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Climate Change Impacts on California Vegetation: Physiology, Life History, and Ecosystem Change

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CLIMATE CHANGE IMPACTS ON CALIFORNIA VEGETATION: PHYSIOLOGY, LIFE HISTORY, AND ECOSYSTEM CHANGE

A White Paper from the California Energy Commission's California Climate Change Center

Prepared for: California Energy Commission
Prepared by: University of California, Berkeley

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DISCLAIMER

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Acknowledgements are provided in each section of this paper.

PREFACE

The California Energy Commission's Public Interest Energy Research (PIER) Program supports public interest energy research and development that will help improve the quality of life in California by bringing environmentally safe, affordable, and reliable energy services and products to the marketplace.

The PIER Program conducts public interest research, development, and demonstration (RD&D) projects to benefit California. The PIER Program strives to conduct the most promising public interest energy research by partnering with RD&D entities, including individuals, businesses, utilities, and public or private research institutions.

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In 2003, the California Energy Commission's PIER Program established the California Climate Change Center to document climate change research relevant to the states. This center is a virtual organization with core research activities at Scripps Institution of Oceanography and the University of California, Berkeley, complemented by efforts at other research institutions.

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ABSTRACT

Dominant plant species mediate many ecosystem services, including carbon storage, soil retention, and water cycling. One of the uncertainties with climate change effects on terrestrial ecosystems is understanding where transitions in dominant vegetation, often termed *state change,* will occur. The complex nature of state change requires multiple lines of evidence. Here, we present four lines of inquiry into climate change effects on dominant vegetation, focusing on the likelihood and nature of climate change–driven state change. This study combined physiological measurements, geographic models, historical documented cases of state change, and statewide plot sampling networks together with interpolated climate grids. Together these approaches suggest that the vulnerability to state change will be driven by the proximity of climatic conditions to biological thresholds for dominant species. The sensitivity of the dominant species is a much greater driver of climate vulnerability compared to the degree of climate change seen by a particular place (Section 1). Furthermore, in some cases, physiological measurements on those species can inform the nature of these thresholds (Section 3). The study team's review of past state change events suggests connections between particular state changes (e.g., forest to shrubland) and particular triggers (e.g., fire; Section 2). The effect of fire is particularly important, as it will likely interact with climatic change with implications for the success of different life history strategies among woody plants (Section 4). Our work suggests that the biological thresholds of dominant species will play a crucial role in the vulnerability of California terrestrial ecosystems. Understanding where climate change will push dominant species past these thresholds should be a major focus of future research.

Keywords: state change, ecosystem services, terrestrial ecosystems, thresholds, vulnerability, exposure, sensitivity

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Introduction

The objectives of this study were to examine projections for climate-induced change in vegetation, ecological mechanisms of vegetation change, and associations of species physiology and life history with distributions on climate gradients. This paper includes four studies addressing this theme. Section 1 presents a new probabilistic model of vegetation distributions in the Bay Area in relation to climate, and forecasts of how climate change will shift these distributions. Section 2 is a review of known mechanisms of vegetation change in coastal California (with a brief analysis of similar mechanisms in the Sierra Nevada). These two studies will be linked to address whether the changes forecast due to climate change are consistent with historically observed changes, and if so what the role of various mechanisms may be in the future (e.g., fire, disease, drought). These two studies were initiated with funding from the Gordon and Betty Moore Foundation, and completed under the current set of California Energy Commission vulnerability studies.

Sections 3 and 4 examine relationships between individual species or functional groups and climate, in an effort to develop a stronger mechanistic understanding of the physiological and ecological factors that may underlie the predictions emerging from species distribution modeling. Section 3 presents a review of plant functional traits in relation to species range limits along precipitation and temperature gradients. Section 4 examines the distribution of contrasting post-fire life history strategies in woody plants (e.g., seeding, resprouting) in relation to climate and fire, providing a basis for forecasting climate change impacts on these functional groups, independent of individual species distributions.

Each section of this paper is expected to be published as a separate paper in the primary literature, and can be read independently of the others.

Section 1: A New Method for Estimating the Probability of Climate-Change Induced Ecosystem Change in Complex Landscapes

Authors: W. K. Cornwell, A. Flint, L. Flint, S. Weiss, and D. D. Ackerly

Abstract

Climate change is expected to profoundly affect terrestrial vegetation. Understanding spatial variability of these impacts is critical to development of conservation strategies and projections of ecosystem services under future climates. This section presents a probabilistic model of the projected impacts of climate change on the distribution of vegetation types in the San Francisco Bay Area using a novel application of multinomial logistic regression. The output of this method is a vector of the relative probability of occupancy by each of a set of vegetation types, for each pixel in the landscape. The overall vulnerability of vegetation to climate change can then be quantified as the change in the probability vectors modeled under present versus future climate. The change in this vector captures the likelihood of long-term, climate-driven vegetation change for each pixel, without relying on deterministic predictions of present and future vegetation types, a determinism that is at odds with current theories of community dynamics. This measure of climate-induced vulnerability can be further decomposed as the product of two components, one reflecting the intrinsic sensitivity of the vegetation to climate and the second measuring the exposure to (i.e., magnitude of) climate change. Based on a new set of high-resolution downscaled climate projections for coastal California, including an estimate of the annual climatic water deficit, this project demonstrated that the vulnerability of vegetation distributions is almost entirely due to variation in sensitivity of individual patches, and not to differences in the magnitude of climate change. This new methodology leads to a clear hypothesis about climate effects on vegetation: the proximity of local climate to the biological thresholds for a particular vegetation type are the key determinant of spatial variation in ecosystem vulnerability.

Introduction

In ecology, change is a constant. One especially dramatic class of change is vegetation state transitions—the shift in the physiognomy of the dominant species of plants from, for example, forest to a grassland. These changes, mediated by turnover in the dominant plant species, may have enormous effects on biodiversity, ecosystem services, and conservation efforts in a local area (Chan et al. 2006). Global change has the potential to effect these types of changes all across the world with significant implications for both conservation and human welfare (Schröter et al. 2005).

The vulnerability of ecosystems to change can be thought of as a function of the sensitivity of the organisms involved and the exposure—the magnitude of the climatic change at that particular place (Turner et al. 2003); this framework is being increasingly used in social sciences (Ionescu et al. 2009) but is equally useful when applied to ecosystems and organisms. The magnitude of climatic change—the exposure of a given place to the shift in climate—is becoming increasingly well-defined (Overpeck et al. 2011). However, biological sensitivity is more difficult to quantify. With respect to plants, climate change-induced transitions occur against a background of the effects due to landuse, disturbance, history, disease, and a variety of other mechanisms (Turner 2010). Isolating climate vulnerability from the array of ecological mechanisms is not trivial. A considerable body of literature has addressed this topic, in a range of contexts such as succession, restoration, and alternative stable states (May 1977; Suding and Hobbs 2009; Turner 2010).

There are several approaches to quantify the vulnerability of vegetation to climate change and related factors. The first is observational: documented state changes at particular places that can be inferred to be climate-driven (Sturm et al. 2001). The second utilizes experimental approaches to test factors that influence transitions between different vegetation types (Suding and Hobbs 2009). The third is the species distribution model (SDM) approach, which treats each species (or vegetation type) as a separate entity, with an individualistic response to different climate variables (Araújo and Guisan 2006). And finally, dynamic global vegetation models provide a mechanistic approach to mapping major vegetation types in relation to climate and climate change (Woodward and Lomas 2004). Despite the clear conceptual interconnections, these approaches have developed somewhat independently. At present observations of climate-induced changes are spread across the world, with numerous documented cases of poleward and uphill movement (Parmesan 2006). While this may be true on average, complex, local climate gradients (Daly et al. 2010) and the multivariate climate tolerances of many organisms (Williams et al. 2004) necessitate a more nuanced set of methods to determine where local vulnerability—defined for this case as the probability of a site experiencing climate change-induced state change—is highest. At the interface of these largely separate lines of inquiry is the need to have a predictive model that could forecast the probability of climate change-induced vegetation transitions (Miller et al. 2007).

To address this, we present a new, probabilistic model of how climate and topography affect vegetation. One key feature of this model is that the current state of vegetation is modeled probabilistically—a given place in the landscape is represented as a vector of probabilities. This non-deterministic behavior is important especially in systems well known to have alternative stable states (May 1977; Turner 2010). Because the model derives a relationship between spatially explicit predictors and the vector of probabilities, climate change can then be represented as a modification in this vector of probabilities. The relative vulnerability of vegetation to state change can be quantified as the magnitude of the climate-driven shift in the probability vector. We apply this new tool to a high-resolution vegetation map (30 meter mapping units) in the San Francisco Bay Area to ask the following questions: (1) Can we quantify climate vulnerability on the regional-to-local scale? (2) What is the likelihood and nature of vegetation change in the Bay Area with climate change?

Site Description

The San Francisco Bay Area

Vegetation in the San Francisco Bay Area today consists of a complex mosaic of vegetation types, including herbaceous grasslands, shrublands, chaparral, woodlands, and closed forests. The distribution of vegetation types is determined in part by edaphic, topographic, and climatic factors. In many cases, though, several different vegetation types could exist at a particular combination of these factors. Which type is observed depends on a diverse array of historical factors, including fire, grazing, human land use, and disease distribution. The vegetation of the Bay Area is in flux, due to climate change, nitrogen deposition, historical and ongoing species invasions, and changing human land use. Understanding the interactions of these factors is critical in predicting future vegetation changes and guiding management decisions.

Methods

Vegetation Layer

We used a detailed vegetation map for the San Francisco Bay Area, which was originally produced based on remote sensing (Parker and Matyas 1979; Matyas and Parker 1980), and subsequently went through several rounds of refinement by local experts (Bay Area Open Space Council 2011). The map is at the 30 m by 30 m grain size.

We considered only the parts of Bay Area vegetation that were not intensively used by humans, excluding developed areas, wind farms, and agriculture. Areas where housing is mixed with native vegetation are included. We also excluded vegetation types that occupied less than 2,000 hectares of area and those on specialized edaphic features (e.g., serpentine); this left $1.5 * 10^7$ pixels with 23 vegetation types, covering 13,500 sq. km. One important aspect of the vegetation types in the Bay Area is that 17 of 23 types are determined by the identity of the dominant woody species (e.g., redwood forest). The map contains no information in the map about subdominant species, so vegetation types in this analysis can be thought of as the areas where a particular shrub or tree species is dominant.

Climate and Water Deficit Layers

We used macroclimate data from the PRISM climate project (Daly et al. 2008). After model selection (see below), only three macro-climate layers remained: Summer (JJA)[1] maximum temperature, Winter (DJF) minimum temperature, and mean annual precipitation (Daly et al. 2008). Because of its importance in determining coastal vegetation patterns (Grace 1988), we also used a mean wind speed layer.[2] We used a measure of seasonal water deficit, calculated following Stephenson (1990), which was calculated at the 270 m scale (Flint and Flint 2012). For future projections we used Geophysical Fluid Dynamics Laboratory (GFDL-A2) for the mid-century (2041–2070), with water deficit projected using the same methodology. All climate layers

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[1] JJA = June, July, August; DJF = December, January, February

[2] California Wind Resource Maps. http://www.energy.ca.gov/maps/renewable/wind.html.

were disaggregated to 30 m to match the scale of the vegetation map, recognizing that this results in values from adjacent cells were not calculated independently.

Digital Elevation Model (DEM) and Soil-based Layers

We used the United States Geological Survey's (USGS)1 arc-second digital elevation model (DEM) to generate a map of annual potential insolation accounting for solar tracks and hill shading (ARC-GIS 9.3 software, ESRI, Redlands, California). Minimum soil depth was based on the USGS STATSGO database.[3] Vegetation on serpentine parent material, on which distinctive vegetation develops in the Bay Area, was excluded from this analysis. These sites, which are of intense conservation interest, have been the focus of other detailed work (Harrison and Rajakaruna 2011).

Probabilistic Vegetation Model

All statistical vegetation models use the current distribution of vegetation and create a statistical link between current abiotic variables and vegetation types. This link is then used with future abiotic conditions, including both the variables that will change (e.g., temperature and precipitation) and those that will not (e.g., soil depth). The model then creates a forecast of areas that may experience a state change for a given climate forecast. Traditional vegetation models assume a deterministic link between abiotic variables and vegetation types. Given the well-documented complexity of this link for California vegetation (see review in Section 2), a probabilistic approach offers a both better representation of current ecological concepts (Seabloom et al. 2003; Suding and Hobbs 2009). Our newly developed probabilistic model is built on the statistical method of multinomial logistic regression.

Logistic models are well known and used in ecology (Keating and Cherry 2004), including their use in binomial vegetation modeling (Calef et al. 2005). In the conventional case there are two possible outcomes (Hosmer and Lemeshow 2000), which is limiting in any ecological setting in which there are more than two possible vegetation types. Here we use an extension of this statistical theory called multinomial logistic regression to build a probabilistic vegetation model (PVM). These models are only different than traditional logistic regression in that they allow n possible outcomes for every pixel; although these models are computationally intensive, they have been thoroughly studied (Agresti and Agresti 1996). The structure and goal of the predictive part of the model is identical to traditional logistic models. A PVM estimates multiple probabilities, with the constraint that there is only one possible outcome—the vector of probabilities must sum to one.

The key assumption of PVM is what is called "independence of irrelevant alternatives" (Hosmer and Lemeshow 2000). In terms of this analysis, this assumption represents a condition that the relative probability of alternative outcomes is not affected by the inclusion of an irrelevant

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[3] Natural Resources Conservation Service, United States Department of Agriculture. U.S. General Soil Map (STATSGO2). Available online at http://soildatamart.nrcs.usda.gov.

alternative. For example, the probability of chaparral versus grassland is not affected by the inclusion of redwood forest. We argue that this is a reasonable assumption for vegetation modeling—there is not a known ecological mechanism that would allow an absent, unsuitable vegetation type to affect the dynamics of two other vegetation types. Vegetation modeling in the context of climate change is a novel application for this statistical framework, and one that we argue has a number of conceptual advantages.

Like the general form of species distribution modeling (Araújo and Guisan 2006), this statistical framework can use any shape function to model the relationship between climate and the likelihood of a given vegetation type. We used all the predictive layers discussed above as inputs, with both linear and quadratic terms for each predictor, such that the probability of a given vegetation type can have an optimum with a decline in probability toward the extremes. Note that unlike some species distribution models, such as Maxent (Phillips et al. 2004), there are no step functions possible in the model fit.

We used a maximum conditional likelihood fitting of the coefficients. The observed fit was highly repeatable with different random samples (that is, training datasets) of the vegetation layer up to a sample size of $N=10^5$. Reported results use a random sampling of the vegetation with $N=10^6$. At these sample sizes, performance of the model is identical for training and test datasets. Model fit can be quantified using standard statistical tools—e.g., Akaike information criterion (AIC). Here, because of the large sample sizes and the risk of over-parameterization, we have used Bayesian information criterion (BIC), which has a larger penalty for additional terms compared to AIC, to examine the relative contribution of different predictors. All of the predictors (including linear and quadratic terms) were included in the best fitting model. The model uses R libraries *nnet* (Venables and Ripley 1999) and *raster* (Hijmans and van Etten 2011).

For each pixel in the dataset we generated current estimates of the probability vector of that pixel being in each state. In some cases the model predicted a pixel with a high degree of certainty (i.e., one vegetation type has a high predicted probability). More often, the model found two to three potential vegetation types for that particular topography-climate combination. We suggest that the actual current vegetation at those sites is a mix of historical and current factors (e.g., priority effects) and chance. While we have attempted to assemble the most ecologically relevant predictor layers, information—especially spatial information—is always incomplete. Both the particular nature of history and priority effects, which are thought to be especially important in California (Seabloom et al. 2003), and the uncertainty of our predictive layers contribute to the uncertainty in the model results.

We then used the current parameterization of the model together with the future layers to estimate the vector of probabilities for the future scenarios. The probability of a climate-driven transition for each pixel can then be quantified as the difference between the past and future vectors; we define this difference as vulnerability. Present-to-future dissimilarity can be quantified in a number of ways; here we use Bray-Curtis dissimilarity which is good at detecting underlying multivariate ecological gradients (Faith et al. 1987), is bounded between 0 and 1, and has a useful linear behavior for these types of data (Rödder and Engler 2011). We define present-to-future dissimilarity as the vulnerability of the dominant vegetation to state change. Because climate vulnerability does not take into account the current state of each pixel, this output variable should be read as the climate vulnerability of pixels of that type as estimated from the model, not of those specific pixels. For this case we define exposure as the multivariate distance in climate space for each pixel from the current to the future predictions. (All climate variables are z-transformed to make units comparable.) Sensitivity of each pixel is defined as vulnerability per unit (multivariate) climate change.

To complement our fine-grain model over a limited spatial extent, we also performed statewide modeling using Maxent of the dominant species for Bay Area vegetation types. The methods followed Loarie et al. (2008) with several modifications. We used 1971–2000 climate normals on an interpolated 30 arc-second scale for precipitation, summer maximum temperature, and winter minimum temperature (PRISM climate; Daly et al. 2008) to fit a climate suitability model. We then projected this model fit into future scenarios downscaled from the Geophysical Fluid Dynamics Laboratory (GFDL) and parallel climate model (PCM) global circulation models from the fourth assessment of the Intergovernmental Panel on Climate Change (IPCC AR4; Solomon et al. 2007; downscaling from Flint and Flint 2012).

Results

The model results suggest that vulnerability to vegetation change will occur in small patches across the Bay Area (Figure 1.1). These vulnerable places are where the vector of probabilities for the current time period is very dissimilar from the modeled future. Other places may still experience state changes, due to a collection of ecological processes (Suding and Hobbs 2009), but the model estimates that the forecast change in the climate is unlikely to be the driver of a state change (Figure 1.2).

The transitions are forecast to be a collection of different types of changes; the most common being transitions from forest ecosystems to more shrub-dominated vegetation. Chamise (*Adenostoma fasciculatum*), a drought-tolerant shrub that regenerates by sprouting after fire, is forecast to increase its abundance (Figure 1.3). This change was consistent with a statewide analysis that showed much increased climate suitability for *Adenostoma fasciculatum* in the Bay Area, although not a marked increase on the statewide extent. Other vegetation types show complex spatial patterns, with increases and decreases spread throughout the modeled extent.

