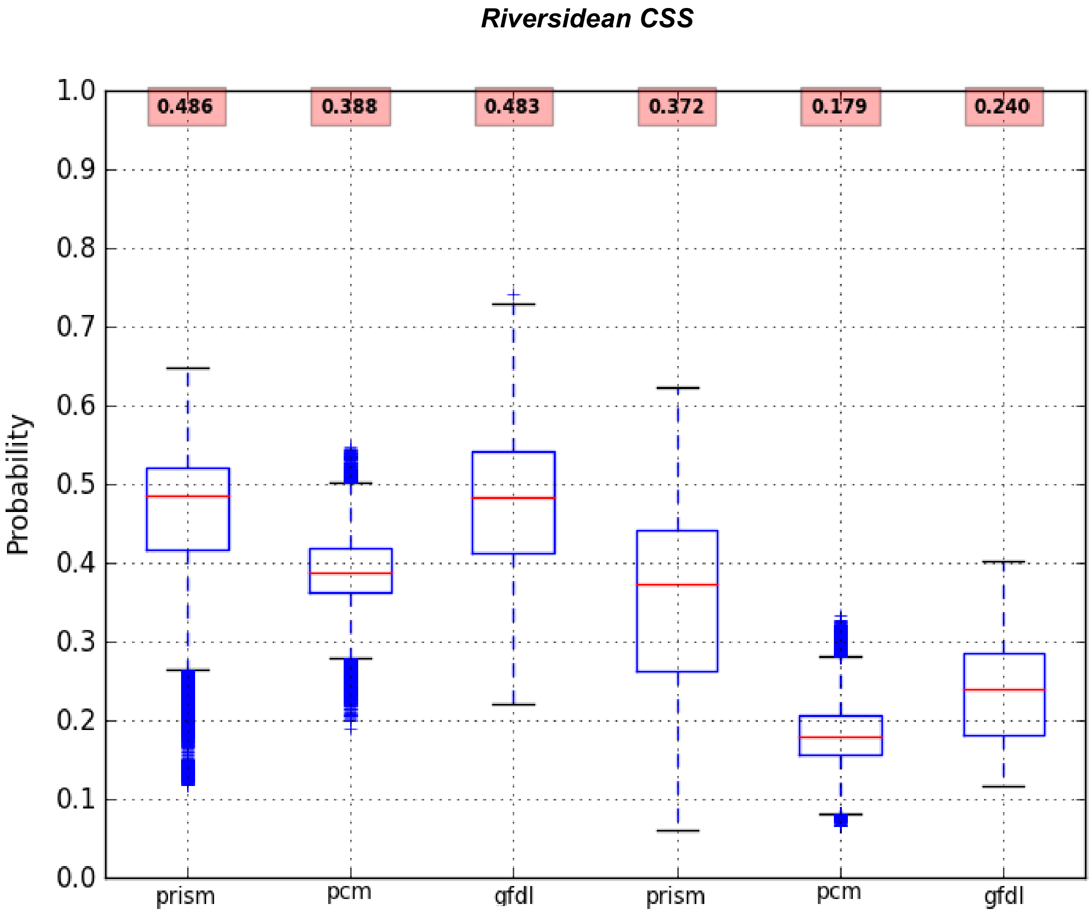

Riversidean CSS
Probability
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.486
0.388
0.483
0.372
0.179
0.240
prism
pcm
gfdl
prism
pcm
gfdl