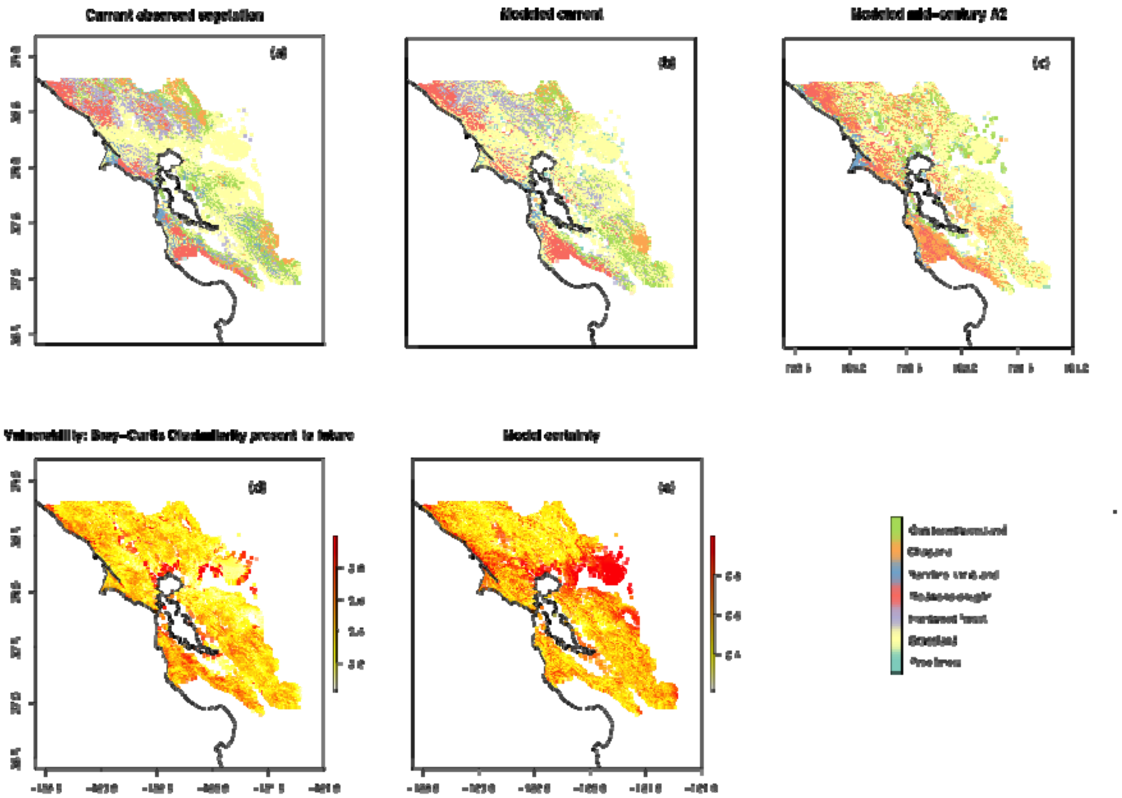

Figure 1.1. (a) Current Vegetation Map for the Bay Area Extent. For graphical display, vegetation types are aggregated from 23 (which were modeled as separate alternatives) to 7 in panels (see legend). (b) Modeled current and (c) modeled mid-century GFDL A2 vegetation is shown in panel with the same aggregation of vegetation types. Both (b) and (c) show the most-likely vegetation type. Panel (e) shows the modeled likelihood of the most likely vegetation type. Note that there is wide range in model certainty, indicating that alternative states are more prominent feature in certain parts of the region compared to others. Panel (d) shows the Bray-Curtis dissimilarity from present to future. For example, that there is high dissimilarity in the driest parts of Redwood-Douglas Fir distribution in the south bay. The model suggests that because of climate change these areas are much more likely to be chaparral in the future. Along the coast (e.g., in Point Reyes), the model suggests that winter warming will facilitate the spread of *Baccharispilularis* shrubland into coastal grassland.

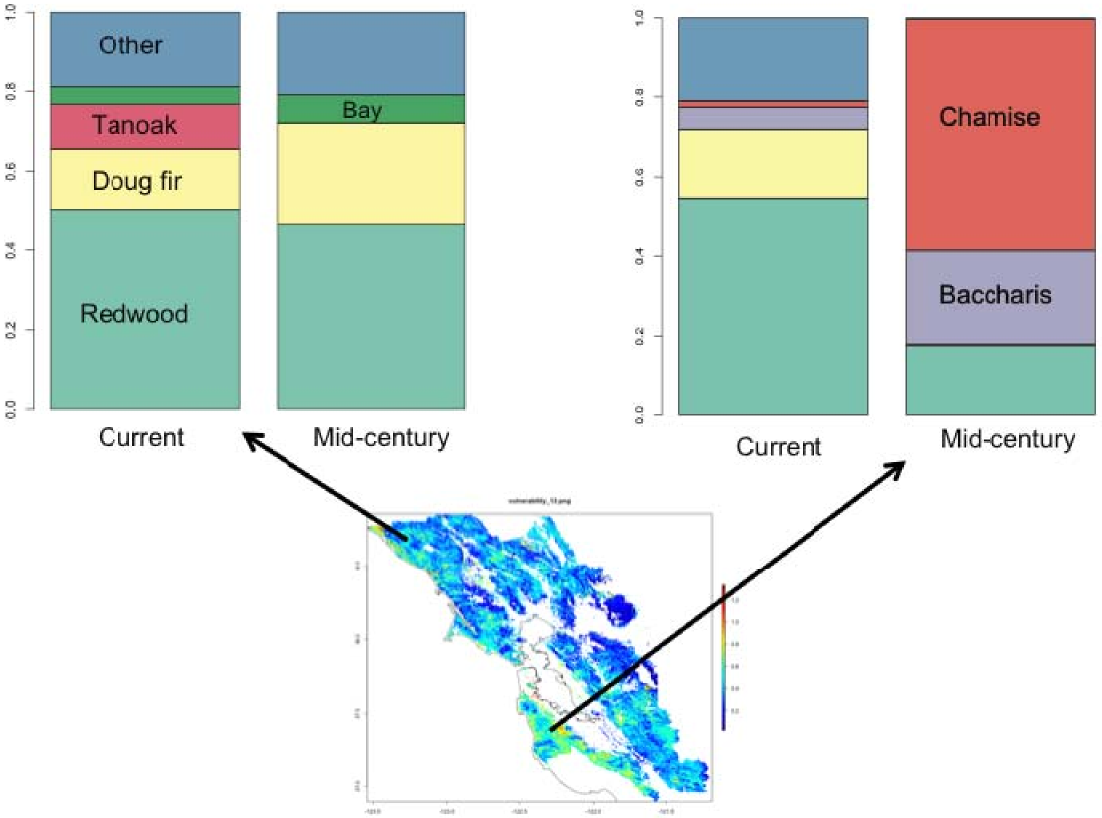

Figure 1.2. Examples of Two Pixels from Figure 1.1. The left pixel is relatively invulnerable; that is, redwood is the most likely vegetation type now and that will remain the case in the future projections. In contrast, the pixel shown to the right currently has redwood as the most probable type, but the conditions are forecast to change such that chamise is forecast to become the most likely type in the new conditions.

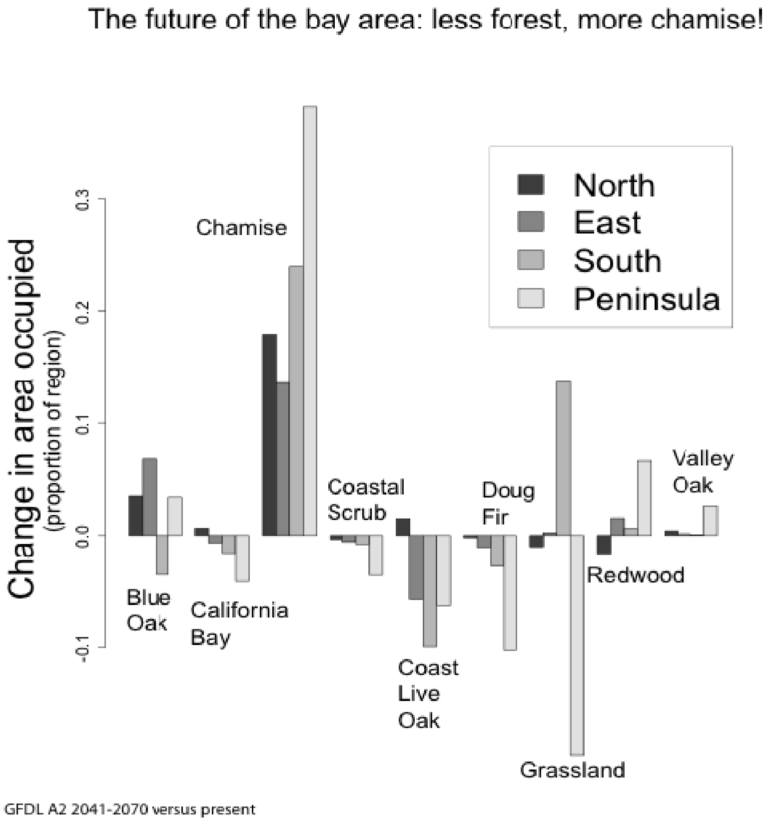

Figure 1.3. Summed Probabilities for the North Bay (Marin, Napa, and Sonoma Counties), East Bay (Solano, Alameda, and Contra Costa Counties), South Bay (Santa Clara County), and Peninsula (San Mateo and San Francisco Counties). The bars show the forecast change in probabilities across all natural area pixels for each sub-region, normalized to the amount of natural area in each sub-region.

Current downscaling techniques estimate that there is considerable variation across the Bay Area in the exposure of different places to climate change; for example, some areas close to the coast will experience much less change in summer maximum temperatures. Nonetheless, this is a relatively small effect (r^2=0.18) with much more of the among site variance explained by the intrinsic sensitivity of the vegetation (Figure 1.4). Examination of these patterns reveals that the primary factor influencing sensitivity is the proximity of a patch of vegetation to a climatic threshold causing transitions to another vegetation type (results not shown). In other words, vulnerability is determined by the biological threshold of a vegetation type at a pixel, in combination with the climate proximity to that threshold; this is much more important than the magnitude of climate change at that pixel.

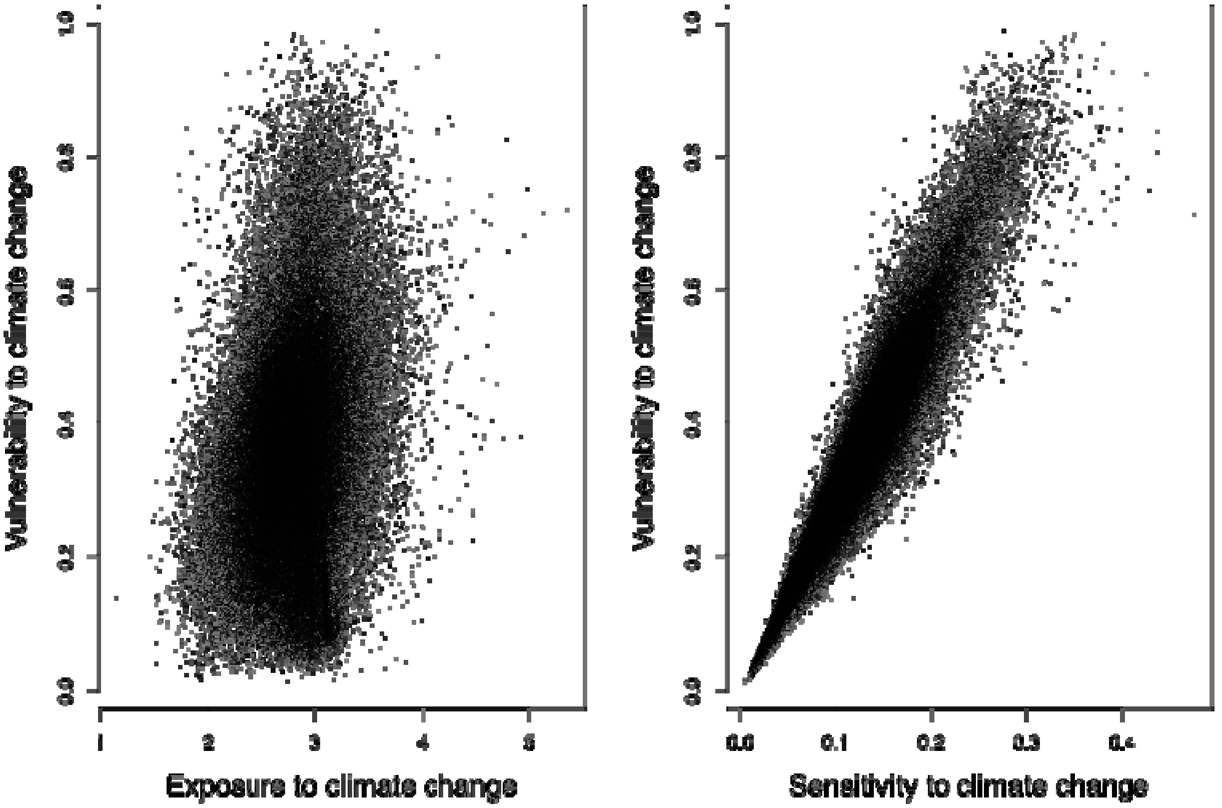

Figure 1.4. A Decomposition of the Climate Vulnerability from Figure 1.1d into Exposure (the Euclidean Distance in Normalized Climate from the Present to the Future) and Sensitivity (the Relative Sensitivity of the Vegetation per Unit of Multivariate Climate Change)

Considering each vegetation type separately, movement of vegetation types is forecast to occur at multiple scales. Some dominant species are forecast to move to more northern-facing, lower-insolation slopes and toward the coast (for Blue Oak, see Figure 1.5). In general the vegetation types forecast to become successful at a point are already found in the local vicinity: we find that 54 percent of the forecast transitions in the Bay Area require less than one kilometer of movement for the successful (i.e., newly establishing) vegetation type (Figure 1.6). A smaller but still important portion of the landscape (8 percent of forecast transitions) is forecast to become suitable for vegetation that is not close by.

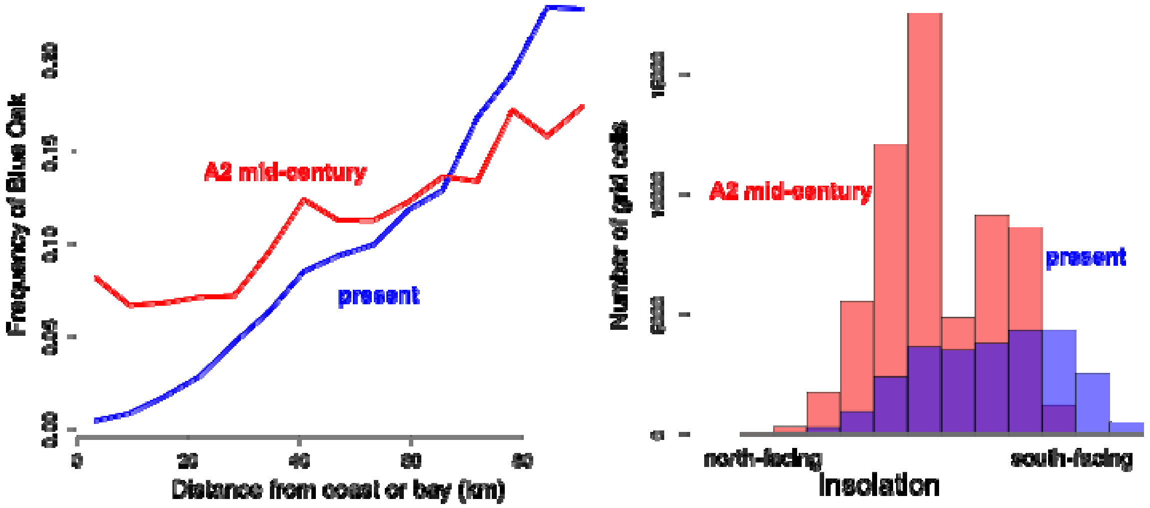

Figure 1.5. Spatial Movement of Blue Oak from the Current to the GFDL A2 Mid-century Projections. Red shows the future; blue show the present. The left panel shows regional movement from the inland areas toward the cooler summer max temperatures of the coast. The right panel shows local movement from higher insolation (south-facing) slopes to lower insolation (north-facing) sites. The y-axis in the right panel is the number of 30 x 30 m pixels forecast with Blue Oak forest as the most probable vegetation type.

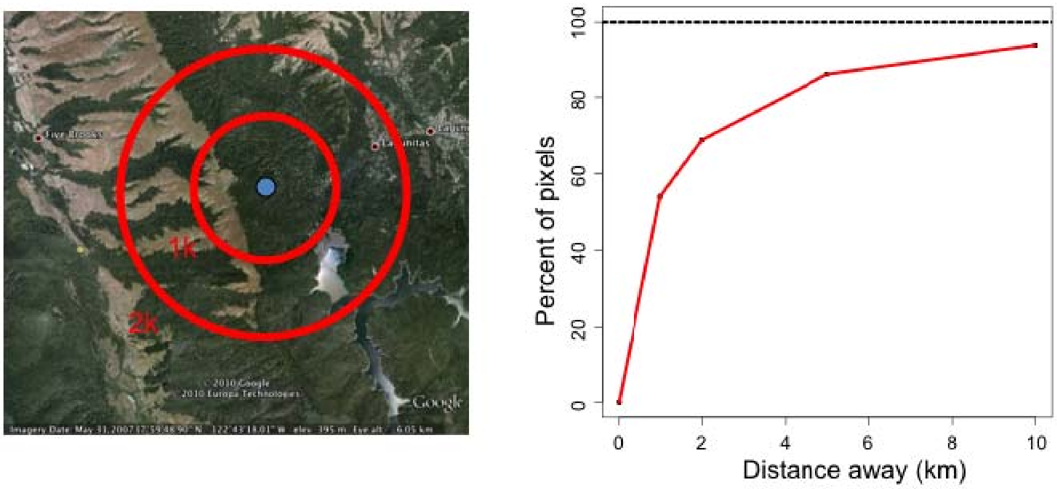

Figure 1.6. Spatial Movement of Blue Oak from the Current to the GFDL A2 Mid-century Projections. Red shows the future; blue show the present. The left panel shows regional movement from the inland areas toward the cooler summer max temperatures of the coast. The right panel shows local movement from higher insolation (south-facing) slopes to lower insolation (north-facing) sites. The y-axis in the right panel is the number of 30 x 30 m pixels forecast with Blue Oak forest as the most probable vegetation type.

Discussion

As the evidence for patchy changes in dominant plant species across the globe accumulates (Sturm et al. 2001), it is increasingly clear that some places will be more vulnerable to climate-induced changes than others. We present a new modeling framework that offers a probabilistic view of the future of vegetation in the San Francisco Bay Area. We find that climate change will have a fundamental and large magnitude effect on the terrestrial vegetation of the Bay Area, with a shift from forest toward shrub-dominated ecosystems; although this model has much finer-grain forecasts than previous work, this is qualitatively similar to the results presented by (Stralberg et al. 2009). The pace and spatial structure of this transformation and the urgency for conservation is dependent on a variety of factors, some of which we have some scientific basis to predict (e.g., herbivory, land use) and others that are more difficult to predict (e.g., disease, timing of a landscape-scale fire). In addition there is a suite of non-climate factors, especially succession and alternate stable states, that affect the current state of each patch of land (Turner 2010). We argue that because of the suite of deterministic and chance events (e.g., lightning strikes) that govern vegetation transitions (Suding and Hobbs 2009), a probabilistic framework is the appropriate framework for examining vegetation dynamics in response to a changing climate.

With this framework, we estimate in our model the importance of exposure of different places to climate change and the thresholds for change. We estimate that most of the forecast change is not due to exceptionally high exposure in some places, but rather to the climate proximity to biological thresholds. It is worth noting that we find this despite the absence of the possibility of biological step functions in our model. We suggest that what we model as a gradual change in probabilities of the occurrence of particular vegetation types will often be realized as a step change after some kind of trigger (Suding and Hobbs 2009). Nonetheless, we argue that the modeled change should be interpreted as a climate-driven change in the probability of this type of event occurring. We argue that any realistic quantitative representation of vegetation transitions must include both the climate forcing and non-climate, stochastic elements. The frequency of stochastic events may change with anthropogenic climate forcing (Rahmstorf and Coumou 2011). Although the specific nature of this change is unknown, when it is well understood, it can be incorporated in this model as part of the climatic forcing.