FIGURE I-7

Scrub Oak

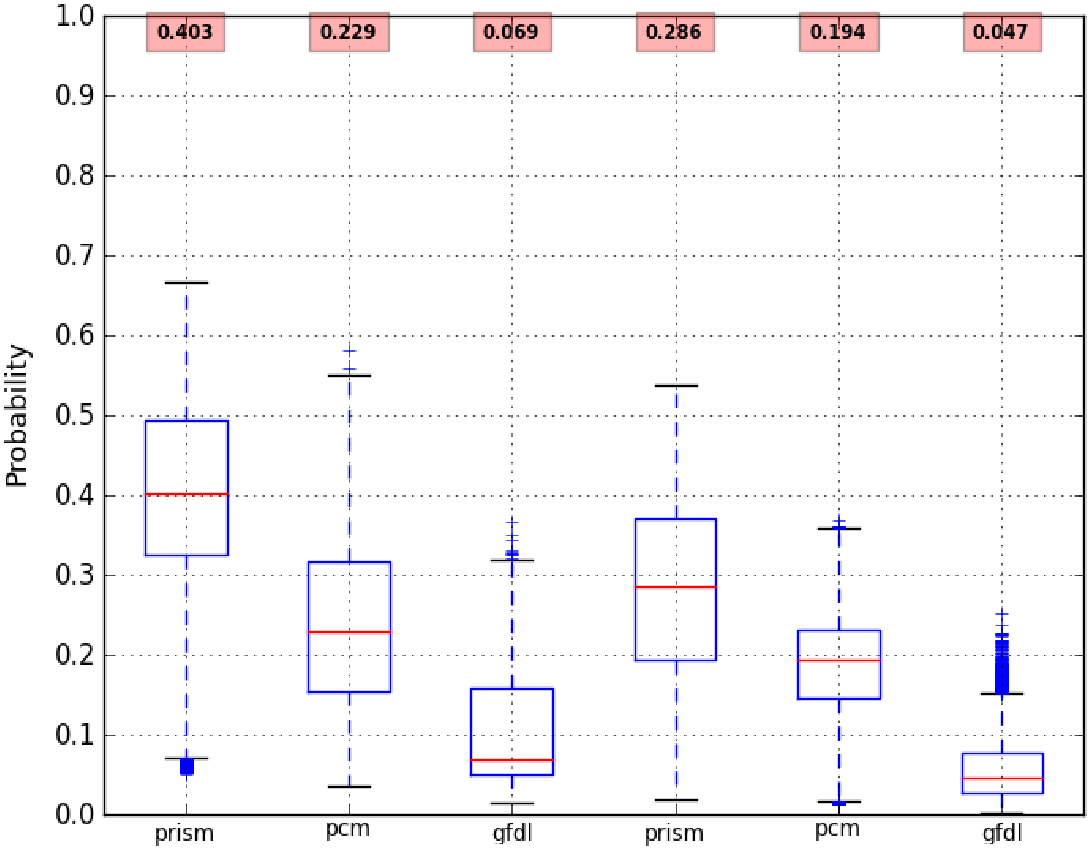


FIGURE I-8

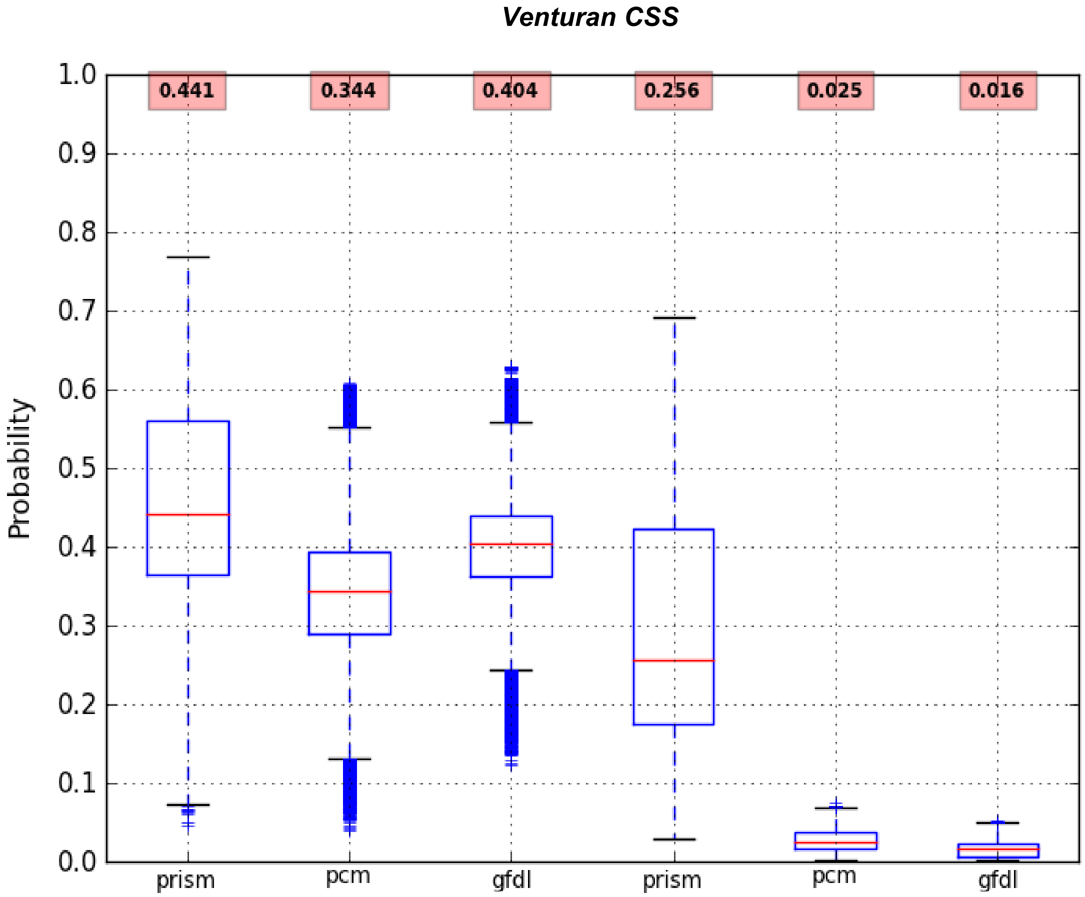

Venturan CSS
Probability
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.441
0.344
0.404
0.256
0.025
0.016
prism
pcm
gfdl
prism
pcm
gfdl

Table 1

Occurrence points relative to bounds for the SW Ecoregion and SMMNRA. Most of the occurrence points for the targeted species were recorded in SMMNRA and are geographically biased.

Species Name	**Common Name**	**Total Points in SW Region**	**Points outside SMMNRA**	**Points in SMMNRA**	**% in SMMNRA**
Ceanothus leucodermis	Chaparral Whitethorn	79	71	8	10.1%
Quercus berberidifolia	Scrub Oak	837	542	295	35.2%
Salvia apiana	White Sage	123	71	52	42.3%
Arctostaphylos glauca	Big Berry Manzanita	100	55	45	45.0%
Ceanothus cuneatus	Buckbrush	160	82	78	48.8%
Cercocarpus betuloides	Mountain Mahogany	732	264	468	63.9%
Ceanothus crassifolius	Hoaryleaf Ceanothus	221	63	158	71.5%
Eriogonum fasciculatum	California Buckwheat	926	198	728	78.6%
Arctostaphylos glandulosa	Eastwood's Manzanita	123	16	107	87.0%
Prunus illicifolia	Hollyleaf Cherry	251	32	219	87.3%
Rhus ovata	Sugar Bush	771	91	680	88.2%
Artemisia californica	California Sagebrush	1294	124	1170	90.4%
Yucca whipplei	Our Lord's Candle	835	68	767	91.9%
Heteromeles arbutifolia	Toyon	1096	76	1020	93.1%
Salvia mellifera	Black Sage	1169	77	1092	93.4%
Ceanothus oliganthus	Hairy Ceanothus	153	9	144	94.1%
Malosma laurina	Laurel Sumac	1587	91	1496	94.3%
Ceanothus megacarpus	Bigpod Ceanothus	1170	25	1145	97.9%
Opuntia littoralis	Western Prickly Pear	118	2	116	98.3%
Rhus integrifolia	Lemonade Berry	346	2	344	99.4%
Encelia californica	California Encelia	556	3	553	99.5%
Ceanothus spinosus	Greenbark Ceanothus	556	1	555	99.8%
Salvia leucophylla	Purple Sage	646	0	646	100.0%
TOTAL		**13849**	**1963**	**11886**	

Table 2

Community and Species Model Important Variable Selection Comparison

Important variables selected by MaxEnt are listed in each left column under each community. The right column under each community lists the number of species in the community for which that variable was likewise important. Bold font variables are those selected as important by the community model (and inclusively, the species model). Regular font variables were important for species only. Variety in variable selection was greater among species than among community models. BIO18: Summer Rain; BIO4: Temperature Seasonality; BIO24: Aridity; BIO5: Max Summer Temperature; BIO20: Growing Season Length; BIO12: Annual Precipitation;

Ceanothus megacarpus		**Riversidean Scrub**		**Diegan CSS**		**Venturan CSS**		***Ceanothus crassifolius***		**Scrub Oak**		***Ceanothus cuneatus***		**Northern Mixed**	
Number of species in community		Number of species in community		Number of species in community		Number of species in community		Number of species in community		Number of species in community		Number of species in community		Number of species in community	
3		3		4		4		3		3		4		8	
BIO18	3	**BIO18**	2	**BIO18**	3	**BIO4**	4	**BIO18**	2	**BIO18**	3	**BIO18**	3	**BIO18**	5
BIO4	3	**BIO24**	2	**BIO24**	3	**BIO20**	3	**BIO5**	2	BIO4	3	**BIO4**	3	BIO4	5
BIO24	2	**BIO4**	2	**BIO4**	3	BIO5	2	**BIO24**	1	**BIO24**	2	Soil pH	3	**BIO24**	3
BIO5	2	**BIO5**	2	**BIO5**	1	**BIO18**	1	BIO4	1	**Soil pH**	2	BIO20	2	BIO5	3
		BIO20	1	BIO12	1	**BIO24**	1	**BIO20**	1	Insolation	1	BIO5	1	BIO20	2
		BIO12	1	Soil H20	1	BIO12	1	BIO12	1			BIO12	1	BIO12	2
				Insolation	1	Soil H20	1	Soil H20	1			Soil Depth	1	Soil pH	2
														Insolation	2
														Soil H20	1

Table 3

Probability Sums for Suitable Habitat in SMMNRA by Community for Each Global Climate Model and Modeling Approach

Summed values for the probabilities extracted from the model grids. Each grid contained nearly three million pixels. These values are the basis for the percentage decrease graphs in Figure 10, Community Response to Climate Change as Percent Change in SMMNRA Suitable Habitat Probability Sums.

	SMMNRA Suitable Habitat Probability Sums							
Climate Model	Ceanothus crassifolius	Ceanothus cuneatus	Ceanothus megacarpus	Diegan CSS	Northern Mixed	Riversidean Sage Scrub	Scrub Oak	Venturan CSS
	Modeled Communities							
PRISM	59030	42357	60199	59663	50673	55259	48456	54672
PCM A2	45450	26398	56801	61882	33222	46792	28291	41003
GFDL A2	26322	10397	34675	71802	8692	57747	11920	48570
	Intersected Communities							
PRISM	42065	29275	59783	54704	22181	42199	33615	35952
PCM A2	16499	10741	58962	39430	7661	21838	22040	3282
GFDL A2	9316	2008	38011	38372	1564	28780	6390	2020

Table 4

Wilcoxon-Mann-Whitney Test on Suitable Habitat Probability Medians for Difference in Current and Averaged Climate Change GCMs Across Communities

The first column "Current Climate Median" are median values for probability distributions extracted from current climate grids; "Averaged Climate Change Median" are the distributions extracted from averaged PCM A2 and GFDL A2 for that community; "Difference" is the difference for those; p value is the probability that the two samples came from populations with equivalent distributions. *n*=100.

Wilcoxon-Mann-Whitney Test

Community	Current Climate Median	Averaged Climate Change Median	Difference	*p* Value
		Modeled Communities		
Ceanothus crassifolius	0.515	0.298	0.217	< 2.2e-16
Ceanothus cuneatus	0.381	0.142	0.239	< 2.2e-16
Ceanothus megacarpus	0.504	0.384	0.120	< 2.2e-16
Diegan CSS	0.511	0.571	-0.06	< 2.2e-16
Northern Mixed	0.434	0.176	0.258	< 2.2e-16
Riversidean Sage Scrub	0.501	0.432	0.069	1.52E-05
Scrub Oak	0.397	0.164	0.232	< 2.2e-16
Venturan CSS	0.438	0.363	0.075	1.33E-08
		Intersected Communities		
Ceanothus crassifolius	0.367	0.113	0.254	< 2.2e-16
Ceanothus cuneatus	0.260	0.050	0.21	< 2.2e-16
Ceanothus megacarpus	0.500	0.435	0.065	4.49E-12
Diegan CSS	0.479	0.311	0.168	< 2.2e-16
Northern Mixed	0.184	0.035	0.149	< 2.2e-16
Riversidean Sage Scrub	0.377	0.211	0.166	< 2.2e-16
Scrub Oak	0.296	0.125	0.172	< 2.2e-16
Venturan CSS	0.260	0.022	0.238	< 2.2e-16

Table 5

Sorting By Increasing Response To Averaged Climate Change Between Mesic And Non-Mesic Communities

Within each table, the percent change in probability sums for climate change within SMMNRA relative to habitat probability sums for current climate are listed in order of increasing value. Bolded community names are non-mesic; regular font are mesic. The rank for percent change (1=least, 8 = most) for the modeled community is listed in the right-most column for each table. Note that changes in rank emphasize how each modeling approach picks up different trends based on species drought tolerance; the modeled communities sort by drought tolerance more coherently than the intersected models.

GFDL A2

Modeled		Intersected		
Community	% Change	Community	% Change	Rank (Modeled) by Increasing % Change
Diegan CSS	0.20	**Diegan CSS**	-0.30	1
Riv Scrub	0.05	**Riv Scrub**	-0.32	2
Venturan CSS	-0.11	**C. megacarpus**	-0.36	4
C. megacarpus	-0.42	**C. crassifolius**	-0.78	5
C. crassifolius	-0.55	Scrub Oak	-0.81	6
Scrub Oak	-0.75	N Mixed	-0.93	8
C. cuneatus	-0.76	C. cuneatus	-0.93	7
N Mixed	-0.83	**Venturan CSS**	-0.94	3

PCM A2

Modeled		Intersected		
Community	% Change	Community	% Change	Rank (Modeled) by Increasing % Change
Diegan CSS	0.04	**C. megacarpus**	-0.01	2
C. megacarpus	-0.06	**Diegan CSS**	-0.28	1
Riv Scrub	-0.15	Scrub Oak	-0.34	8
C. crassifolius	-0.23	**Riv Scrub**	-0.48	3
Venturan CSS	-0.25	**C. crassifolius**	-0.61	4
Northern Mixed	-0.34	C. cuneatus	-0.63	7
C. cuneatus	-0.38	N Mixed	-0.66	6
Scrub Oak	-0.42	**Venturan CSS**	-0.91	5

Figure 1. Study Area and Regional Context for SMMNRA. The left and right diagonal cross-hatched area combined is the California Floristic Province (CFP). The right diagonal crosshatched area alone is the Southwestern California (SW) region. The Santa Monica Mountains National Recreation Area (SMMNRA) is represented by the black polygon.