Range shifts are expected to be one of the primary responses of species to climate change, and there is no reason to expect that the dominant plant species will be an exception (Jackson and Overpeck 2000; Nathan et al. 2011). This question has been largely examined from the perspective of species-based models (Guisan and Thuiller 2005; Loarie et al.2008). In contrast, this model examines change from a land-based perspective, with a fine-resolution approach. We find that on a land-area basis, the majority of transitions are forecast to be local (Figure 1.6) involving shifts in vegetation types within local landscapes. In other cases (8 percent of forecast transitions), longer distance movement will be required. The small-scale adjustments forecast by this model are only evident because of the small-grain analysis, and will be missed by coarser-grain, larger-extent modeling approaches. We argue that the small-scale topographic shifts of species may be the most common climate-driven change in many landscapes. Further, local-scale migration has important conservation implications: for any given conservation area, the climatic diversity and the potential (or lack thereof) for species to move locally need to be a key part of conservation planning with respect to climate (Ackerly et al. 2010). This can be thought of as part of adaptive capacity (Smit and Wandel 2006).

We suggest that the formalization of ecosystem vulnerability has important implications for conservation planning. The model framework presented here can clearly separate areas that are more or less likely to experience a climate-induced state change. Both types of areas are important for conservation. Areas where redwood forest (for example) is forecast to persist have a very high conservation value, and will be unlikely to require a great deal of active management to ameliorate climate change. Other areas that are forecast to transition to blue oak woodland (for example, see Figure 1.5) also have high conservation value, but the actual transition to blue oak rather than to exotic invaders may require substantial active management. Conservation prioritization for any given piece of land should be aware of this possibility—and an assessment of its likelihood—in the long-term planning process.

Conclusion

We have developed a modeling framework that incorporates the well-known probabilistic nature of California ecosystems into a model of climate effects on ecosystems. As predictive geographic layers improve, model performance (Figure 1.1e) will also improve, although this improvement is bounded by the true stochasticity of the system. The specific results for the Bay Area stress the biological thresholds of the dominant species as being the chief control on where geographically climate change-induced state change may occur. The model output highlights these areas, along with an estimate of uncertainty.

On a regional scale, a range of conservation implications arise from this type of work. There is an emerging sense that conservation planning should balance a preference for preservation (e.g., saving the last Black Oak forest in a given region, even as the climate moves) with an active role in managing transitions as they continue to occur. Much of the Bay Area is developed, creating anthropogenic dispersal barriers that will clearly affect the future of some natural areas. Our results suggest that a scientific understanding of the multivariate climate thresholds of the dominant species, coupled with interactions with other ecological processes, will be crucial information for understanding climate effects on ecosystems.

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Section 2. Mechanisms of Vegetation Change in Coastal California, with an Emphasis on the San Francisco Bay Area

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The Bay Area

Vegetation in the San Francisco Bay Area today consists of a complex mosaic of vegetation types, including herbaceous grasslands, shrublands, chaparral, woodlands, and closed forests. The distribution of vegetation types is determined in part by edaphic, topographic, and climatic factors. In many cases, though, several different vegetation types could exist at a particular combination of these factors. Which type is observed depends on an array of historical factors, including fire, grazing, human land use, and disease distribution. The vegetation of the Bay Area is in flux, due to climate change, ongoing and historical species invasions, disturbance history, and changing human land use. Understanding the interactions of these factors is critical in predicting future vegetation changes and guiding management decisions. This section provides a review of major mechanisms that influence vegetation change in coastal California, based on a review of available literature (Table 2.1). This provides a critical context for understanding how changing climate may affect these transitions.

Invasions

European settlers brought a large number of exotic species to California, many of which became naturalized and invasive, particularly in grasslands. Most of the problematic species were introduced in the nineteenth century, and by the 1860s–1880s, most grasslands were dominated by exotic annual grasses (Burcham 1956; Heady 1977; Heady et al. 1988). Historical accounts and photographs from the beginning of the twentieth century portray grasslands entirely converted to exotic annuals (D’Antonio et al. 2007; Hopkinson and Huntsinger 2005). The invasion may have been promoted by droughts in the late 1800s and intense grazing pressure (D’Antonio et al. 2007; Corbin and D’Antonio 2004; George et al. 1992).

The completeness of the invasion of California’s grasslands makes it difficult to estimate their composition prior to European settlement. These communities have often been thought to be dominated by native perennial grasses (Clements 1934; Burcham 1956), but many may have consisted primarily of native annual forbs (Hamilton 1997; Schiffman 2007; D’Antonio et al. 2007; Minnich 2008). Wet and coastal areas may have been dominated by perennial grasslands, while drier, interior sites might have been forb-dominated (D’Antonio et al. 2007). Using soil phytolith records, Hopkinson and Huntsinger (2005) were unable to find evidence for long-term occupation of the East Bay hills by perennial grasses. Instead, they speculate that northern coastal sage scrub, dominated by *Baccharispilularis*, likely covered much of the East Bay hills, with some forests containing *Sequoiasempervirens*, *Quercus* spp., and *Umbellularia californica*.

Table 2.1. Summary of Observed or Experimentally Induced Vegetation Transitions in the Coastal California

Transition	Mechanisms	Time Scale of Transition	Reference
Grassland - Shrubs	Protection from grazing and fire	10–20 years, 0.7%/year, 1%/year, 0.4%/year	McBride and Heady 1968, Russell and McBride 2003, McBride 1974, Plant et al. 1999, Keeley 2005, Callaway and Davis 1993, Tyler et al. 2007
Grassland - Shrubs	High Rainfall	5 years	Biswell 1954, Williams et al. 1987
Grassland - Shrubs	Small fires, intense grazing		Biswell 1954
Grassland - Oak Savanna	Time	Decades, 20-50 years, 100+ years	George and Alonso 2008, Plant et al. 1999, Vayssieres and Plant 1998
Grassland - Doug Fir	Protection from grazing and fire	~50 years	Russell and McBride 2003, Kennedy and Sousa 2006
Grasslands - Tanoak	Time		Kennedy and Sousa 2006
Grassland Maintained	Grazing		George and Alonso 2008, Callaway and Davis 1993, McBride 1974, Tyler et al. 2007, Biswell 1954
Grassland Maintained	Fire		George and Alonso 2008, Tyler et al. 2007, Biswell 1954
Shrubs - Chaparral	Time	0.1%/year	Gray 1983, Callaway and Davis 1993
Shrubs - Bay	Time		McBride 1974
Shrubs - Oak	Time	~50 years, 0.3%/year	McBride 1974, Callaway 1992, Callaway and Davis 1993
Shrubs Maintained	Protection from grazing, allelopathy?		Tyler et al. 2007
Shrubs Maintained	Fire		McBride 1974
Shrubs - Grassland	Fire	49% converted in 76 years, 0.3%/year	Callway and Davis 1993, Talluto and Suding 2008, Minnich and Dezzani 1998, Tyler et al. 2007, Plant et al. 1999, Keeley 2005, Keeley 2002
Shrubs - Grassland	Grazing		Tyler et al. 2007
Shrubs - Grassland	Invasion of exotic annuals		Minnich and Dezzani 1998
Shrubs - Grassland	N deposition		Talluto and Suding 2008
Chaparral - Montane Hardwood		60 years	Thorne et al. 2008
Chaparral - Grasslands	Fire		Haidinger and Keeley 1993
Chaparral - Oak woodland	Fire suppression	13 years, 0.1%/year	Van Dyke et al. 2001, Callaway and Davis 1993
Chaparral - Douglas Fir	Facilitation by Arctostaphylos		Dunne and Parker 1999

Table 2.1. (continued)

Oak Savanna - Grassland	Crown fire	1–5 years	Vayssieres and Plant 1998, George and Alonso 2008, Huntsinger and Bartolome 1992
Oak Savanna - Grassland	Cutting	1–5 years	Vayssieres and Plant 1998, George and Alonso 2008, Huntsinger and Bartolome 1992
Oak Savanna - Grassland	Natural mortality	50–200	Vayssieres and Plant 1998
Oaks (Q. douglasii) - Grassland	Grazing	60 years, 0.03%/year	Callaway and Davis 1993, Thorne et al. 2008
Oak - Bay	Time		McBride 1974
Oak - Bay	SOD	decade	Brown and Allen-Diaz 2009
Oak - Bay	Grazing		Safford 1995
Oak (Mixed Blue/Live) - Chaparral	Intense Fire		George and Alonso 2008
Oak (Mixed Blue/Live) - Live Oak	Intense Fire		George and Alonso 2008
Oak Forest - Oak Woodland	Fire		George and Alonso 2008
Oak Woodland - Oak Forest	Fire suppression	30–50 years	George and Alonso 2008, Vayssieres and Plant 1998, Holzman and Allen-Diaz 1991
Oak/Grass - Oak/Shrub	Time	Slow, 10–15 years, if at all	Hunstinger and Bartolome 1992
Oak/Pine-Grassland - Grassland	Drought, crown fire, herbicide, cutting		Plant et al. 1999
Oak/Pine-Grassland - Oak/pine-Shrubs	Protection from fire and grazing	Decades	Plant et al. 1999
Oak/Pine-Shrubs - Grassland	Drought, crown fire		Plant et al. 1999, Huntsinger and Bartolome 1992
Oak/Pine-Shrubs - Oak/Pine-Grassland	Grazing or moderate fire		Plant et al. 1999, Huntsinger and Bartolome 1992
Oak/Pine-Shrubs - Shrubs	Herbicide, fire, removal of trees		Plant et al. 1999, Huntsinger and Bartolome 1992
Ponderosa Pine - Douglas Fir		60 years	Thorne et al. 2008
Ponderosa Pine - Montane Hardwood		60 years	Thorne et al. 2008
Ponderosa Pine/Jeffrey Pine - White Fir/Incense Cedar	Lengthened Fire Intervals	60 years	Minnich et al. 1995

Native perennial grasslands, to whatever extent they occurred prior to human settlement, were nearly completely type-converted to exotic annual grasses. This change has important consequences for ecosystem properties. For example, exotic annual grasses tend to produce shallower but denser root systems and to be active earlier in the spring than perennial grasses. Thus, exotic grasses decrease near-surface soil water in this season relative to native species, but can leave deep soil water at elevated levels late in the season (Holmes and Rice 1996; D'Antonio et al. 2007).

The arrival of invasive species likely contributed to other type conversions as well. Exotic annual grasses suppress oak seedling establishment more than their native counterparts (Tyler et al. 2006 and references therein), possibly contributing to reduced regeneration of oak seedlings in recent decades. In dry years, oak seedling success is very low on dry south-facing slopes in competition with grass, while in wet years or on north-facing slopes, oak seedlings are more successful competitors (Griffin 1971). Exotic annuals can invade recently burned woody vegetation types more rapidly than native species, promoting their conversion to grassland (Zedler et al. 1983).

Though grasslands are the most heavily impacted by invasive species, other vegetation types have been affected as well. The understories of oak woodlands have been converted to annual grasses (Tyler et al. 2006). Cape ivy (*Delairea odorata*) has invaded a variety of habitats in the Bay Area, and is often found in the understory of forests, where it reduces native and exotic plant diversity alike (Alvarez and Cushman 2002). *Eucalyptus globulus* is an abundant exotic tree in many areas of California, where it can invade intact chaparral (Underwood et al. 2007) and is particularly common in human-modified areas (Nowak 1993).

Succession

In the absence of disturbances such as fire or grazing, successional processes can lead to vegetation type conversions. A common successional pathway in California is from grasslands to shrublands to woodlands or forests. For example, in coastal southern California, grasslands slowly convert to coastal sage scrub. With time, coastal sage scrub itself gives way to chaparral or oak woodland (Callaway and Davis 1993).

For at least the last 50 years, shrubs have been rapidly spreading into grassland in many parts of California (e.g., Biswell 1954; McBride and Heady 1968; McBride 1974; Williams et al. 1987). This may represent a long-term response to reduced grazing pressure and increased fire suppression over the last century (Keeley 2005). *Baccharispilularis* is one of the most common grassland-invading shrubs in the Bay Area (McBride 1974; Havlik 1984). It spreads into grasslands most aggressively in unusually wet years, or years with unusually late spring rains (Williams et al. 1987; Williams and Hobbs 1989). Several invasive shrubs, including gorse and French broom, can also invade grasslands. In the absence of grazing and fire, coastal prairies can be replaced in as few as 15–25 years by scrub species (Ford and Hayes 2007), while exotic annual grasslands may be converted in as few as 2–5 years (Hobbs and Mooney 1986).

Over time, tree species may regenerate under shrublands, grow taller than the shrubs, and eventually the system may become a woodland or forest. Shrubs such as *Baccharis*, *Salvia leucophylla,* and *Artemisia californica* can have direct facilitative effects on tree seedlings, by providing protection from grazing and a moister microenvironment (Callaway and D'Antonio 1991; Callaway 1992; Callaway and Davis 1998). In the East Bay hills, *Baccharis* stands can be invaded and replaced by *Quercus agrifolia* and *Umbellularia californica* (McBride 1974; Safford 1995). This process takes approximately 50 years, and may be slowed by grazing (McBride 1974). After 70 years without fire, oak forests can replace chaparral (Van Dyke et al. 2001). On Mt. Tamalpais and other sites in the Bay Area, Douglas fir has overtopped manzanita chaparral in recent years (Dunne and Parker 1999). Senescent manzanitas and chamise growing under oaks can be observed in various locations, suggesting that chaparral has been replaced by woodlands (personal observation, though it is possible that the shrubs establish in occasional forest gaps and do not reflect a past vegetation transition).

Fire

Ample evidence supports the central role of fire in controlling vegetation composition in California. Most often, fire has been shown to contribute to conversion from woody to herbaceous vegetation, such as coastal sage scrub to grassland (Callaway and Davis 1993; Talluto and Suding 2008), oak woodland to grassland (George and Alonso 2008), chaparral to grasslands (Haidinger and Keeley 1993), or shrublands (including coastal sage scrub and *Baccharis* scrub) to grasslands (Keeley 2002; Keeley 2005; Tyler et al. 2007). Conversion from woody to herbaceous vegetation appears to be particularly favored by repeated burning of a site with only one or a few years to recover, especially due to elimination of obligate seeding chaparral shrubs (Zedler et al. 1983; Haidinger and Keeley 1993). The introduction of highly aggressive herbaceous weeds has likely contributed to the ease with which woody vegetation is converted following fire (Zedler et al. 1983). Moderate burn intervals can also favor the conversion of woodlands to *Baccharis* scrub (McBride 1974).

Prior to human settlement, fire was rare, which likely contributed to vegetation much more strongly dominated by woody plants (Keeley 2005). Grasslands likely occurred, but primarily as isolated patches in areas recovering from fire. It is difficult to know the composition of these grasslands, because few remnant native grasslands occur today, and their composition might not reflect the historically dominant grassland vegetation (Hamilton 1997).

Beginning some 12,000 years ago, Native Americans had significant effects on fire frequencies in the Bay Area (Greenlee and Langenheim 1990; Keeley 2005; Anderson 2007; Reiner 2007). With human settlement, fire frequency increased substantially. This likely led to an increase in herbaceous cover.

The arrival of Europeans to the Bay Area in large numbers brought reduced fire frequencies (Greenlee and Langenheim 1990; Keeley 2005). However, woody plant encroachment into grasslands and forblands, which is expected following reduced fire frequency, was prevented by a simultaneous increase in grazing pressure (see below). In addition, European settlers brought with them a suite of non-native plant species (see above). The combined effects of aggressive annual grass introductions and grazing pressure may have actually contributed to further expansion of grassland.

Strong fire suppression began in the twentieth century, while grazing pressures also began to decrease. Accordingly, in many places woody plants have been gradually and episodically recruiting within grasslands (Biswell 1956; McBride and Heady 1968; McBride 1974; Havlik 1984; Bakeman and Nimlos 1985; Williams et al. 1987; Vayssieres and Plant 1998; Russell and McBride 2003).

Grazing

Grazing can have major effects on plant community composition in California (Jackson and Bartolome 2007). In many cases, it is useful to think of grazing as a disturbance that affects the successional status of a community. Following the basic description of succession in the Bay Area (above), grazing will tend to push communities toward herbaceous compositions at the expense of woody species. For example, grazing has been shown to promote the conversion from oak woodland to grassland (Callaway and Davis 1993), shrubland to grassland (Tyler et al. 2007) and to maintain grassland in the face of potential invasion by shrubs or other woody species (McBride 1974; Callaway and Davis 1993; Plant et al. 1999; Russell and McBride 2003; Tyler et al. 2007; George and Alonso 2008). Grazing can also cause the understory of oak woodlands to transition from shrub dominance to grass dominance (Huntsinger and Bartolome 1992).

These broad generalizations can oversimplify the effects of grazing in several ways. For example, the timing of grazing can have important effects on community composition, favoring either shrubs or grasses, depending on season (Biswell 1954).

Grazing may also favor one successional endpoint over another. In the East Bay Hills, for example, intense grazing tends to favor *Umbellularia californica* over *Quercus* spp. (Safford 1995). Oaks and foothill pine can increase in cover through time, even under grazing pressure, through both the growth of large mature trees and recruitment of new individuals (Holzman and Allen-Diaz 1991).

The flora of California evolved under the influence of a wide variety of now extinct herbivores. These included giant ground sloths, horses, camels, deer, elk, bison, tapirs, mastodons, and mammoths. In part due to the activities of these large mammals, and in part because of climate differences, it is likely that the vegetation of California near the end of the Pleistocene was more open, with a significant grassland component (Edwards 2007).

Increasing aridity in the Holocene combined with human hunting pressure led to the demise of most of the Pleistocene megafauna. Both Tule elk and pronghorn antelope survived this period, and apparently grazed the grasslands of California in large herds prior to European contact (Edwards 1992). The loss of most large mammals likely contributed to increased abundances of shrubs and trees. Note that this mechanism is in the opposite direction of the fire hypothesis described above (and see Keeley 2005). The arrival of humans at first decreased the role of large mammals, which would promote woody vegetation but increased the frequency and role of fire, which on balance will tend to promote herbaceous dominated areas. The implications of these two massive ecological changes on the geographic extent of grassland or forbland is not known.

Widespread introduction of domestic livestock began approximately 200 years ago. The first livestock arrived in 1769 with Spanish settlers, with heavy grazing beginning just a few years later. Initial grazing pressure was concentrated on the coast, but beginning in 1824, began to spread inland. Since that time, cattle populations have typically been between 4 and 5 million, while sheep have typically been at about 2.5 million until a decline beginning in 1960 brought the population to its current level of about 0.5 million (Jackson and Bartolome 2007). Historically, this grazing pressure likely maintained grasslands in the face of woody plant invasions, and probably contributed to the success of exotic annual grasses (Elliot and Wehausen 1974; Burcham 1975).

Unusual Weather Events

In much the same way that grazing, fire and disease can trigger transitions between vegetation types, episodic unusual weather can also cause such transitions. Extreme rainfall or drought, hot spells and prolonged cold periods can all act as agents of mortality, and shift the balance of establishment in favor of different species; these factors can cause vegetation state changes and can interact with other drivers of changes.