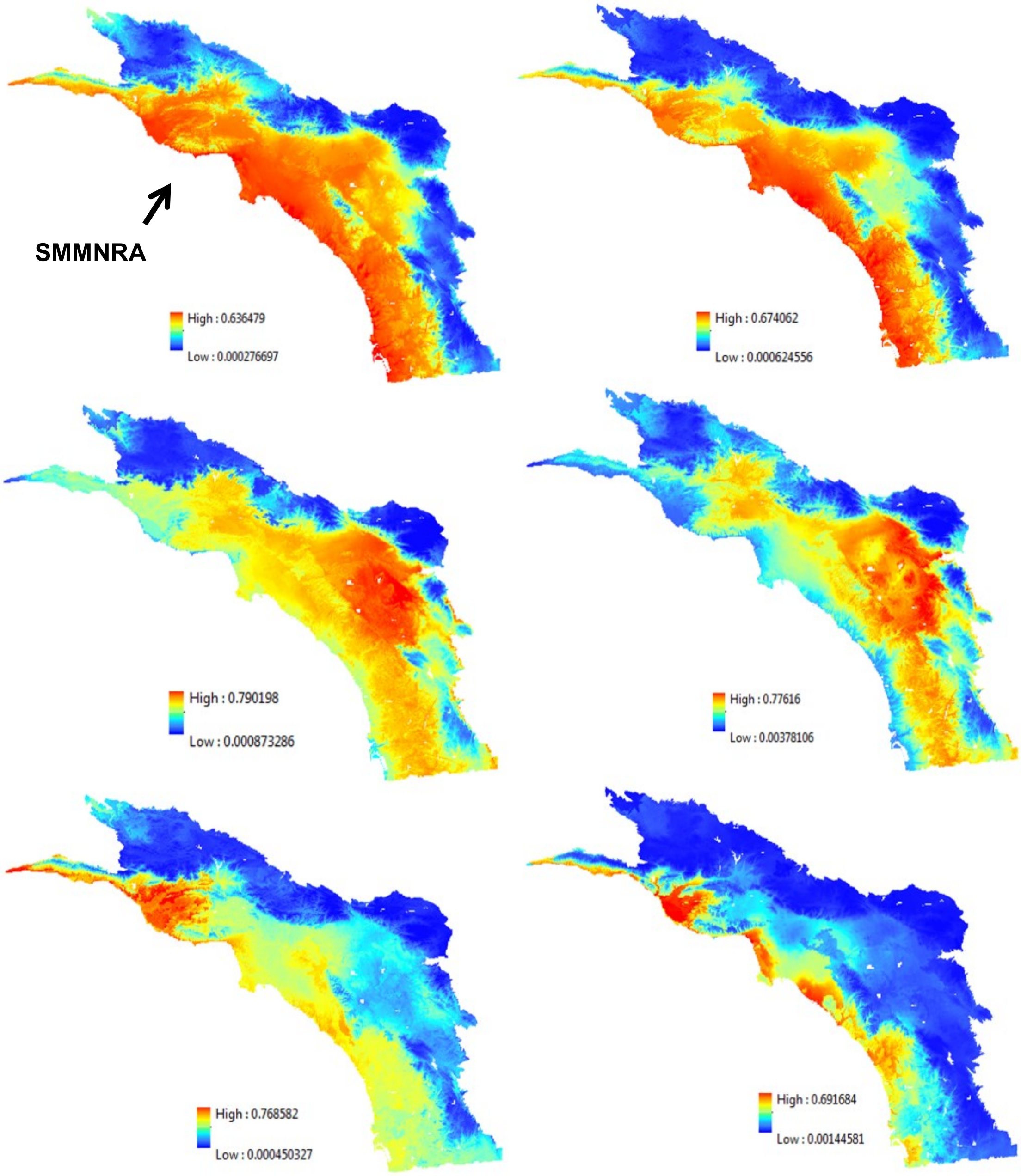


Figure 2. South West Ecoregion Modeled Distributions for CSS. Left column: grouped species models; Right column: intersected species models. Top Row: Diegan CSS; Middle Row: Riversidean Sage Scrub; Bottom Row: Venturan CSS. Warmer colors indicate higher probabilities for suitable habitat. SMMNRA is approximately located where black arrow is in Diegan CSS Modeled Community image. Note that each legend scale for suitable habitat probabilities is relative.

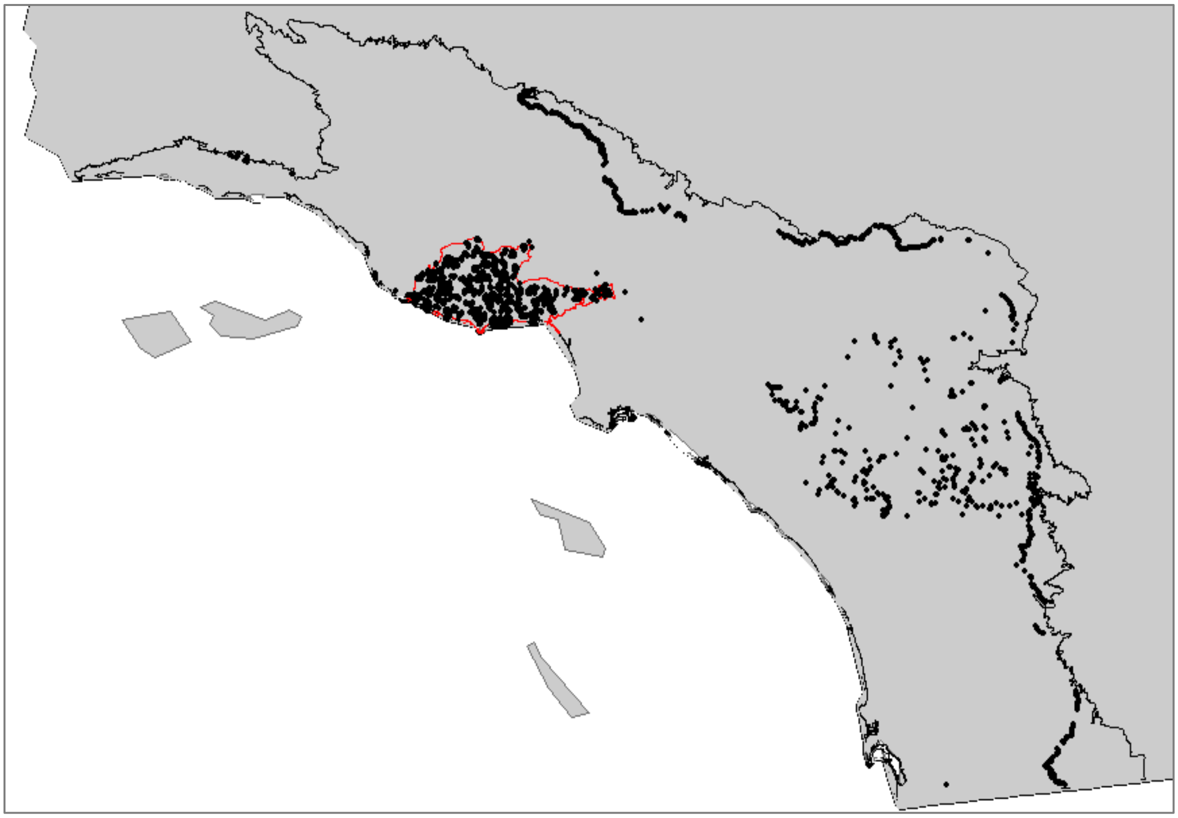


Figure 3. Spatial Bias of Species Occurrences. The distribution of all 13,849 data points for the targeted species within the SW region (indicated by black border). Of these, 11,886 points are within SMMNRA (indicated by the red border).

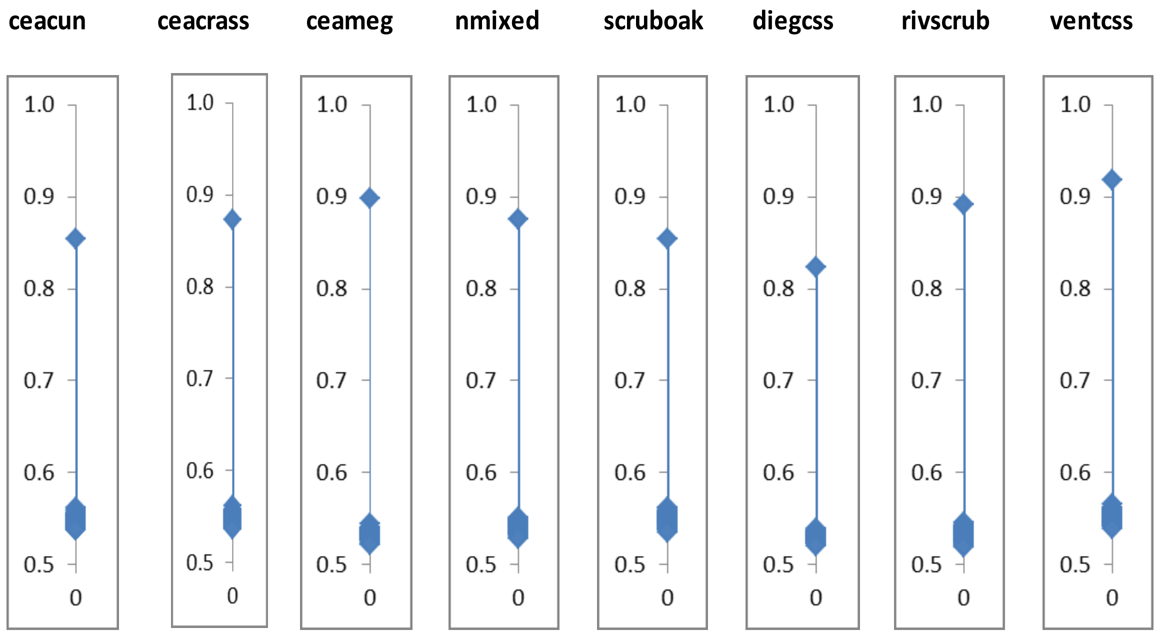


Figure 4. Results Demonstrating Environmental Bias in the Occurrence Data Using Null a Model Comparative Procedure (Raes and ter Steege, 2007). The lower collection of grouped points represents the AUC values of 99 SDMs built with randomly drawn locations from one representative environmental grid used in the study, BIO12 (Annual Precipitation). The upper point represents the AUC value for the real SDM for each community using the actual occurrence locations. The SDMs built with randomly drawn environmental data were run with the same settings as the real SDM.

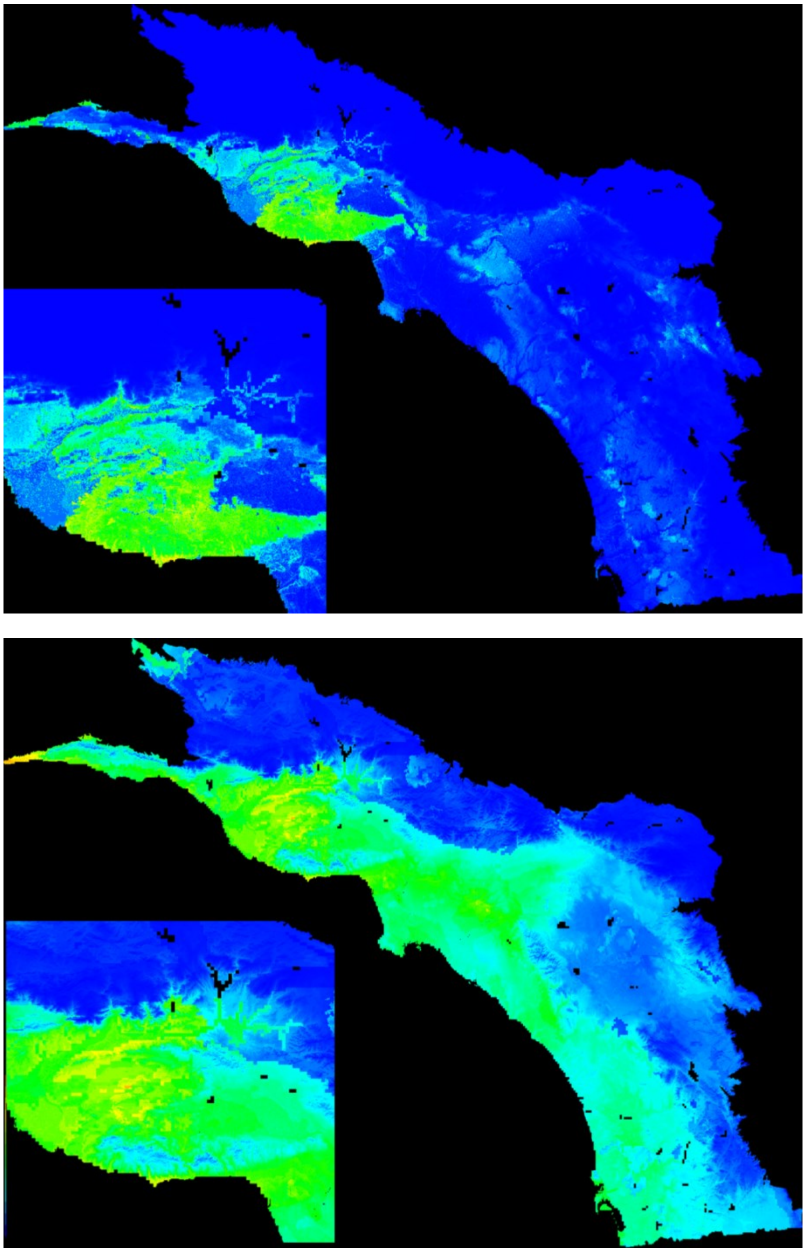


Figure 5. Target Group Background Versus Background From The Entire SW Region. On the top is the predicted distribution for Venturan CSS over the study area using a random sample of points from the entire SW region for the background. The inset is a close up of SMMNRA, showing little differentiation within its bounds. On the bottom, the predicted distribution based on target group background points is more reasonable, shifting predictions northwestward into Ventura County and increasing discrimination within SMMNRA. Note the distribution has moved away from the high elevation peaks and chaparral areas within SMMNRA, visible in the inset in the lower figure (the light blue band replacing green). Warmer colors mean higher probabilities for suitable habitat. Note that this model is a calibration-stage model, and was not the one used for the current climate Venturan CSS in the study