As discussed above, *Baccharis pilularis* can invade grasslands, particularly in wet years. *Baccharis* establishment in grasslands depends on unusually wet years because *Baccharis* seedling root growth is fairly slow. By spring, annual grasses are fully active and rapidly transpiring, causing a drying of the upper soil layer (Eliason and Allen 1997). Recently established *Baccharis* roots are too short to access deeper water, causing seedling death (Williams and Hobbs 1989). Once established after a wet year, however, *Baccharis* roots are sufficiently deep to utilize deeper soil water, increasing survival through the dry season. Thus, a brief period of unusually heavy rainfall can trigger the transition from grassland to *Baccharis* (Williams et al. 1987). In southern California, seedlings of several shrubs (*Artemisia californica, Salvia apiana, Eriogonum fasciculatum* and *Lotus scoparius*) show similar positive responses to years with high rainfall (DeSimone and Zedler 1999).

On the other end of the precipitation spectrum, unusually intense or prolonged droughts can also lead to vegetation type conversions. A drought in the mid-1800s likely promoted the invasion of annual grasses into California’s perennial grasslands and forblands (D’Antonio et al. 2007; Corbin and D’Antonio 2004; George et al. 1992). Prolonged drought can also lead to oak mortality, resulting in the long-term replacement of oak forests with grasses (Plant et al. 1999; Huntsinger and Bartolome 1992).

Sudden Oak Death

Despite the rapid spread of this disease and its severe impacts on oak populations, relatively little is known about how composition of the vegetation should change in affected forests. Unsurprisingly, these changes include declines in oak basal area. Where oaks co-occur with

California bay laurels, bays are expected to increase (Moritz et al. 2008; Brown and Allen-Diaz 2009). In other areas, oaks co-occur with redwoods, so redwoods are expected to increase (Moritz et al. 2008).

Nitrogen Deposition

Human activities have resulted in increased nitrogen (N) deposition in many areas (Padgett et al. 1999; Fenn et al. 2003). Because N is an important limiting nutrient for plant growth, one might expect N deposition to have consequences for community composition and vegetation structure. Relatively little research has addressed the possible role of N deposition in vegetation transitions in California. However, some evidence from southern California suggests that, in areas of low fire frequency, N deposition tends to favor the transition of coastal sage scrub to grassland (Talluto and Suding 2008). Nitrogen deposition also appears to favor exotic grass invasion into serpentine communities in the Bay Area (Weiss 1999).

Resistance to Change

Several factors can prevent expected transitions between vegetation types or contribute to the persistence of existing vegetation. Type conversions can show time lags, in which long-lived individuals of a dominant species are slow to establish at a new site or slow to vacate a newly unsuitable site. Another source of potential time lags is dispersal limitation. As well, under certain conditions, dispersal limitation can lead to transitions to unexpected vegetation types. Finally, communities can show positive feedback loops that tend to cause stable vegetation even in the presence of changing environmental conditions.

Conversions between vegetation types might not be immediate. For example, slow-growing trees can take decades to establish themselves in new habitats and, in the absence of major disturbances, might take decades to senesce and give way to herbaceous species. Thus, certain expected transitions might not occur on the time scales relevant to most land managers. In California, *Quercus* spp. typically produce very few seedling recruits each year, and these usually recruit near existing adults (Huntsinger and Bartolome 1992; Tyler et al. 2006; George and Alonso 2008). Thus, even if a particular location becomes suitable habitat for oaks, it might take decades or centuries for an oak woodland to appear there.

Similarly, the transition to a new vegetation type assumes that propagules of the invading species are available. In some cases, this assumption might be invalid. If the species constituting the new vegetation type are unable to reach the area, a transition might not occur without assisted migration. Alternatively, a transition may still occur, but to an unexpected new type. Here, we make an important distinction between two types of causes of vegetation transitions. In the first type, the transition from type A to type B is caused by a trigger (such as a disturbance or climate change) that makes the conditions unsuitable for supporting type A. In this case, even in the absence of propagules of species from type B, type A will still decline. As A declines, and B is unable to reach the site, it could be invaded by a third, unexpected vegetation type. On the other hand, the conversion from A to B could be because, while the site can still support A, B is now more suitable for the environmental conditions. In this case, A will persist at the site unless propagules of B arrive.

Communities may also maintain themselves by positive feedback loops, or switches (Wilson and Agnew 1992). A switch occurs when a community produces some effect on its environment, which in turn benefits that community. Had initial conditions differed (such as the community composition), the switch might have "flipped" the other way, possibly favoring a different plant community. When trying to predict vegetation shifts and transitions, these switches are important. Failure to recognize them could produce an erroneously rapid estimate of vegetation transitions, as switches promote vegetative stasis. Some examples of positive feedback mechanisms can be found in the vegetation types of the Bay Area.

Grasses, and in particular exotic annual grasses, can contribute to the rapid accumulation of fine fuels, leading to increased fire severity and frequency (Reiner 2007). This establishes a potential positive feedback loop, by which grasslands promote fires, and are in turn promoted by them (D'Antonio and Vitousek 1992).

Shrubs can exclude herbaceous species by several mechanisms. After 2–3 years of growth, *Baccharis* can form a closed stand. Herbaceous seed dispersal into *Baccharis* stands is low (Hobbs and Mooney 1986), small rodents and birds shelter in *Baccharis* stands and consume developing herbaceous seedlings (Bartholomew 1970; Christensen and Muller 1975; Hobbs and Mooney 1986; DeSimone and Zedler 1999), and low light levels under canopies may exclude herbaceous seedlings (Christensen and Muller 1975; Keeley 1999). As a result, herbaceous plant density under Baccharis plants can be <0.1 plant per square meter (m^2) (McBride 1974). Some shrubs and chaparral species, such as *Salvia leucophylla, Artemisia californica, Lotus scoparius,* and *Adenostoma fasciculatum* may produce allelopathic compounds that tend to stabilize community composition by excluding potential invaders (Christensen and Muller 1975; Halsey 2004; Haubensak and Parker 2004). Thus, even in the face of climate changes that could promote a transition to grassland, the low invasibility of intact shrub vegetation by herbaceous plants will tend to slow or resist this transition.

Redwoods also show an important positive feedback mechanism. Their height allows them to collect fog water, much of which drips to the forest floor where it increases soil moisture. This moist environment fosters the establishment of redwood seedlings, and supports a very different understory environment than would occur without fog input (Dawson 1998). Removal of redwoods should produce a drier environment that would be less suitable for redwood reestablishment. This example illustrates that communities stabilized by positive feedback mechanisms might undergo rapid transitions if the feedback mechanism is disrupted.

Conclusions

One of the unique features of the vegetation of coastal California is the existence of grasslands, shrublands, chaparral, woodlands, and closed forests in close proximity. There are a collection of processes that have been observed to trigger state changes among these vegetation types. Our review of the literature suggests that fire, grazing, and unusual weather events may trigger these transitions even in the absence of climatic change. This suggests that climate change will be layered on top of an already complex system, with a complex history, internal dynamics, and trigger events. An understanding of the likelihood and nature climate change induced state change requires understanding these dynamics.

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Section 2 Appendix. Vegetation Change in the Sierra Nevada

Authors: C. R. Dolanc and J. H. Thorne

This study focused on the major vegetation types of the west slope of the Sierra Nevada and their likelihood of transition from one type to another. Vegetation types reflect those as described in Barbour et al. (2007). Potential transitions or conversions from one type to another were determined via literature review (see References and Table A2.1) and range from suggested or predicted transitions to actual, observed transitions. Figures A2.1–3 show the vegetation types, superimposed on the standard montane zones (see Barbouret al. 2007) as described for the Sierra Nevada. Potential transitions/conversions from one type to another are represented as arrows between types. For all three figures, red arrows indicate either proposed or observed transitions driven by climate change; black arrows represent transitions driven by other mechanisms not directly attributable to climate change. Wide arrows indicate greater support in the literature for that particular transition. Table 1 contains the literature used to determine all potential transitions.

The common vegetation types within each montane zone typically transition from one to another via succession or disturbance (Figure A2.2), while transitions across montane zones probably require climate change (Figure A2.3). For example, a natural cycle of succession and disturbance is well established in the literature for “oak woodland,” “chaparral,” and “grassland” vegetation types, but to move from one of these types to a type historically relegated to the lower montane, such as “ponderosa pine,” would likely require a long-term climatic shift that, e.g., increases annual precipitation markedly (Figure A2.3). Similarly, transitions between “mixed-conifer,” “montane chaparral,” and “ponderosa pine” within the lower montane zone are relatively common. But to transition from “red fir” to “mixed-conifer” would probably require a long-term reduction in snowpack (Barbour et al. 1991; Figure 3).

Vegetation types are displayed on an axis of moisture (Figures A2.2, A2.3) because moisture availability has a profound effect on vegetation in the Sierra Nevada. Unlike many other mountain ranges, the Mediterranean, summer-dry climate probably drives much of the heterogeneous nature of the range, making changes in precipitation via climate change potentially more important in the Sierra Nevada than other mountains in North America.

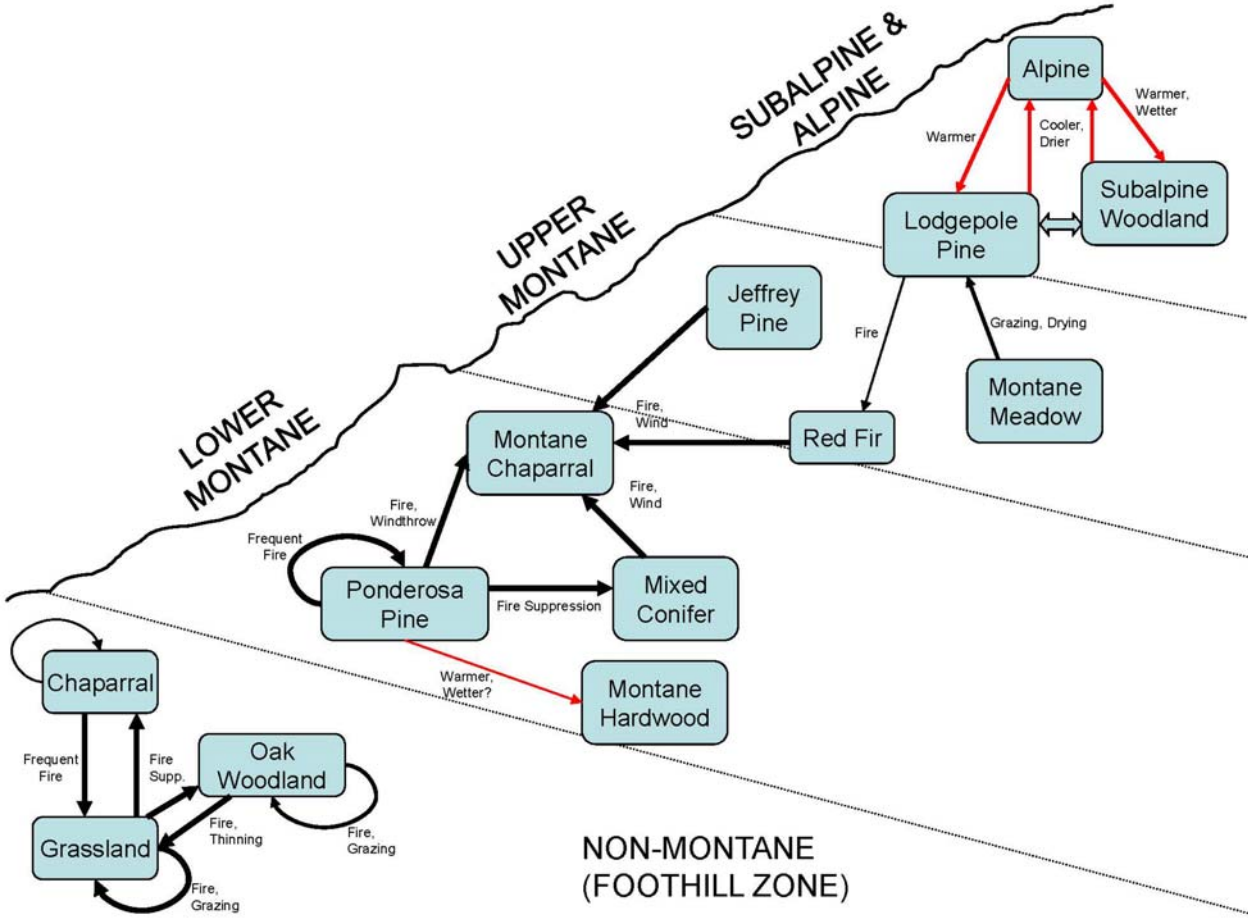

Figure A2.1. Major Vegetation Types Found on the West Slope of the Sierra Nevada, and the Transitions Between Them. Arrows represent potential type conversions/transitions. Red arrows represent transitions driven by climate change. Those at high-elevations have some support in the literature. Black arrows are other types of mechanisms. The amount of support/acceptance in the literature is represented by the width of the arrows.

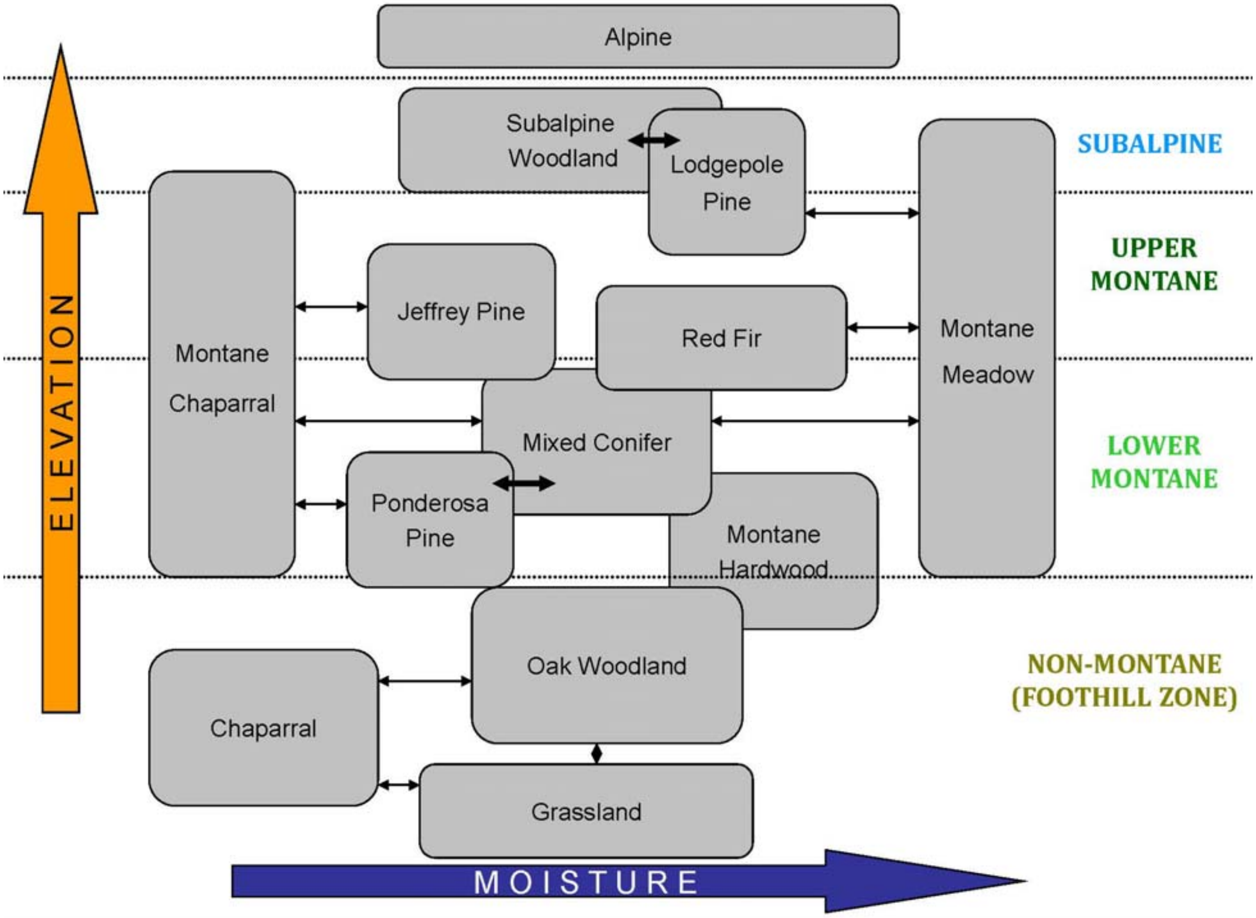

Figure A2.2. The Same Vegetation Types as Those in Figure A2.1, Arranged on Axes of Elevation and Moisture. The black double-headed arrows represent established transitions that are mostly well-documented and shown on the previous slide. Note that most of these are lateral transitions, within major zones. The amount of support/acceptance in the literature is represented by the width of the arrows. Overlapping polygons are intended to represent vegetation types that can merge in some locations or may be considered the same type by some authors.

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Figure A2.3. Vegetation Types as Described in Figures A2.1 and A2.2, with Red Arrows Added to Represent Transitions Driven by Climate Change. In order to cross montane zones (move vertically), climate change is required for most situations. Arrows represent both predicted shifts, as well as some already reported. The point of the arrow indicates what the beginning of the arrow will/has become; e.g., alpine has become subalpine woodland. Overlapping polygons are intended to represent vegetation types that can merge in some locations or may be considered the same type by some authors.

Table A2.1. References Observing and/or Predicting Transitions from One Major Vegetation Type to Another for the West Slope of the Sierra Nevada, Along with the Proposed Mechanism of Transition, Evidence for Transition, Location Within the Sierra Nevada, and Time Scale of Transition. Full citations for each reference can be found in the Literature Cited section following.