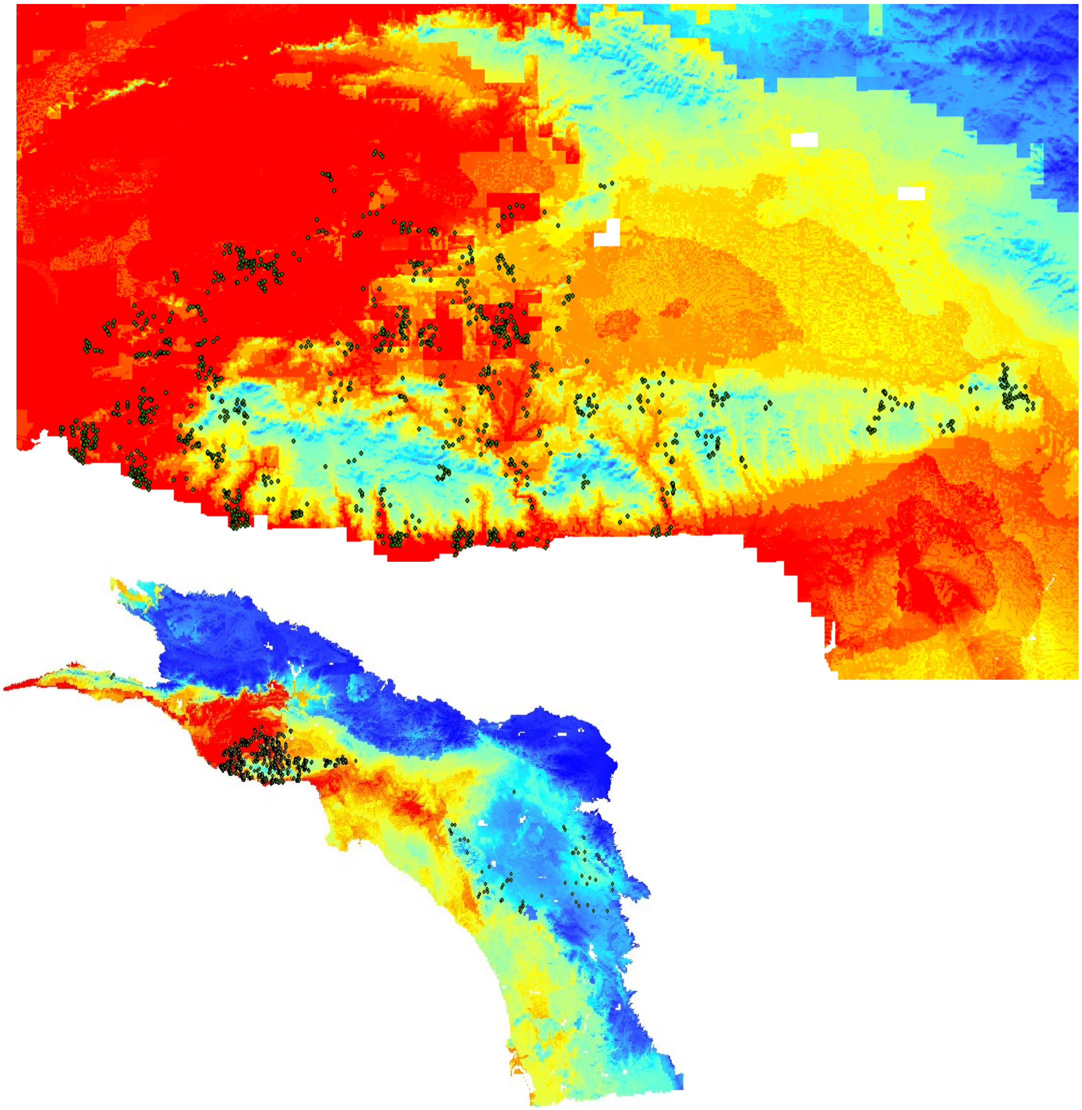


Figure 6. Model for Venturan CSS with Target Group Background Overlaid with Occurrence Points For the Assembly. On the lower panel is the SW regional view. The close up of SMMNRA is on the upper panel. Warmer colors indicate higher predicted probabilities for suitable habitat.

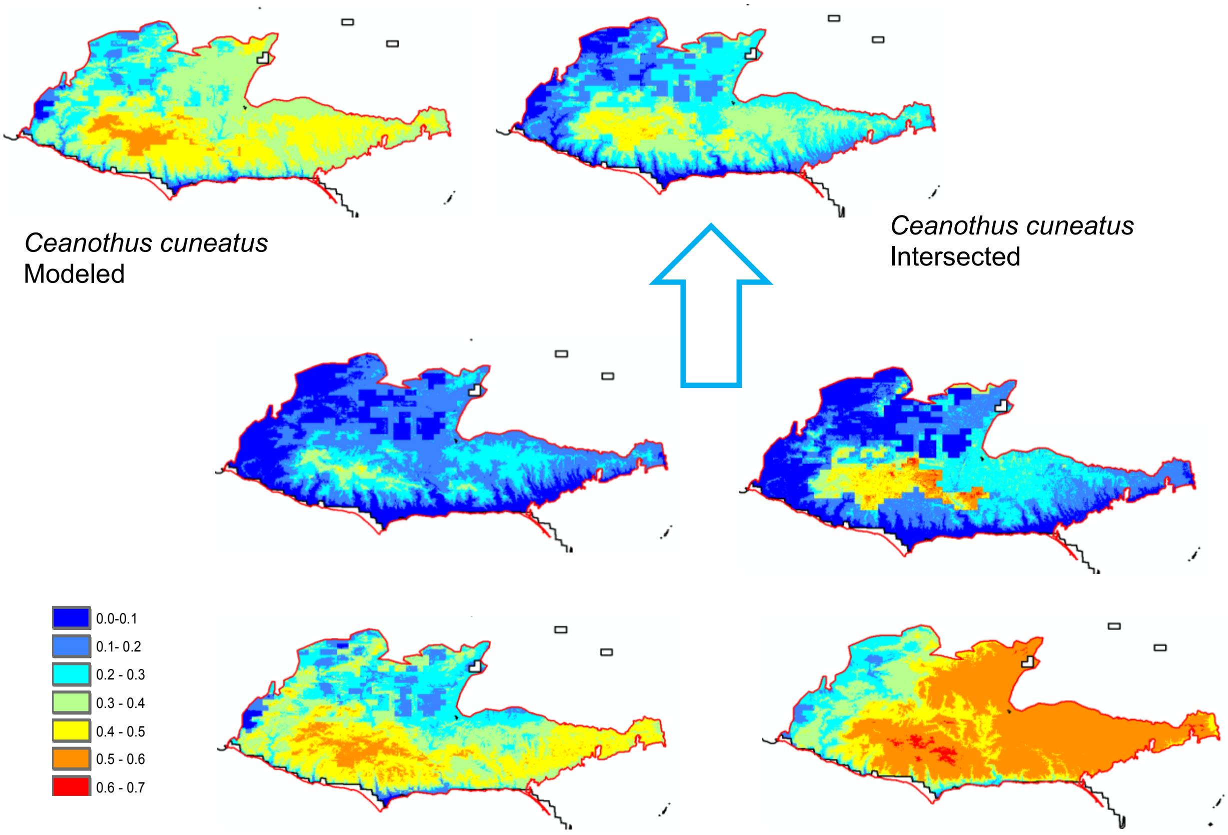


Figure 7. *Ceanothus cuneatus* Community Model for SMMNRA. Mapped suitable habitat depicting the Ceanothus cuneatus community based on the modeled community upper left, and based on the intersected model upper right. The component species models are shown below the blue arrow. Species models, clockwise from left: *Quercus berberidifolia, Ceanothus cuneatus, Rhus ovata, Cercocarpus betuloides*. The color ramp legend lower left gives the range of values for the probability of suitable habitat from pixels in the models, from a minimum of 0.0 to a maximum of 0.7, based on a scale 0.0 to 1.0. Higher values (warmer colors) indicate where higher probabilities for suitable habitat are located. Boxplots for the community distributions are shown in Figure 8.

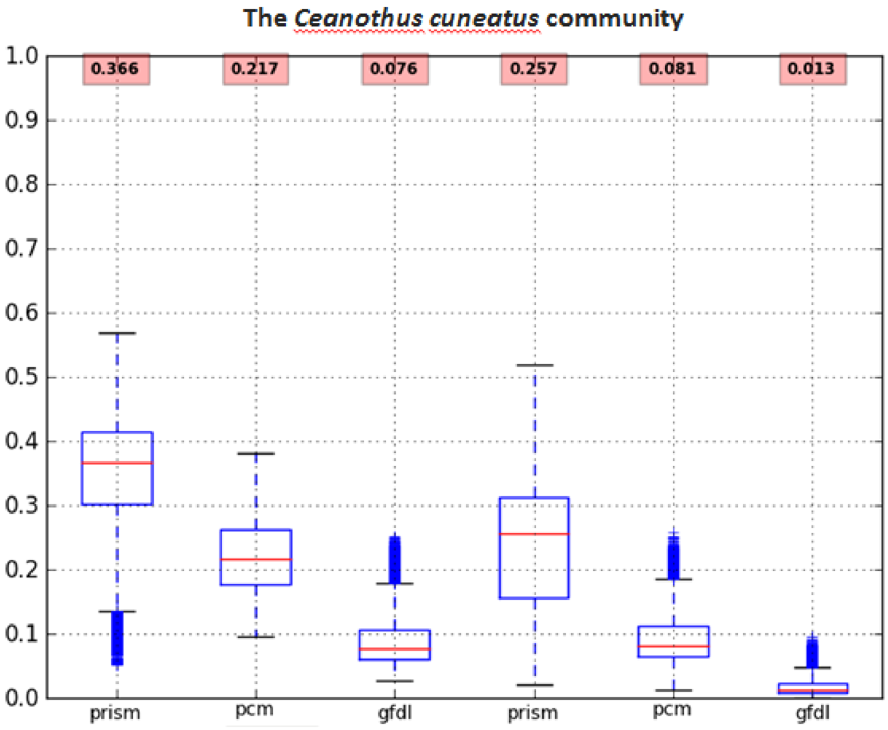
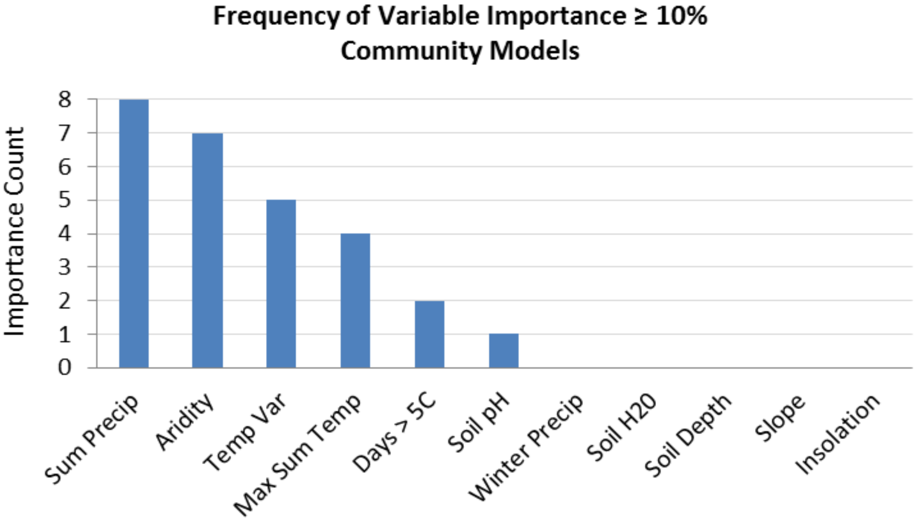


Figure 8. Boxplots illustrating the contrast between modeling approaches . The boxplots represent the probability distributions for suitable habitat within SMMNRA's bounds for the *Ceanothus cuneatus* community. Their mapped distributions are depicted in Figure 7.
In the graph series: Graphs 1-3 are the community models (grouped species): the boxplots from left to right are the distribution for current climate (PRISM graph 1),warmer and wetter (PCM A2-graph 2) and warmer and drier GCMs(GFDL A2 graph 3). Graphs 4-6 are for the same species but as intersected species models to form the community. The y-axis is the scale for the probability values for suitable habitat extracted from the models. Median values for each probability distribution are given in the pink boxes at the top of each graph . The intersected models (Graphs 4-6) had lower median values across GCMs for most communities.



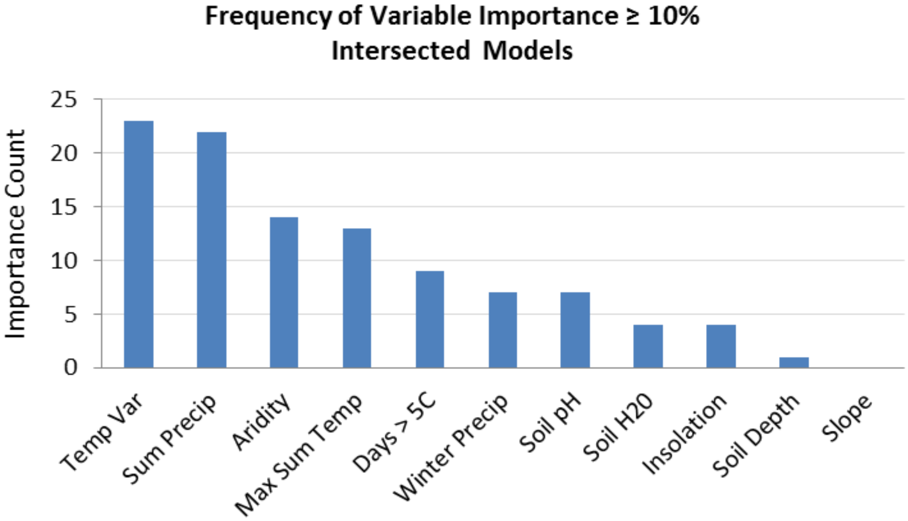
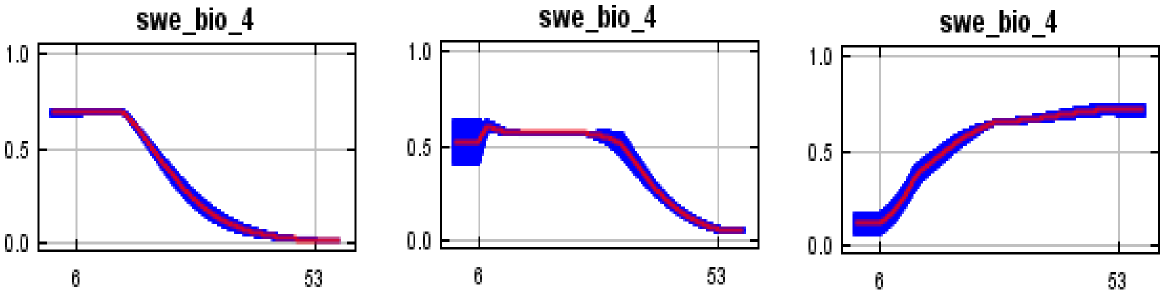