Reference	Transition	Mechanism proposed	Evidence for mechanism	Location	Time Scale of transition
Anderson and Moratto 1996 (SNEP)	Grassland maintained	Fire, Thinning	Interviews, historical records	entire SN	1900 - current
Anderson and Moratto 1996 (SNEP)	Ponderosa Pine Woodland maintained	Fire, Thinning	Interviews, historical records	entire SN	1900 - current
Anderson and Moratto 1996 (SNEP)	Oak Woodland maintained	Fire, Thinning	Interviews, historical records	entire SN	1900 - current
Anderson and Moratto 1996 (SNEP)	Chaparral maintained	Fire, Thinning	Interviews, historical records	entire SN	1900 - current
Anderson and Moratto 1996 (SNEP)	Meadows maintained	Fire, Thinning	Interviews, historical records	entire SN	1900 - current
Anderson 1994	Oak Woodland maintained	Fire, Thinning	Interviews, historical records	entire SN	1900 - current
Anderson 1994	Mixed-conifer maintained	Fire, Thinning	Interviews, historical records	entire SN	1900 - current
Anderson 1994	Montane Hardwood maintained	Fire, Thinning	Interviews, historical records	entire SN	1900 - current
Anderson 1994	Chaparral maintained	Fire, Thinning	Interviews, historical records	entire SN	1900 - current
Biswell 1974 (see van Wagtendonk and Fites-Kaufman 2006)	Grassland - Chaparral	Fire suppression		SN Foothills	
Biswell 1974 (see van Wagtendonk and Fites-Kaufman 2006)	Chaparral - Grassland	Frequent Fire		SN Foothills	
Parsons and deBennedetti 1979	Ponderosa Pine - Mixed Conifer	Fire suppression	Stage and age distribution data	Sequoia and Kings Canyon NPs	1920-1970

Table A2.1. (continued)

Reference	Transition	Mechanism proposed	Evidence for mechanism	Location	Time Scale of transition
Parsons and deBennedetti 1979	Giant Sequoia mixed conifer - white fir mixed conifer	Fire suppression	Stage and age distribution data	Sequoia and Kings Canyon NPs	1920-1970
Vankat 1977	Ponderosa Pine - Mixed Conifer	Fire suppression			1920-1970
Vankat 1977	Montane Chaparral - Mixed Conifer	Fire suppression			1920-1970
Vankat and Major 1978	Grassland - Blue Oak Woodland	Grazing Cessation/Fire suppression	Repeat photography and stand demography	Sequoia NP	1920-1970
Vankat and Major 1978	Montane Chaparral - Mixed Conifer	Fire suppression	Repeat photography and stand demography	Sequoia NP	1920-1970
Vankat and Major 1978	Ponderosa Pine - Mixed Conifer	Fire suppression	Repeat photography and stand demography		1920-1970
Vankat and Major 1978	Giant Sequoia mixed conifer - white fir mixed conifer	Fire suppression	Repeat photography and stand demography		1920-1970
Pitcher 1987	Montane chaparral - Red fir	Fire suppression	Stage and age distribution data	Sequoia NP	
Pitcher 1987	western white pine - Red fir	Fire suppression	Stage and age distribution data	Sequoia NP	
Kilgore 1971 (see van Wagtendonk and Fites-Kaufman 2006)	lodgepole pine - red fir	Fire			
Bock and Bock 1977 (see van Wagtendonk and Fites-Kaufman 2006)	Jeffrey pine - montane chaparral	High-severity Fire		Donner Ridge	

Table A2.1. (continued)

Reference	Transition	Mechanism proposed	Evidence for mechanism	Location	Time Scale of transition
Bock and Bock 1977 (see van Wagtendonk and Fites-Kaufman 2006)	Jeffrey pine - Red fir	Fire suppression		Donner Ridge	
Lorentzen 2004 (see van Wagtendonk and Fites-Kaufman 2006)	aspen - lodgepole pine	Fire suppression			
McCain Et al. 2003 (See Jones et al. 2005)	aspen - conifers (lodgepole in SN)	Grazing/browsing		Rocky Mts	
White 1998 (See Jones et al. 2005)	aspen - conifers (lodgepole in SN)	Grazing/browsing			
Jones et al. 2005	lodgepole pine - aspen	conifer thinning	manipulative study - removal of competing conifers	Lassen NP	
McClaran and Bartolome 1989	Blue Oak woodland maintained	Frequent Fire	age distribution and fire scars from tree cores	UC Sierra Foothill Field Station	
Busch and Smith 1995	Riparian Woodland - Riparian scrubland	Water table and salinity alterations	Community analysis and physiological measurements	SW US (not in SN)	
Sawyer et al. 2009 (MCV)	Ponderosa Pine - Mixed Conifer	Logging/Fire suppression			
Minnich and Everett (see Sawyer et al. 2009 p. 194)	Ponderosa Pine - Mixed Conifer	Ozone pollution			
Thorne et al. 2008	Ponderosa Pine - Montane hardwood		Mapping (comparison of historical and modern vegetation maps)		1935-1995

Table A2.1. (continued)

Reference	Transition	Mechanism proposed	Evidence for mechanism	Location	Time Scale of transition
Thorne et al. 2008	Blue Oak woodland - grassland		Mapping (comparison of historical and modern vegetation maps)		
Thorne et al. 2008	Foothill pine woodland - grassland		Tree ring analysis and demographic data		
Dull 1999	Montane meadow - shrubs	Grazing	Palynological analysis	Southern SN, Kern River basin	1800-current
West 2003	Pine woodland - red fir forest	Climate change (cooler and wetter)	Palynological analysis	Lassen NP	12,500 YBP to 3100 YBP
West 2003	sagebrush steppe - pine woodland	Climate change (warmer and wetter)	Palynological analysis	Lassen NP	3100 YBP to present
Anderson 1990	Montane chaparral - subalpine woodland	Climate change (wetter)	Palynological analysis	Tioga Pass	6000 BP to present day
Anderson 1990	Montane chaparral - Red fir	Climate change (wetter)	Palynological analysis	Tioga Pass	6000 BP to present day
Anderson 1990	subalpine woodland - alpine	Climate change (cooler)	Palynological analysis	Tioga Pass	3000 BP to 2500 BP
Cole 1983	dry woodland - mixed conifer forest	Climate change (wetter)	Palynological and fossil analysis	Kings Canyon NP	Pleistocene to Modern day
Cole 1983	pinyon pine/sagebrush scrub - subalpine woodland	Climate change (wetter)	Palynological and fossil analysis	Kings Canyon NP	Pleistocene to Modern day

Table A2.1. (continued)

Reference	Transition	Mechanism proposed	Evidence for mechanism	Location	Time Scale of transition
Lloyd and Graumlich 1997	subalpine woodland - alpine	Climate change (drier)	Tree ring analysis and demographic data	SN crest near Mt Whitney	1000 YBP to Modern day
Lloyd and Graumlich 1997	alpine - subalpine	Climate change (warmer and wetter)	Tree ring analysis and demographic data	SN crest near Mt Whitney	1001 YBP to Modern day
Gruell 2001	Montane chaparral - forest		Repeat photography	SN	1850 - present

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Section 3: Understanding the Physiology Underlying Species Climate Suitability: Correlating Physiology and Climate Suitability

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The anticipated impacts of global climatic change have brought greater focus and urgency to understanding why species live where they do (Parmesan and Yohe 2003; Araújo and Rahbek 2006). This is of importance both for protecting existing habitat and projecting ranges under future scenarios (Thomas et al. 2004; Araújo et al. 2004; Schroter 2005; Hannah et al. 2007). Most distributional models use some form of climatic suitability analysis—a description of the habitat appropriate for a given species, based on climatic parameters describing the areas where it is currently found (Elith et al. 2006, 2011; Phillips, Anderson, and Schapire 2006; Phillips and Dudík 2008). While much valuable insight has been gained from such models, they have several important drawbacks. First, they assume that species are in equilibrium with their environments, making it difficult to project the future ranges of rapidly expanding groups such as invasive species (Thuiller et al. 2005; Hijmans and Graham 2006; Richardson and Pyšek 2006). Second, the area where a species is currently found may not be equivalent to the area where climatic parameters are suitable for the species, due to competition, dispersal limitation, and other factors (Araújo and Guisan 2006; Pearson et al. 2006;Jackson and Overpeck 2000).

Ideally, complementary modeling efforts should be developed based on the underlying physiology of the organisms studied. A fully mechanistic model, however, represents a major challenge, especially at a landscape scale. Here, we present a preliminary step toward a physiologically based model, by comparing climate suitability as analyzed by Maxent with traits related to temperature tolerance and precipitation requirements (Pearson and Dawson 2003; Beale, Lennon, and Gimona 2008; Maharjan et al. 2011).

The goals of this analysis are two-fold. First, we aim to test whether there is overlap between the predictions made by climate and the patterns observed in physiology. If strong correlations appear, this suggests that realized climate envelopes align closely with physiology, and adds to our confidence in predicting range shifts in response to future climates through these methods. If only weak relationships are observed, this points to a larger role for interspecies interactions and other conditions, rather than climate, in setting currently observed biogeographical ranges. A second aim has more immediate practical use. Strong correlations between physiological traits and climatic parameters might make it possible to create a predictive tool which, given a few traits of interest, could suggest whether high temperature, precipitation, or freezing represents the most important threat or limitation to a plant not currently included in the dataset.

Climate change is expected to have major effects on the size, shape, and distribution of California’s many microclimates. This has dramatic implications for the distribution of plant communities within the state (Loarie et al. 2008: Loarie et al. 2009; Ackerly et al 2010,; Ackerly 2012). California's climate can be described on two axes: one, running north to south, is a water availability gradient, from desert to Mediterranean chaparral to temperate rainforest. The other, running east to west, is a gradient of temperature extremes, from a mild climate with few frosts and low highs near the coast, to a continental climate with cold winters and hot summers inland (Ackerly et al. 2010). The state's varied topography adds extreme cold temperatures at alpine elevations. As a result, water availability and the frequency of freezing are two important climatic determinants of species occurrence within the region (Cornwell and Ackerly 2009; Ackerly et al. 2010). The many different combinations that result from these two intersecting gradients, plus other regional and local variation, provide the climatic conditions for the state's high number of different plant communities (Bakker 1984; Barbour and Billings 2000).

Climatic change will relax one of these limits while intensifying the other. Winter frost events are expected to decrease (Ackerly 2012), while water deficit is expected to increase, due to greater evaporative demand, particularly in the summer. Understanding the physiological basis of individual species’ climatic thresholds for minimum temperature, maximum temperature, and water availability is the first step toward forecasting winners and losers under changing climate scenarios.

In this analysis, we seek to match climatic conditions directly with physiological traits. If we are successful in doing so, we will gain a powerful new tool for predicting how any species whose functional traits are known, or can be measured, may respond to changes in rainfall, temperature, and freezing regime. Our analysis consists of matching modeled climate suitability data for a variety of California species with physiological traits hypothesized to be important determinants of sensitivity to drought and freezing. We have included two measurements of physiological drought: precipitation (as a measure of water availability), and maximum temperature (as a measure of evaporative demand). We also examined one measure of freezing: minimum temperature.

A number of physiological traits have been previously linked to drought survival in the scientific literature (Table 3.1). In particular, leaf-related traits such as stomatal conductance (G_s) and maximum photosynthetic assimilation rate (A_{max}) are important in determining the balance of water transpired per unit carbon gained (Farquhar and Sharkey 1982). Other leaf-related traits, such as specific leaf area (SLA) and leaf (or, for compound leaves, leaflet) size have been shown to vary directly with exposure to sunlight at local scales (Parkhurst and Loucks 1972; Hirokazu 2003; Falster and Westoby 2003); they also vary with climate at landscape and worldwide scales (Ackerly and Reich 1999; Wright et al. 2005; Moles et al. 2011). Water-transport related traits, such as stem-specific conductivity (K_s), leaf-specific hydraulic conductivity (K_L), and xylem pressure at 50 percent loss of conductivity (P_{50}), are also believed to be important in determining how plants respond to water stress—and even what conditions are “stressful” or “unstressful” for a given species (Tyree and Ewers 1991; Sperry et al. 1994; Pockman and Sperry 2000; Sperry 2000; Sperry, Meinzer, and McCulloh 2008; Meinzer et al. 2009).

Traits associated with surviving cold conditions are still more specific (Table 3.1). A key determinant of whether plants survive frost is the degree to which the water transport system is blocked by air forced out of the sap during freezing (embolism). Post-freeze embolism has been shown to be lower in species with narrow xylem vessels under a variety of conditions (Sperry and Sullivan 1992; Sperry et al. 1994; Langan, Ewers, and Davis 1997). As a result, narrow vessels are strongly associated with resistance to freezing (Pockman and Sperry 1996; Ewers et al. 2003; Stuart et al. 2007). However, other traits such as K_s and P_{50} may also be important in determining how the vascular system recovers from air blockages. Leaf traits are less explored, but may be important, particularly in evergreen species, as leaf density (measured here as SLA) and leaf size may affect the thermal properties and freezing rates of leaf tissues (McBurney 1992; Wanner and Junttila 1999; Ball et al. 2002).

Table 3.1. Relationships Between Traits and Climate as Predicted from the Literature (See Trait Definitions in Table 3.2)

	Mean Annual Precip	Max Temp	Min Temp
Max height	↗	↘	–
P_{50}	↗	↘	↘
K_s	↗	↘	↘
K_L	↗	↘	↘
Predawn Ψ_{min}	↗	↘	–
ACD	↗	↘	↘
SLA	↗	↘	↗
G_s	↗	↘	–
Leaf size	↗	↘	↗
Leaf N	↗	↘	↗
N_{area}	↘	↗	↘

↗	Positive correlation predicted
–	No correlation predicted
↘	Negative correlation predicted

Methods

Trait Database

We compiled previously published data on 28 whole-plant, stem, and leaf traits for 82 woody angiosperm species native to California (Table 3.2; note that some of the data points were measured on plants growing outside of California.) Of the 28 traits initially collected, some were redundant and/or closely related, and therefore excluded. For example, the initial dataset included three measures of xylem vulnerability to cavitation: P_{50}, P_{12}, P_{88},and the slope of the line connecting these three points. In the final analysis, only P_{50} was used. Ultimately, 12 traits were selected as best representing different aspects of physiological function, with as little overlap as possible (Table 3.2).

Table 3.2. Trait Data Compiled for This Study. Traits marked with an asterisk were included in the analysis. The total number of species for which measurements were found for each trait is given at right.

Trait	Description	Why excluded	Number of Species (82 Total)
* Max height	Maximum height of species		56
Act height	Actual height of individual	Closely correlated with max height, lower sample size	31
* P_{50}	Xylem pressure at 50% loss of conductivity		80
P_{12}	Xylem pressure at 12% loss of conductivity	Closely correlated with P_{50}	54
P_{88}	Xylem pressure at 88% loss of conductivity	Closely correlated with P_{50}	57
Slope	Slope of xylem vulnerability curve	Closely correlated with P_{50}	57
* K_s	Stem-specific hydraulic conductivity		67
* K_L	Leaf-specific hydraulic conductivity		30
* Predawn Ψ_{min}	Minimum pre-dawn xylem water potential observed		36
Midday Ψ_{min}	Minimum mid-day xylem water potential observed	Closely correlated with Predawn Ψ_{min}	62
* ACD	Average conduit diameter		57
D_h	Hydraulically-weighted conduit diameter	Closely correlated with ACD; lower sample size	38
* SLA	Specific leaf area (leaf area/unit mass)		57
* G_s	Stomatal conductance		30
* A_{max}	Maximum CO_2 assimilation rate		10
$\delta^{13}C$	Water-use efficiency as measured using stable isotope ratio	Very low sample size available	4
* Leaf size	Area of leaf or, for compound leaves, leaflet		34
* Leaf N	Leaf nitrogen per unit mass		48
* N_{area}	Leaf nitrogen per unit area		32

Climate Suitability Modeling

We compared each trait to climate suitability data extracted using a MaxEnt model (Phillips et al. 2006). MaxEnt models utilize species occurrence data from herbarium records or field observations and relate these observations to climate and other spatial data to develop predictive models of environmental suitability across a species' range (Figure 3.1). The models output a suitability parameter that can be loosely interpreted as the probability that a species will occupy each pixel on the landscape (Elith et al. 2011). The MaxEnt analyses used here followed methods in Loarie et al. (2008), using minimum temperature, maximum temperature, and total precipitation as predictor variables, instead of the multivariate climate axes used in the earlier analysis.

MaxEnt is capable of producing two different types of suitability response curves. Both types describe which values of the climatic parameter are suitable for the species examined. The first type of curve holds all other variables constant while estimating the effect of manipulating a focal variable. The result describes the marginal effect of that one variable (Figure 3.1). The drawback to this approach, however, is that it may be misleading for highly correlated variables, where it is difficult to truly measure the effect of one variable and hold others constant. For instance, it may not be meaningful to manipulate total annual precipitation while holding quarterly precipitation constant. For this reason, MaxEnt also provides a second type of response curve. In this case, values of the focal variable are recorded as they occur in relation to other variables across the landscape. Therefore, in this type of curve, only combinations of climatic variables that actually occur are considered. This is sometimes described as an "observed" response curve, but this can be misleading, because both types of response curves are based on observed species locations. We use the term "realized" response curve to describe this second type of curve (Figure 3.1).

Matching Trait Data and Climatic Suitability

Three parameters were extracted from suitability curves for each species, for both realized and marginal responses on gradients of precipitation, maximum temperature, and minimum temperature (resulting in six different measurements in all.) For each species, we selected the lower edge, optimum, and upper edge of the portion of the response curve that includes 90 percent of known observations. These points were used as parameters for comparison with physiological values in subsequent analyses. Because our primary interest is to examine changes at the edge of climate suitability limits, the analysis and discussion presented here focus on upper and lower bounds of this distribution. Correlations with optimum values are reported for completeness, but not discussed in the text.

We used correlations to test for relationships between physiological traits and marginal and realized suitability on several climate axes. Because the number of traits and climate variables explored was large, we report both the actual p-value and a multiple-comparison adjusted p-value for each correlation (first/second for each p-value reported, respectively). The adjusted p-values use the method of Benjamini and Hochberg (1995). Multiple linear regression, with back-and-forward stepwise model selection, was used to test several different models for the lower limit of precipitation, the upper limit of high temperature, and the lower limit of low temperature. Before analysis, all data were centered to facilitate analysis, but not scaled, so that the final model could easily be understood in the original units. Original units were used for all variables except precipitation, and area-based physiological measurements, which were strongly log-normal and were log-transformed. Each model was checked for high correlation between explanatory variables using the Variance Inflation Factor (VIF; as implemented in the R stats package, R Development Core Team 2011). Variables that resulted in a VIF over 6 were not used together in a single analysis.

Results

Traits Related to Precipitation

We found stronger correlations with the lower edge of realized precipitation suitability than marginal precipitation suitability (Table 3.3). Only one trait, leaf size, was significantly correlated with the lower edge of both marginal and realized precipitation (Figure 3.2A) It was positively correlated with both, indicating that species with smaller leaves reach their climatic limits at comparatively low precipitation values. K_s (Figure 3.2B) was positively correlated with the lower edge of realized precipitation only. N_{area} (Figure 3.2C), predawn Ψ_{min}, and K_L were negatively correlated with the lower edge of realized precipitation. This suggests that higher stem conductivity, lower nitrogen per unit area, more negative predawn water potentials, and lower conductance per unit leaf area are all associated with species that reach their climatic limits at higher precipitation values.

We also found several strong correlations with the upper edge of both marginal and realized precipitation suitability. A positive correlation was observed with leaf size (Figure 3.3A) maximum height (Figure 3.3B), and stem-specific conductivity. This indicates that taller plants, larger leaves, and more conductive stems are found in species that reach their climatic limits at wetter values. As with the lower limits of precipitation suitability, we found moderately strong and significant negative correlations with leaf-specific conductivity (Figure 3.3C). This suggests that stems are more conductive for a given leaf area in plants that reach their distribution limits in drier areas. Maximum assimilation rate was not significantly correlated with the upper bound of precipitation suitability, but relatively high R^2 values (albeit with small sample sizes) suggest that further investigation of this trait may be warranted.

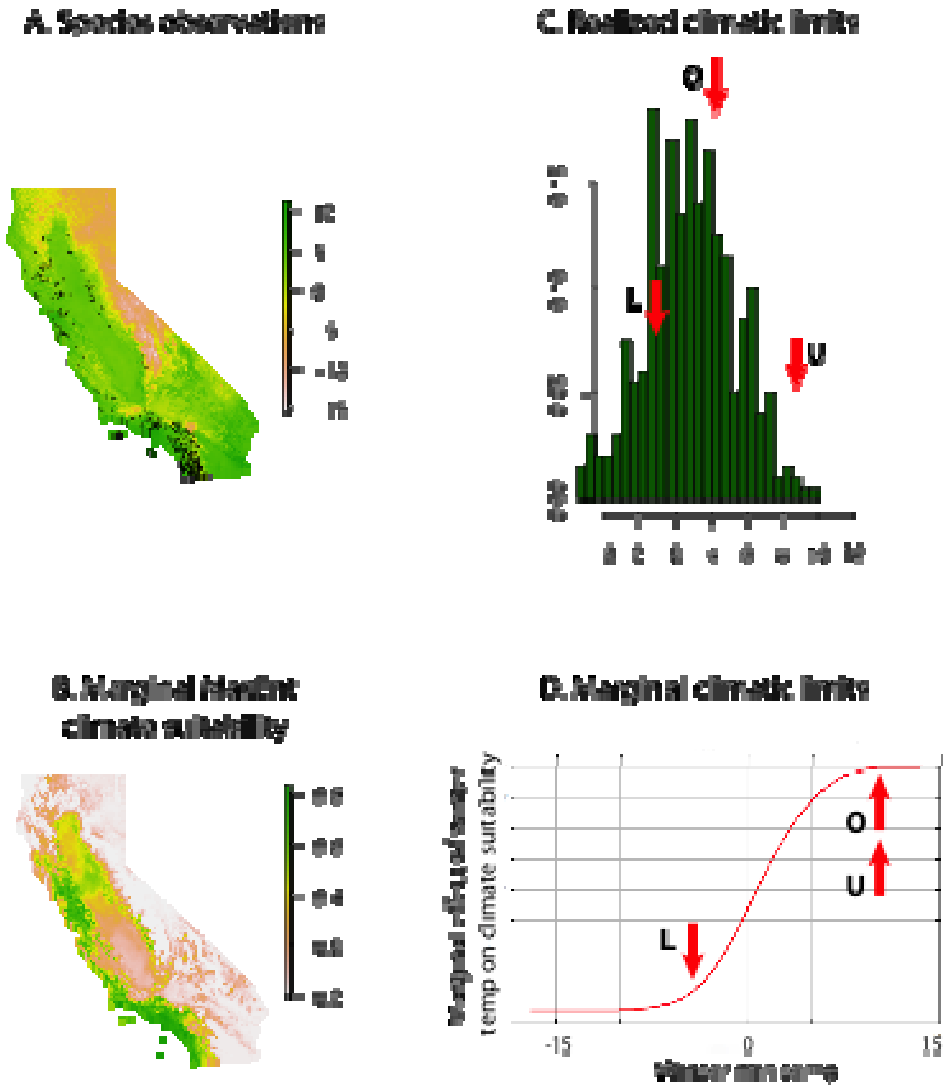

Figure 3.1. Extracting Climatic Suitability Limits from MaxEnt Modeling. Species observations (A) are used to construct a climate suitability model (B). The effect of each variable within the model is measured while holding other variables constant (marginal climate, D). We then extracted lower limits (L), optima (O), and upper limits (U) corresponding to 90 percent of species occurrences (C). Note that in some cases (e.g., D) optima may be the same as either upper or lower limits.

Table 3.3. Correlations Between Physiological Traits and Different Aspects of Precipitation Suitability

Marginal Precipitation

			Lower Edge				Optimum				Upper Edge			
	n	*df*	*R*	*p*	*adj. p*	R^2	*R*	*p*	*adj. p*	R^2	*R*	*p*	*adj. p*	R^2
Max height	56	54	-0.08	0.5723	0.6646	0.01	0.32	0.0166 *	0.0497 *	0.10	0.42	0.0013 **	0.0083 **	0.18
P_{50}	80	78	-0.10	0.3548	0.4730	0.01	-0.06	0.6264	0.6939	0.00	-0.09	0.4466	0.5537	0.01
K_s	67	65	-0.01	0.9660	0.9681	0.00	0.26	0.0318 *	0.0738	0.07	0.43	0.0003 ***	0.0057 **	0.18
K_L	30	28	-0.30	0.1062	0.1777	0.09	-0.55	0.0015 **	0.0083 **	0.31	-0.55	0.0015 **	0.0083 **	0.31
Predawn Ψ_{min}	36	34	-0.13	0.4537	0.5537	0.02	-0.27	0.1086	0.1777	0.07	-0.13	0.4448	0.5537	0.02
ACD	57	55	0.07	0.6189	0.6939	0.00	0.33	0.0136 *	0.0481 *	0.11	0.09	0.5066	0.5980	0.01
SLA	57	55	0.06	0.6831	0.7420	0.00	0.25	0.0595	0.1127	0.06	0.30	0.0222 *	0.0571	0.09
G_s	30	28	0.28	0.1309	0.2005	0.08	0.33	0.0764	0.1374	0.11	0.29	0.1138	0.1781	0.09
A_{max}	10	8	-0.46	0.1861	0.2791	0.21	-0.69	0.0261 *	0.0649	0.48	-0.67	0.0337 *	0.0757	0.45
Leaf size	34	32	0.50	0.0029 **	0.0138 *	0.25	0.57	0.0004 ***	0.0057 **	0.33	0.54	0.0009 ***	0.0075 **	0.29
Leaf N	48	46	0.06	0.6905	0.7420	0.00	-0.05	0.7544	0.7987	0.00	0.02	0.8882	0.9135	0.00
N_{area}	32	30	-0.32	0.0709	0.1309	0.10	-0.41	0.0213 *	0.0567	0.16	-0.36	0.0417 *	0.0844	0.13

Realized Precipitation

			Lower Edge				Optimum				Upper Edge			
	n	*df*	*R*	*p*	*adj. p*	R^2	*R*	*p*	*adj. p*	R^2	*R*	*p*	*adj. p*	R^2
Max height	56	54	0.31	0.0194 *	0.0545	0.10	0.36	0.0063 **	0.0245	0.13	0.43	0.0009 ***	0.0075 **	0.19
P_{50}	80	78	-0.19	0.0998	0.1710	0.03	-0.13	0.2632	0.3716	0.02	-0.12	0.3008	0.4166	0.01
K_s	67	65	0.37	0.0019 **	0.0099 **	0.14	0.42	0.0004 ***	0.0057	0.18	0.46	0.0001 ***	0.0057 **	0.21
K_L	30	28	-0.36	0.0504	0.0980	0.13	-0.49	0.0056 **	0.0237	0.24	-0.52	0.0032 **	0.0145 *	0.27
Predawn Ψ_{min}	36	34	-0.40	0.0154 *	0.0483 *	0.16	-0.21	0.2272	0.3272	0.04	-0.14	0.4167	0.5455	0.02
ACD	57	55	0.21	0.1133	0.1781	0.04	0.10	0.4413	0.5537	0.01	0.09	0.5024	0.5980	0.01
SLA	57	55	0.23	0.0888	0.1559	0.05	0.29	0.0289 *	0.0693	0.08	0.27	0.0422 *	0.0844	0.07
G_s	30	28	0.38	0.0380 *	0.0804	0.14	0.24	0.2008	0.2950	0.06	0.19	0.3273	0.4446	0.03
A_{max}	10	8	-0.74	0.0140 *	0.0481 *	0.55	-0.74	0.0148 *	0.0483	0.54	-0.72	0.0197 *	0.0545	0.51
Leaf size	34	32	0.53	0.0014 **	0.0083 **	0.28	0.59	0.0002 ***	0.0057	0.35	0.56	0.0006 ***	0.0066 **	0.31
Leaf N	48	46	-0.08	0.5842	0.6676	0.01	-0.01	0.9681	0.9681	0.00	0.02	0.8801	0.9135	0.00
N_{area}	32	30	-0.58	0.0006 ***	0.0066 **	0.33	-0.47	0.0065 **	0.0245	0.22	-0.37	0.0367 *	0.0800	0.14

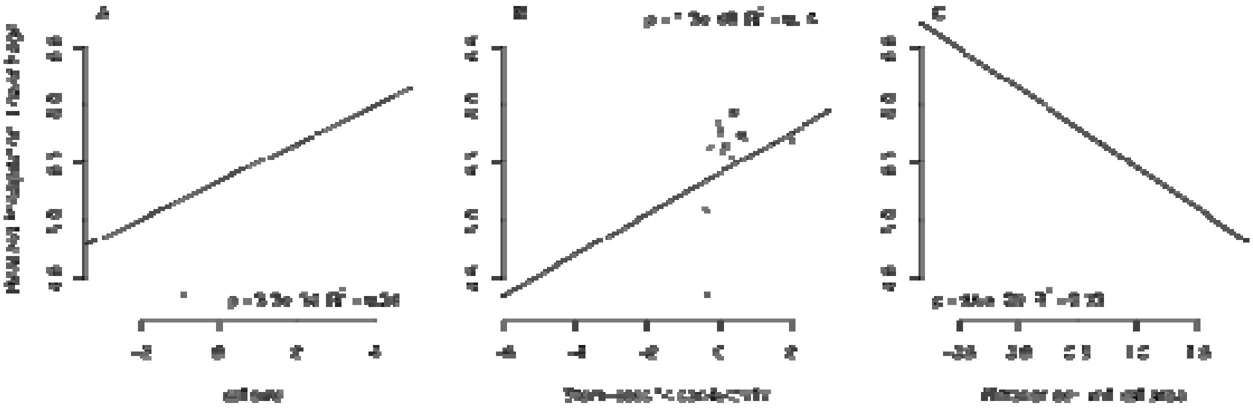

Figure 3.2. Relationships with the Lower Edge of Realized Precipitation Suitability

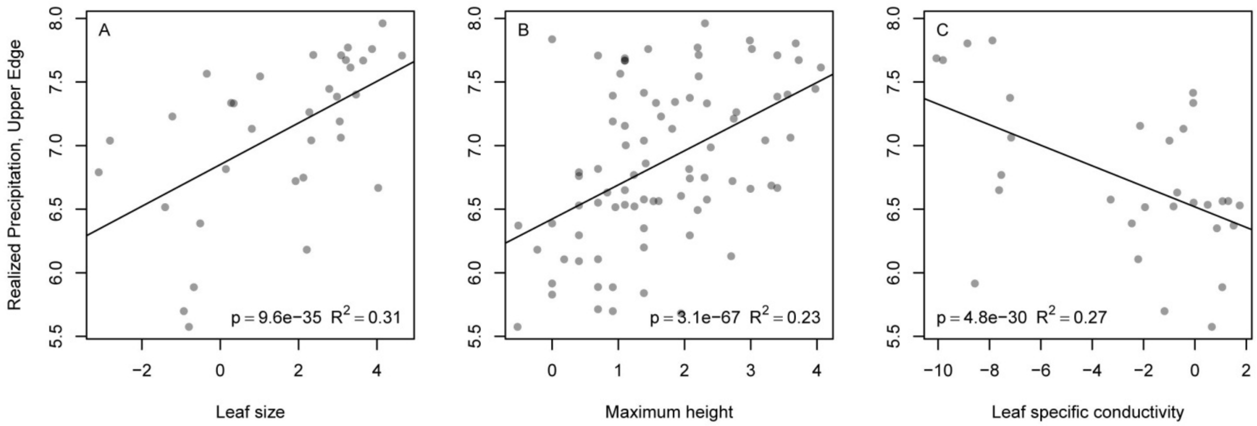

Figure 3.3. Relationships With the Upper Edge of Realized Precipitation Suitability

Table 3.4. Predictive Models for the Lower Edge of Realized Precipitation Suitability Models pr1 and pr2 Represent Different Sets of Parameters for Which Complete Data Were Available (Sample Sizes Shown). Nested models share the same "pr" number, with "s" indicating the model selected through stepwise regression. Akaike information criterion (AIC) results shown relate only to each set of nested models. Precipitation and all area-based measurements are log transformed; all data shown is centered, but not scaled. Significance: $p < 0.001$ shown bold italic, $p < 0.01$ shown bold, $p < 0.05$ shown italic.

	Realized Precipitation Suitability, lower edge ~	*n*	AIC	Multiple R^2	Adj R^2	Intercept	K_s	Leaf size	Max height	N_{area}	P_{50}	SLA	N_{area}:P_{50}	N_{area}:Max height	P_{50}:Max height	N_{area}:P_{50}:Max height
pr1	Leaf size + N_{area} + SLA + P_{50} + K_s + Max height	21	31	0.58	0.40	0.13	-0.04	0.03	0.12	-0.63	-0.12	0.24				
pr1s	N_{area} + P_{50} + Max height	21	26	0.56	0.48	0.14			0.12	***-0.84***	*-0.09*					
pr2	N_{area} * P_{50} * Max height	29	36	0.59	0.45	*0.20*			**0.26**	-0.55	-0.07		0.01	0.05	-0.06	0.14
pr2s	N_{area} + P_{50} + Max height + N_{area}:Max height	29	33	0.55	0.48	*0.20*			**0.18**	-0.51	-0.06			0.24		

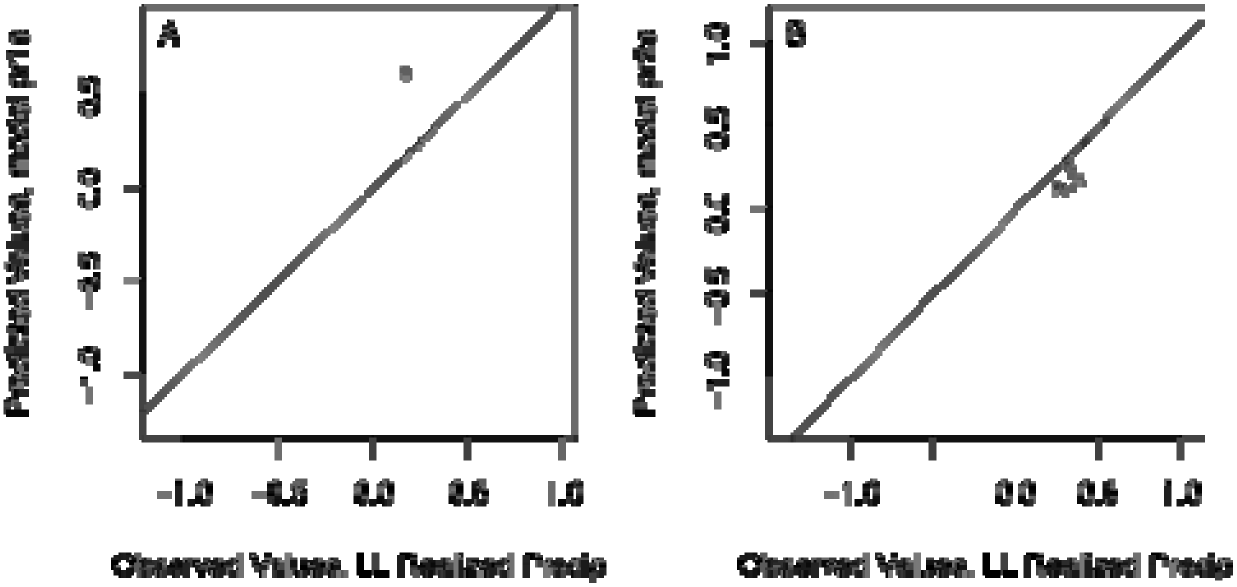

Figure 3.4. Multiple Regression Models for Precipitation. Relationships between predicted and observed data are shown for the most explanatory models of the lower edge of realized precipitation suitability.

Multiple Trait Models for Predicting Precipitation Suitability

Selection of explanatory variables for the multiple regression models was limited by the degree of overlap in data availability for different traits. Table 3.4gives the result of testing several different sets of compatible variables; two of the most explanatory models are shown (Figure 3.4). The number of data points available for each combination of variables is given under *n*. In each case, a saturated model for each set of variables is shown, followed by a model selected using Akaike information criterion (AIC)-based stepwise regression. We were able to improve on the predictive potential of any variable used alone. In spite of its high individual correlation, leaf size was not selected as an important explanatory variable in any model. Instead, N_{area} emerged as one of the better predictors of precipitation suitability, and models including N_{area} were able to account for 55 to 59 percent of variation in the data (Table 3.4).

Max height and P_{50} also made significant contributions to the explanatory power of these models, suggesting that there is a role for leaf-level, stem-level, and whole-plant traits in predicting precipitation limits. These results suggest that climatic limits may be closely associated with leaf traits; in particular, with photosynthetic efficiency, as N_{area} is expected to be strongly related to the amount of Rubisco in the leaf (Reich and Oleksyn 2004; Wright et al. 2004). However, there is also interplay between the xylem and the leaves: K_s was retained in model pr1s, and P_{50} was retained in model pr2s, showing that these two variables explained additional aspects of variation.

Traits Related to Maximum Temperature

Correlations with maximum temperature were, in general, weak, and only a few traits were significantly correlated with this aspect of climate (Table 3.5). This pattern has been noted previously in other systems (Woodward 1987). An exception was A_{max}, which was positively correlated with up to 43 percent of variation in realized maximum temperature, and 62 percent of marginal maximum temperature. However, this was not significant, and due to the small sample size (*n* = 10) should be considered, at best, a promising direction for further study.

Among other relatively good predictors of maximum temperature limits were many of the same traits found to be highly correlated with precipitation limits. This included leaf size (Figure 3.5A) and max height. Both of these were negatively correlated with maximum temperature, indicating that shorter plants, and plants with smaller (or more highly dissected) leaves reach their climatic limits at warmer values. Stem-specific conductivity was also negatively correlated with realized maximum temperature, indicating that lower conductivities are associated with warmer climatic limits. N_{area} and K_L (Figure 3.5B, C) also had strong relationships with maximum temperature. Both showed a positive correlation, indicating plants with higher N_{area} and $K_L$reach the edge of their distribution in warmer areas.