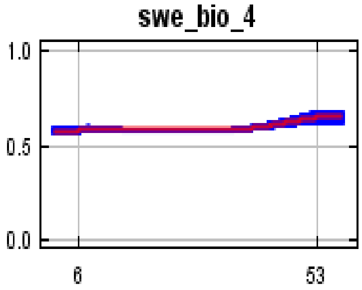
Figure 9. Frequency of Variable Importance ≥ 10 Percent Permutated Value. Frequency of important variables in models as calculated by MaxEnt. Top: Community models; Bottom: Species models. Topographic variables were selected as important more frequently in the species than in the community models. Temperature Variation in the species models replaces Summer Rain as the most frequently important variable in the community models. Note that y axes are different between species and community model bar charts.



Species: *Ceanothus spinosus*

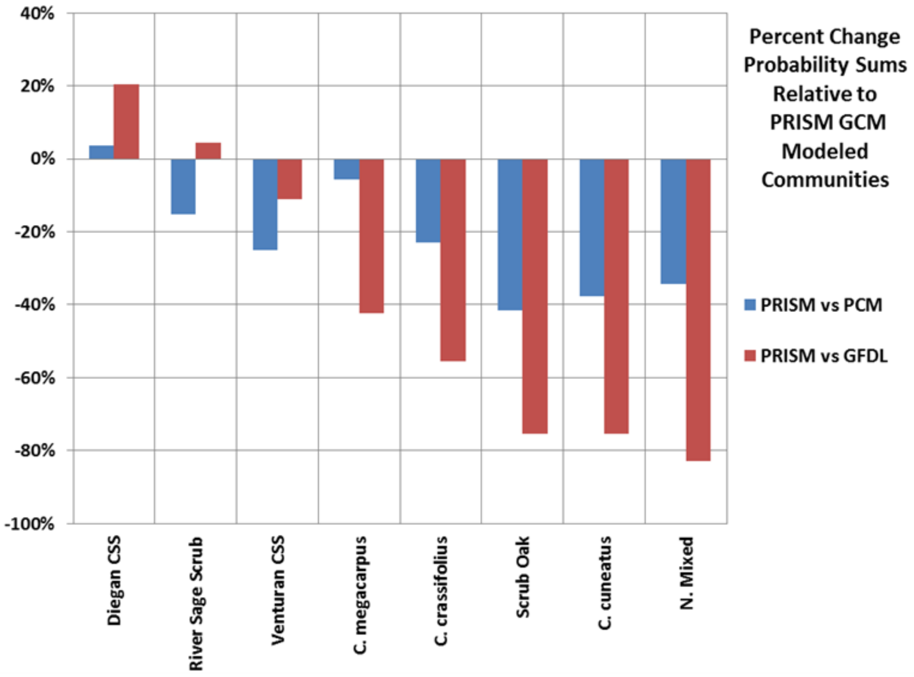
Species: *Heteromeles arbutifolia*

Species: *Quercus berberidifolia*



Community: Scrub Oak

Figure 10. Response Curves For Temperature Seasonality (BIO4) for Modeled Scrub Oak Community. Top Row: Response curves for the component species. Bottom Graph: Response curve for the community. Community curves often had a shape intermediate to the more variable shapes for the species models and appeared to be the average of the species' response curves. The values on the y axis are probabilities for suitable habitat (ranging from 0-1) for the species as x (standard deviation for Temperature Seasonality) is varied. The heading 'swe_bio_4' refers to the environmental variable file name used by MaxEnt for Temperature Seasonality for the Southwest Ecoregion (swe).



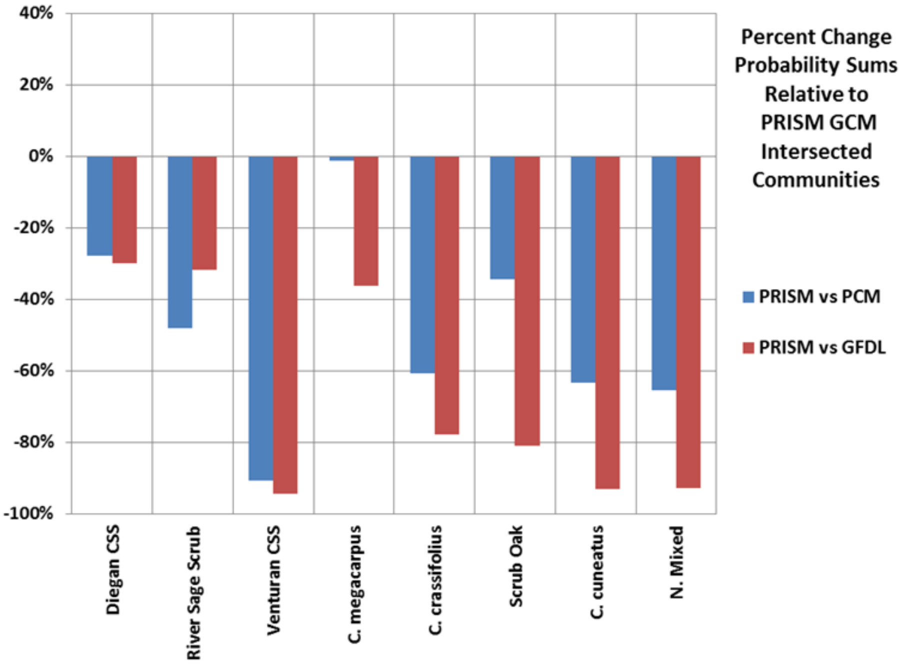


Figure 11. Community Response in SMMNRA to Climate Change as Percent Change for Suitable Habitat Probability Sums Relative to PRISM" (current climate). Top graph: Modeled Communities; Bottom graph: Communities as intersected species models. Projected change in suitable habitat within SMMNRA bounds as a percent difference relative to current climate. GFDL (red bars) is warmer and drier climate; PCM (blue bars) is warmer and relatively wetter. Labels below graphs are the community names.