Table 3.5. Correlations Between Physiological Traits and Different Aspects of Maximum Temperature Suitability

			Marginal Max Temp											
			Lower Edge				Optimum				Upper Edge			
	n	*df*	*R*	*p*	*adj. p*	R^2	*R*	*p*	*adj. p*	R^2	*R*	*p*	*adj. p*	R^2
Max height	56	54	-0.30	0.0238 *	0.1007	0.09	-0.22	0.0957	0.1813	0.05	-0.39	0.0033 **	0.0500	0.15
P_{50}	80	78	-0.04	0.7316	0.7862	0.00	0.07	0.5116	0.6243	0.01	0.15	0.1856	0.3037	0.02
K_s	67	65	-0.25	0.0434 *	0.1203	0.06	-0.19	0.1275	0.2240	0.04	-0.25	0.0377 *	0.1203	0.06
K_L	30	28	0.11	0.5457	0.6250	0.01	0.22	0.2418	0.3585	0.05	0.47	0.0082 **	0.0500	0.22
Predawn Ψ_{min}	36	34	0.01	0.9455	0.9455	0.00	0.17	0.3093	0.4137	0.03	0.37	0.0285 *	0.1051	0.13
ACD	57	55	0.26	0.0504	0.1246	0.07	0.15	0.2711	0.3828	0.02	-0.17	0.2047	0.3275	0.03
SLA	57	55	-0.27	0.0431 *	0.1203	0.07	-0.17	0.2093	0.3275	0.03	-0.14	0.2945	0.4078	0.02
G_s	30	28	0.02	0.9130	0.9391	0.00	0.14	0.4509	0.5741	0.02	-0.28	0.1361	0.2332	0.08
A_{max}	10	8	0.42	0.2275	0.3484	0.18	0.60	0.0661	0.1487	0.36	0.79	0.0071 **	0.0500	0.62
Leaf size	34	32	-0.24	0.1721	0.2881	0.06	-0.30	0.0829	0.1715	0.09	-0.38	0.0276 *	0.1051	0.14
Leaf N	48	46	-0.25	0.0833	0.1715	0.06	-0.06	0.6796	0.7413	0.00	0.06	0.6612	0.7324	0.00
N_{area}	32	30	0.21	0.2474	0.3585	0.04	0.12	0.5273	0.6250	0.01	0.42	0.0173 *	0.0891	0.17

			Realized Max Temp											
			Lower Edge				Optimum				Upper Edge			
	n	*df*	*R*	*p*	*adj. p*	R^2	*R*	*p*	*adj. p*	R^2	*R*	*p*	*adj. p*	R^2
Max height	56	54	-0.38	0.0041 **	0.0500	0.14	-0.39	0.0033 **	0.0500	0.15	-0.35	0.0083 **	0.0500	0.12
P_{50}	80	78	0.07	0.5463	0.6250	0.00	0.09	0.4111	0.5382	0.01	0.17	0.1257	0.2240	0.03
K_s	67	65	-0.30	0.0132 *	0.0730	0.09	-0.32	0.0078 **	0.0500	0.10	-0.32	0.0077 **	0.0500	0.10
K_L	30	28	0.33	0.0795	0.1715	0.11	0.42	0.0220 *	0.1007	0.17	0.37	0.0459 *	0.1224	0.13
Predawn Ψ_{min}	36	34	0.13	0.4545	0.5741	0.02	0.20	0.2489	0.3585	0.04	0.34	0.0419 *	0.1203	0.12
ACD	57	55	0.06	0.6516	0.7324	0.00	0.03	0.8153	0.8508	0.00	-0.03	0.8117	0.8508	0.00
SLA	57	55	-0.29	0.0292 *	0.1051	0.08	-0.30	0.0227 *	0.1007	0.09	-0.25	0.0584	0.1357	0.06
G_s	30	28	-0.13	0.5018	0.6229	0.02	-0.29	0.1230	0.2240	0.08	-0.39	0.0309 *	0.1059	0.16
A_{max}	10	8	0.57	0.0862	0.1724	0.32	0.56	0.0908	0.1766	0.32	0.65	0.0400 *	0.1203	0.43
Leaf size	34	32	-0.34	0.0511	0.1246	0.11	-0.49	0.0030 **	0.0500	0.24	-0.50	0.0024 **	0.0500	0.25
Leaf N	48	46	-0.15	0.3103	0.4137	0.02	-0.09	0.5468	0.6250	0.01	-0.01	0.9363	0.9455	0.00
N_{area}	32	30	0.35	0.0519	0.1246	0.12	0.48	0.0055 **	0.0500	0.23	0.49	0.0049 **	0.0500	0.24

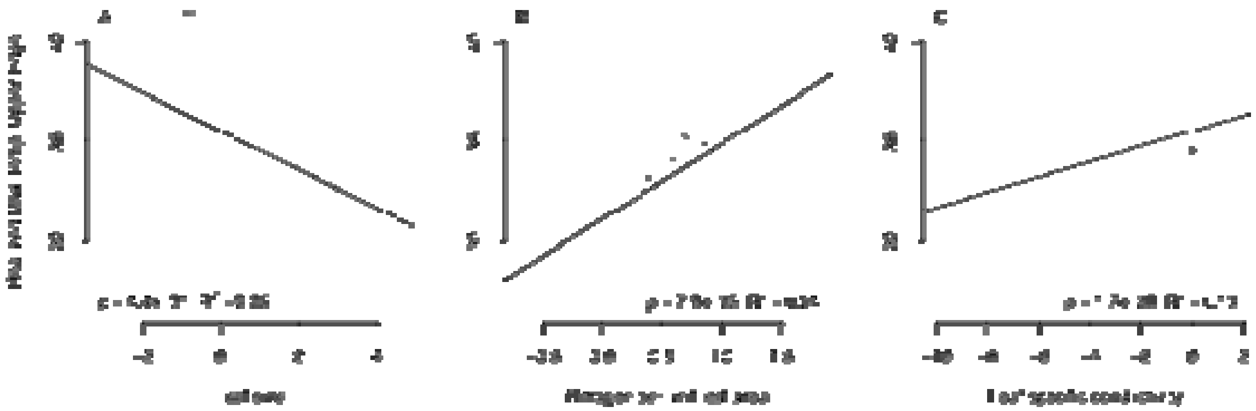

Figure 3.5 Relationships with the Upper Edge of Realized Maximum Temperature Suitability

Table 3.6. Predictive Models for the Upper Edge of Realized Maximum Temperature Suitability Nested Models Share the Same "Max" Number, With "S" Indicating the Model Selected Through Stepwise Regression. AIC results shown relate only to each nested set of models. All area-based measurements are log transformed; all data shown is centered, but not scaled. Significance: $p < 0.001$is shown in bold italic, $p < 0.01$is shown in bold, and $p < 0.05$is shown in italic.

	Realized Maximum Temperature Suitability, upper edge ~	AIC	*n*	Multiple R^2	Adj R^2	Intercept	K_s	Leaf size	Max height	N_{area}	K_s:Leaf size	K_s:Max height	K_s:N_{area}	Leaf size:Max height	Leaf size:N_{area}	Max height:N_{area}
max1	K_s + Leaf size + Max height + N_{area}	112	21	0.36	0.20	-0.50	1.00	0.00	-0.90	*4.80*	-	-	-	-	-	-
max1s	N_{area}	109	21	0.27	0.24	-0.30	-	-	-	*3.60*	-	-	-	-	-	-
max2	(K_s + Leaf size + Max height + N_{area})^2	105	21	0.75	0.49	-1.90	0.70	0.70	-1.30	*5.70*	*2.00*	-1.00	4.00	0.40	0.00	-2.00
max2s	K_s + Leaf size + Max height + N_{area} + K_s:Leaf size + K_s:N_{area} + Leaf size:Max height	100	21	0.73	0.58	*-2.00*	0.30	0.50	-1.10	**5.30**	**1.70**	-	2.60	0.40	-	-

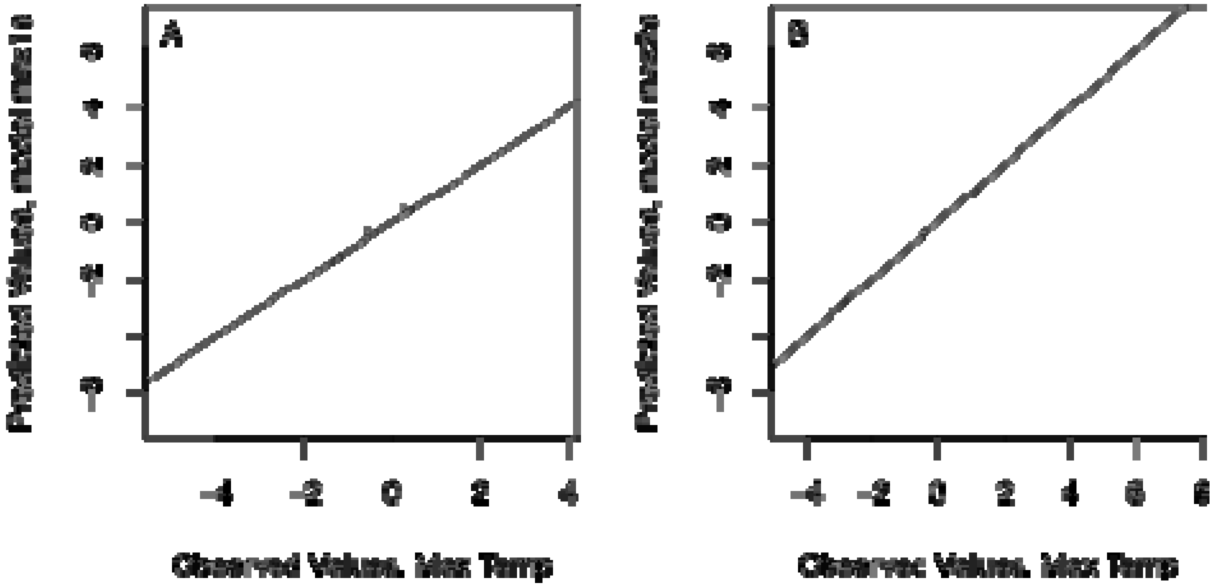

Figure 3.6. Multiple Regression Models for Maximum Temperature. Relationships between predicted and observed data are shown for the most explanatory models of the upper edge of realized high temperature suitability.

Multiple Trait Models for Predicting Maximum Temperature Suitability

As for precipitation, model selection was constrained by the availability of overlapping datasets for different traits. By exploring sets of compatible traits together, however, we were able to find two models with good predictive power (Table 3.6, Figure 3.6). In particular, model max2s, which combines K_s, leaf size, max height, and N_{area}, explained 73 percent of the variation in our data. It is interesting to note that almost all of this explanatory power comes from the inclusion of interactions; analyzed without interactions, the result of the selection process is a model that includes only N_{area}, and has weak explanatory power (multiple $R^2 = 0.27$, model max1s). Each of these models combines leaf and stem traits, suggesting that, as for precipitation, both aspects of physiology contribute to a highly descriptive model of climate suitability.

Minimum Temperature

As expected, average conduit diameter (ACD) was a good predictor of the lowest temperature tolerated by a given species (Figure 3.7A). It was positively correlated with all measures of minimum temperature, but was not as strongly correlated with the lower edge of minimum temperature as might be expected, predicting only 11 percent of marginal and realized lower temperature limits (Table 3.7). It was more significantly correlated with the optimum and upper edge of minimum temperature suitability, predicting up to 26 percent of variation in the upper edge of marginal suitability. Several other traits were good predictors of minimum temperatures, including leaf-related traits, such as K_L, SLA, and leaf size (Table 3.7, Figure 3.7B, C). K_L had a moderate positive correlation. SLA and leaf size had moderate negative correlations. This indicates that species with lower leaf-based conductivities, thinner leaves (possibly associated with deciduous leaf habit), and smaller leaves reach the limits of their distributions in areas with lower minimum temperatures.

In the context of climate change, the upper edge of minimum temperature distribution may be of particular interest, both because it is the direction of likely shifts, and because this is the edge that relates to competitive release. As noted above, ACD was an even stronger predictor of the upper limit of minimum temperature than the lower limit of minimum temperature. As for lower edge, K_L and SLA were also good predictors. All three show the same correlation patterns as with the lower limit of minimum temperature suitability (Figure 3.8).

Table 3.7. Correlations Between Physiological Traits and Different Aspects of Minimum Temperature Suitability

Marginal Min Temp

			Lower Edge				Optimum				Upper Edge			
	n	*Df*	*R*	*P*	*adj. p*	*R^2*	*R*	*p*	*adj. p*	*R^2*	*R*	*p*	*adj. p*	*R^2*
Max height	56	54	-0.04	0.7661	0.9364	0.00	-0.14	0.3008	0.5157	0.02	-0.13	0.3279	0.5490	0.02
P_{50}	80	78	-0.07	0.5608	0.8240	0.00	-0.04	0.7249	0.9157	0.00	0.03	0.7861	0.9434	0.00
K_s	67	65	0.01	0.9159	0.9760	0.00	-0.09	0.4939	0.7433	0.01	-0.11	0.3569	0.5711	0.01
K_L	30	28	0.46	0.0107 *	0.0759	0.21	0.42	0.0223 *	0.1004	0.17	0.38	0.0381 *	0.1523	0.14
Predawn Ψ_{min}	36	34	-0.31	0.0673	0.1794	0.10	-0.19	0.2721	0.4779	0.04	-0.22	0.1950	0.3509	0.05
ACD	57	55	0.33	0.0128 *	0.0759	0.11	0.34	0.0092 **	0.0759	0.12	0.51	0.0001 ***	0.0040 **	0.26
SLA	57	55	-0.32	0.0137 *	0.0759	0.11	-0.20	0.1421	0.3009	0.04	-0.23	0.0895	0.2301	0.05
G_s	30	28	0.01	0.9415	0.9760	0.00	-0.01	0.9603	0.9760	0.00	-0.11	0.5743	0.8270	0.01
A_{max}	10	8	-0.11	0.7673	0.9364	0.01	0.02	0.9607	0.9760	0.00	0.07	0.8406	0.9760	0.01
Leaf size	34	32	-0.24	0.1671	0.3166	0.06	-0.25	0.1617	0.3146	0.06	-0.23	0.1906	0.3509	0.05
Leaf N	48	46	-0.28	0.0571	0.1617	0.08	-0.34	0.0192 *	0.0986	0.11	-0.28	0.0555	0.1617	0.08
N_{area}	32	30	0.03	0.8673	0.9760	0.00	-0.10	0.5976	0.8436	0.01	0.02	0.9210	0.9760	0.00

Realized Min Temp

			Lower Edge				Optimum				Upper Edge			
	n	*Df*	*R*	*P*	*adj. p*	*R^2*	*R*	*p*	*adj. p*	*R^2*	*R*	*p*	*adj. p*	*R^2*
Max height	56	54	-0.25	0.0584	0.1617	0.06	-0.19	0.1614	0.3146	0.04	-0.20	0.1490	0.3064	0.04
P_{50}	80	78	-0.01	0.9092	0.9760	0.00	0.06	0.6207	0.8552	0.00	0.00	0.9760	0.9760	0.00
K_s	67	65	-0.24	0.0528	0.1617	0.06	-0.21	0.0946	0.2350	0.04	-0.12	0.3439	0.5628	0.01
K_L	30	28	0.48	0.0077 **	0.0759	0.23	0.56	0.0014 **	0.0259	0.31	0.58	0.0007 ***	0.0178 *	0.34
Predawn Ψ_{min}	36	34	-0.28	0.1011	0.2426	0.08	-0.25	0.1371	0.3000	0.06	-0.27	0.1103	0.2561	0.07
ACD	57	55	0.33	0.0123 *	0.0759	0.11	0.37	0.0050 **	0.0605	0.13	0.47	0.0002 ***	0.0075 **	0.22
SLA	57	55	-0.37	0.0049 **	0.0605	0.14	-0.33	0.0121 *	0.0759	0.11	-0.25	0.0567	0.1617	0.06
G_s	30	28	0.07	0.7231	0.9157	0.00	-0.07	0.6985	0.9144	0.01	-0.03	0.8865	0.9760	0.00
A_{max}	10	8	0.17	0.6414	0.8552	0.03	0.17	0.6330	0.8552	0.03	0.02	0.9625	0.9760	0.00
Leaf size	34	32	-0.39	0.0208 *	0.0998	0.16	-0.38	0.0284 *	0.1204	0.14	-0.34	0.0514	0.1617	0.11
Leaf N	48	46	-0.28	0.0578	0.1617	0.08	-0.22	0.1375	0.3000	0.05	-0.29	0.0493 *	0.1617	0.08
N_{area}	32	30	0.15	0.4104	0.6424	0.02	0.12	0.4956	0.7433	0.02	0.03	0.8737	0.9760	0.00

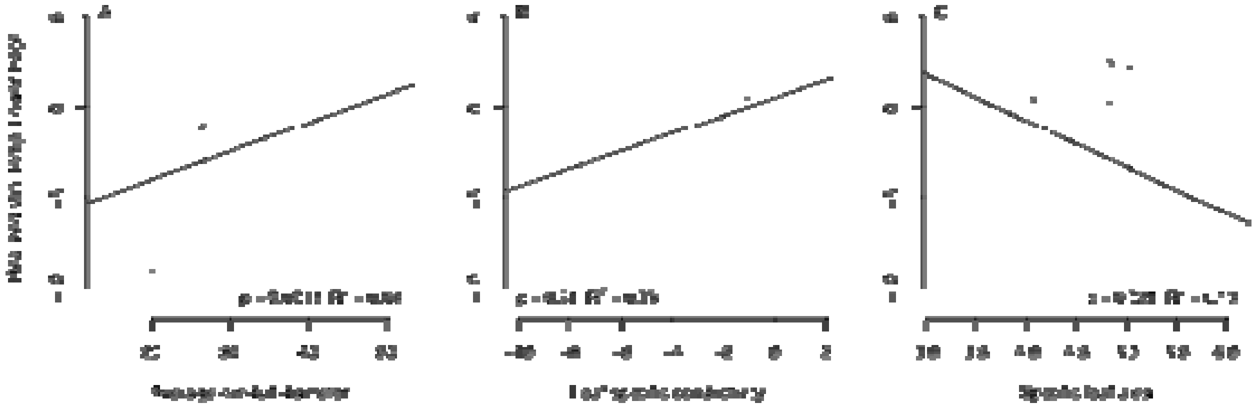

Figure 3.7. Relationships with the Lower Edge of Realized Minimum Temperature Suitability

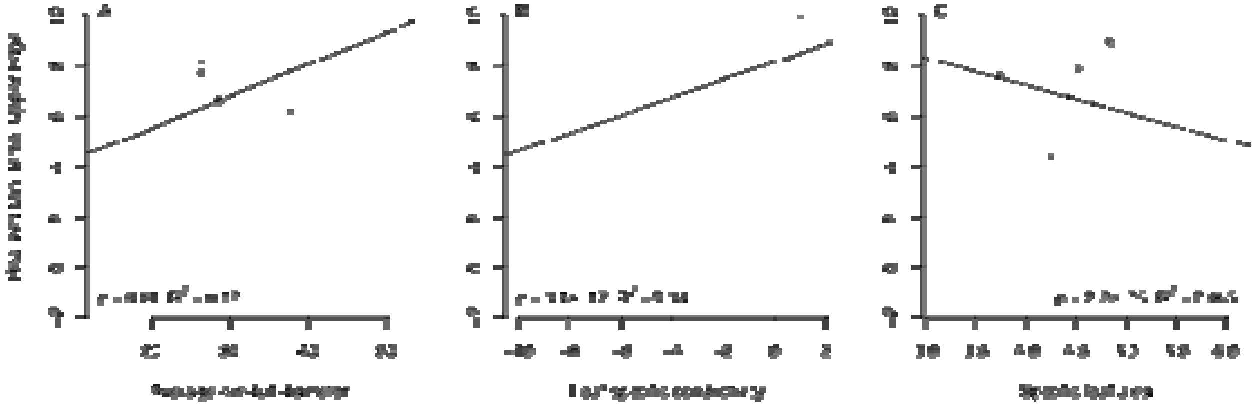

Figure 3.8. Relationships with the Upper Edge of Realized Minimum Temperature Suitability

Table 3.8. Predictive Models for the Upper Edge of Realized Minimum Temperature Suitability Nested Models Share the Same "Min" Number, with "S" Indicating the Model Selected Through Stepwise Regression. AIC results shown relate only to each nested set of models. All area-based measurements are log transformed; all data shown is centered, but not scaled. Significance: $p < 0.001$is shown in bold italic, $p < 0.01$is shown in bold, and $p < 0.05$is shown in italic.

	Realized Minimum Temperature Suitability, lower edge ~	AIC	*n*	M R^2	Adj R^2	Intercept	ACD	K_L	K_s	leaf N	max height	P_{50}	SLA	ACD:max height	ACD:P_{50}	ACD:SLA	max height:P_{50}	max height:SLA	P_{50}:SLA
min1	K_L + ACD + max height + P_{50} + SLA	68	15	0.82	0.73	-0.10	**21.60**	0.10	-	-	-1.70	**-1.30**	1.50	-	-	-	-	-	-
min1s	ACD + max height + P_{50} + SLA	67	15	0.82	0.75	-0.20	***22.40***	-	-	-	**-1.90**	***-1.40***	1.70	-	-	-	-	-	-
min2	K_s + P_{50} + K_L + max height + leaf N	88	16	0.65	0.48	0.90	-	0.40	0.50	-4.90	-1.90	0.00	-	-	-	-	-	-	-
min2s	K_L + max height + leaf N	84	16	0.64	0.55	0.90	-	*0.60*	-	-4.50	-1.30	-	-	-	-	-	-	-	-
min3	K_L + max height + leaf N + SLA + P_{50} + ACD	67	14	0.83	0.69	-0.10	**20.90**	0.10	-	-1.10	-2.00	*-1.30*	2.00	-	-	-	-	-	-
min3s	max height + SLA + P_{50} + ACD	63	14	0.83	0.75	-0.20	***22.40***	-	-	-	**-2.10**	**-1.40**	1.90	-	-	-	-	-	-
min4	(max height + SLA + P_{50} + ACD)^2	174	31	0.61	0.41	-0.40	5.60	-	-	-	*-2.30*	-0.20	0.20	-1.20	-2.40	*-22.00*	0.90	-1.30	0.80
min4s	max height + SLA + P_{50} + ACD + SLA:P_{50} + SLA:ACD	169	31	0.56	0.4	-1.10	*6.70*	-	-	-	**-2.30**	-0.50	1.40	-	-	**-27.00**	-	-	1.20

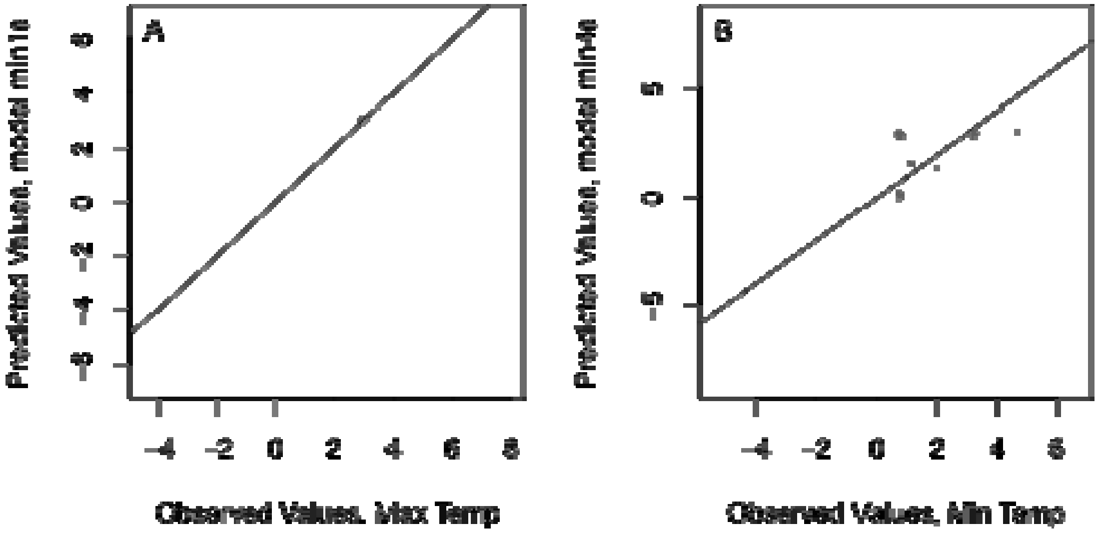

Figure 3.9. Multiple Regression Models for Minimum Temperature. Relationships between predicted and observed data are shown for two of the most explanatory models for the lower edge of realized low temperature suitability.

Multiple Trait Models for Predicting Minimum Temperature Suitability

Although ACD was only a moderately good predictor of minimum temperature suitability on its own, it was an important component of multiple regression models attempting to predict low temperature suitability. Models including ACD were able to explain 56 to 82 percent of variation in minimum temperature suitability (Table 3.8, Figure 3.9). In spite of its apparently strong initial relationship, K_L was retained only when ACD was omitted (min2s). By contrast, several traits that were not significantly correlated with minimum temperature suitability on their own—max height and P_{50}—were frequently retained as informative, and had significant effects, in several models. This suggests that hydraulic conductivity, as well as vessel size, may be important in determining frost survival at broader scales; alternatively, these may be strongly linked to conduit diameter. Leaf habit—i.e., evergreen versus deciduous phenology— was also tested, but was not found to be a significant component of any model. This may be due to the low number of winter-deciduous plants within the California flora, or to the conflation of drought-deciduous and winter-deciduous habits.

Discussion

This analysis explored how well ecophysiological traits correlate with climatic limits, with two goals. The first was to build a foundation for future mechanistic models of plant distribution. The second was to work toward a predictive tool to estimate climatic limits from ecophysiological traits, particularly for cases where these limits are not well understood or not in equilibrium with biogeographical ranges. We explored a large number of physiological traits in relation to climate suitability and found significant relationships with at least some traits for each aspect of climate examined. This suggests that it will be possible to meet both of these goals through the approach described here. Still more encouragingly, each aspect of climate appeared to associate with a distinct set of ecophysiological traits. For example, in our analysis, low precipitation and high maximum temperature were associated with overlapping, but ultimately distinct, sets of functional traits, particularly in multiple regression models. This suggests this physiological approach may be able to predict responses to these two aspects of climate separately.

Each of aspect of climate explored has a presumed “limiting” edge, in relation to mechanistic studies of plant stress (Levitt 1980). For instance, when considering precipitation, the lower edge of precipitation suitability—that is, the drier end—is generally thought of as the most limiting. For maximum temperature, this is the upper edge, and for minimum temperature, the lower edge. In this analysis, we observed strong correlations with *both* edges of suitability for all three aspects of climate—including the presumed non-limiting end. In fact, for minimum temperature, higher R^2 and lower p-values were observed in relation to the upper edge of the limit—the warmer end. This calls attention to the importance of considering these edges in future analyses. For most species, the “non-limiting” edge of their biogeographical range may not be set by physiological tolerance, but by competition with other species. The effect observed here may be a second-order; for instance, it may result from the climatic limits of competitors or other factors correlated with climate, such as fire. This highlights the difference between “fundamental environments" and "realized environments," an important distinction to consider in all climatic distribution models (Jackson and Overpeck 2000).

Several trait correlations were surprising, and merit further investigation. For instance, the negative correlation observed between precipitation limits and predawn Ψ_{min} and K_L is somewhat counterintuitive, but it is not entirely contrary to theory. In the case of Ψ_{min}, this may be due to an avoidance strategy—plants that are very drought tolerant often do not reach low water potentials; rather, they close their stomata and wait out dry conditions. The negative relationship between K_L and precipitation is probably driven by small leaf areas in arid regions. This allows plants to support higher leaf-level rates of transpiration for a given water potential gradient (i.e., in drier soils) than would otherwise be possible. By doing this, they are able to support continued growth, even under dry conditions (Maherali and DeLucia 2000).

The ability of all species to adjust these traits (plastically or genetically) will be an important part of their ability to persist in a changing climate (Jump and Penuelas 2005; Parmesan 2006; Franks, Sim, and Weis 2007). Also important will be the effects of changes in competitive structure as species are released from environmental limitations. For instance, a drop in the frequency of freezing may mean that upslope species are no longer protected from competition with their less-tolerant but faster-growing neighbors (Walther et al. 2002; Kelly and Goulden 2008; Loarie et al. 2009). Complex interactions such as these make an interesting starting point for future experimental work. As more ecophysiological trait data are incorporated into models like those presented here, we will obtain an improved sense of the fundamental climate space which each species is able to occupy. If we can move toward predicting species occurrence from these underlying parameters, rather than from observed limits, we will be able to better quantify areas where species might currently be expected to occur, but do not. Doing so is a first step toward an improved understanding of the role of competitive exclusion and incorporating competition in future predictions.

Several traits stood out as likely to reward further data collection. For instance, we would strongly suggest future researchers interested in the effects of maximum temperature collect A_{max} data, as this trait showed great promise, but was available for only a relatively small subset of the species examined. N_{area} and P_{50} also stood out as highly predictive, and greater overlap between all three of these traits is expected to improve the power of the models presented here.

Because our results are trait-specific, they provide a framework in which to consider species that are not in equilibrium with their communities, such as invasive species (Thuiller et al. 2005; Hijmans and Graham 2006; Richardson and Pyšek 2006). In theory, if key traits are known, it would be possible to use the multiple linear models developed here to predict temperature and precipitation suitability for any species. Such predictions would not be exact, but, with appropriate estimates of uncertainty, they might provide a guide for where best to focus eradication and surveillance efforts.

The same framework also suggests directions for applied land management. In addition to invasive species, predictions could also be made for other species that are either too rare or too poorly cataloged to be included in MaxEnt models. This offers an alternative method for estimating the vulnerability of such species to changing climatic conditions. The type of traits included help make such models accessible. Many, such as SLA and leaf size, are easy to measure, and some, such as maximum height, are readily available in floras (Cornelissen et al. 2003; Moles et al. 2009). Thus, ecophysiological expertise is not required in order to use potential tools that might be developed using this approach.

This last point highlights the potential importance of collecting functional trait data from across the state for future conservation efforts. For instance, further development of an ecological flora of California could make many more measurements of these traits easily accessible to a wide audience (Fitter and Peat 1994; Ackerly 2006). This would potentially allow land managers and conservation workers to make predictions about how any one species might be affected in the face of rising temperatures and changing rainfall conditions.

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Section 4: Fire, Climate, and the Distribution of Shrub Life-history Strategies Across the California Landscape

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Introduction

Spatial modeling is frequently used to connect species distributions to underlying environmental variables. Such models can be useful when trying to predict the impacts of climate change on the distribution of important species. However, models that incorporate community-level data may be more useful for predicting impacts on a large number of species or species that might be overlooked by models that focus on individual species (Ferrier and Guisan 2006). Furthermore, since species within a community vary in their functional strategies, it may be most useful to create models for groups of species based on their functional similarity rather than from broad vegetation type descriptions (e.g., Franklin et al. 2001, 2004; Syphard et al. 2006). In addition, models based on functional groups allow us to generalize beyond the study system and better understand the biological basis for differences among species.

In California shrublands, plants are often categorized into functional groups based on their observed response to wildfire (Hanes 1971; Keeley 1991, 1995; Keeley et al. 2012). These authors have identified three distinct post-fire strategies of sclerophyllous woody shrubs. Facultative sprouters (F) consist of species that employ both vegetative resprouting and fire-stimulated seed germination following top-kill by crown fire. Non-sprouters (NS) do not resprout, but re-establish via fire-stimulated seed germination. Obligate resprouters (R) produce seeds that are killed by fire but survive by vigorous resprouting from underground structures (e.g., lignotubers, roots). Previous fieldwork (Franklin et al. 2004; Keeley 1991; Zedler et al. 1983) and modeling (Franklin et al. 2001; Syphard et al. 2006) with southern California chaparral communities have shown that there is a link between life-history strategy composition and fire frequency. Generally, fire regimes characterized by very frequent (< 20 years) or very unpredictable fire favor R species; whereas, very predictable fire regimes that create consistent post-fire gaps encourage post-fire seeding strategies (Keeley et al. 2012).

Previous studies have also shown that post-fire life-history strategies are linked to suites of traits that may correspond to features of the environment other than wildfire, in particular tolerance of the seasonal water deficit that is characteristic of habitats in California’s Mediterranean-type climate (Ackerly 2004; Pratt et al. 2008; Jacobsen et al. 2007). These studies find that post-fire seeding species are more resistant to water stress-induced tissue damage; whereas, R species are more sensitive to drought stress but avoid damage by utilizing deep roots and by establishing in moister microsites. These divergent water use strategies may result in different habitat requirements for members of different life-history strategies. For example, Hanes’ (1971) extensive field study of community composition in southern California chaparral communities revealed that *Adenostoma fasciculatum* (a common facultative sprouter) dominates drier south-facing slopes; whereas, the cooler, moister north-facing slopes are frequently dominated by obligate resprouting and non-sprouting species. Similarly, Meentemeyer and Moody (2002) used spatially explicit models to show that R species and NS species inhabit different positions along a moisture gradient, with R species being less common in more xeric sites. These studies indicate that water availability may be an important determinant of life history strategy distributions in California shrublands, but the extent of such patterns has yet to be explored.

Although previous studies have shown relationships between life history strategies of California shrubs and various aspects of the environment, we are unaware of any studies that attempt to define the distribution of these life history strategies with respect to multiple environmental variables on a large landscape scale (i.e., the State of California). Our study utilizes a large scale species distribution dataset, together with spatially interpolated climate surfaces and a recent model of fire frequencies in relation to climate, to address this goal. The benefit of such an analysis is the ability to elucidate which features of the environment are most important in determining the distribution of life-history strategies in California shrublands. In addition, such information would serve as a foundation for predictive models that can assess the differential impacts of climate change on each life-history strategy, providing information that would be overlooked by more general community-level models or those that make untested assumptions about which environmental variables are most informative.

Methods

Species distribution and percent cover data from the 1930s Weislander Vegetation Type Map (VTM) were used to assess the distribution of life-history strategies in California shrublands with respect to four environmental variables: precipitation (Precip), maximum summer temperature (Tmax), minimum winter temperature (Tmin), and fire proneness (Fire). A multiple regression model was used to assess the relationship between percent cover of each life history strategy and these environmental variables.

Weislander Vegetation Type Map (VTM)

The 1930s VTM dataset contains species composition and percent cover data for 18,000 plots across a range of California's native plant communities. In our study, a VTM species list and all available plot data were downloaded from the Weislander Vegetation Type Mapping Project: www.vtm.berkeley.edu. This publicly available data included the plot locations that had been digitized from the original hard-copy maps. Our study focused on plots with > 50 percent cover attributed to shrubs categorized into one of three distinct life history strategies (see below). This criteria was used in order to focus our hypothesis testing to dense shrub-dominated communities and exclude shrub distribution patterns in communities dominated by other life-forms (e.g., grasslands, forests) or those with low shrub densities. In total 2,908 VTM plots were used in the analysis (Figure 4.1).

Life Form and Life History Strategy Information

Using the digital VTM species list, a database was created containing life-form and life-history information for each species. Life-form (i.e., grass, herb, shrub, shrub/tree, tree) was recorded for each species based on descriptions from the Jepson Online Interchange (http://ucjeps.berkeley.edu/interchange/) and Calflora (http://www.calflora.org/). We identified 340 species (including subspecies and varieties) as shrub or shrub/tree. The shrub species were grouped into the three functional groups described above based on their published life-history response to wildfire. We were able to locate published life history designations for 212 of the 340 shrub species, including all of the 100 most common shrubs in the VTM dataset. Each life-history strategy (LHS) was found in all shrub-dominated regions surveyed in the VTM dataset (Figure2).

Environmental Variables

High-resolution (30-arc-second) land averages for Precip, Tmax, and Tmin over a 30-year interval (1971–2000) were downloaded from the PRISM Climate Group at Oregon State University, http://www.prismclimate.org. Spatially explicit relative fire probability across California was determined by Parisien and Moritz (2009) using a novel approach to model the "habitat" of fire with respect to 25 environmental variables related to climate, vegetation (fuel), and ignition (Figure 4.1).

Analysis

Multiple regression analyses were conducted in R 2.14.0 (R Development Core Team 2011), treating all plots as independent units. Cover data was converted to relative proportions for each LHS in each plot by dividing the observed cover values by the cumulative cover for all three LHSs. Relative cover values were transformed using the logit transformation (Warton andHui 2011). Environmental variables were converted to normalized values. Both linear and non-linear (quadratic) effects were analyzed using a generalized linear model (glm). Akaike information criterion (AIC) was used to select the best model, testing all combinations of the independent environmental variables. Delta AIC values for each environmental variable in each model were calculated to assess the relative importance of each variable to the model. Overall $r^2$of each model was calculated as 1-residual deviance/null deviance (Menard 2000). Climate-only, fire-only, and combined models were analyzed to assess potential autocorrelation between fire and climate variables, since climate was also used to derive the fire layer (Table2). Residuals from the combined models were examined visually to determine potential spatial autocorrelation in the dataset (Figure 4.3).

Results

The distribution of relative cover values with plot locations revealed distinct spatial patterns for each life history strategy (LHS) (Figure 4.2). Facultative sprouters (F) were more common in southern and central California Coast Ranges. Obligate resprouters (R) had higher relative cover in plots in the Sierra Nevada Range. Non-sprouters (NS) had relatively low cover values throughout the range, with more high cover plots in the Sierra Nevada. Although there were differences in relative cover between LHSs, all three were present throughout the range of plots.

Overall r^2 was highest (and AIC lowest) for models that incorporated linear and quadratic effects, combined climate and fire variables, and logit transformed data (Table 4.2). F cover had a positive linear relationship with Fire and Tmin, and a negative linear relationship with Precip and Tmax. R cover had a negative linear relationship with Fire and Tmin, and positive relationship with Precip and Tmax. NS cover had a positive linear relationship with Precip and negative relationship with Tmax. In general, quadratic relationships were less important than linear relationships (except for NS, which had weak quadratic relationships with Fire and Tmin when linear relationships were non-significant). For this reason, discussion of results will focus on linear relationships between LHS and environmental variables.

Discussion

Facultative Sprouter Life History Strategy

The model for facultative sprouters (F) indicates that they are more common in sites with low precipitation, high fire probability, warmer winter temperatures, and cooler summer temperatures (Table 4.2). These patterns are consistent with the higher relative cover of F in southern California Coast Ranges (Figure 4.2), where summer/winter temperatures are more moderate, precipitation is lower, and fire frequency is higher than more northern and inland sites. These patterns are also consistent with previous studies that indicate the relationship between F species and drought, freezing temperatures, and fire probability.

F species are mainly represented by *Adenostoma fasciculatum, Artemisia californica, Salvia* spp., and resprouting species of *Ceanothus* and *Arctostaphylos* (Table 4.1). Hanes (1971) discovered that many of these species are more common on dryer south-facing slopes in southern California chaparral communities than NS or R species, possibly pointing to a heightened affinity for dry environments. In addition, a few studies have reported increased sensitivity of facultative sprouters to freezing temperatures relative to non-sprouters (Langan et al. 1997; Ewers et al. 2003). Finally, F species are dependent on fire for reproduction, a trait that is adaptive under certain fire regimes characterized by high fire predictability (Keeley et al. 2012).

Obligate Resprouter Life History Strategy

Obligate resprouters (R) are more common in sites with high precipitation, low fire probability, low winter temperatures, and high summer temperatures (Table 4.2). As with F species, these relationships between R species and environmental variables are consistent with their position along geographic gradients of precipitation, temperature, and fire. The more northern and inland distribution of high R species cover correlates with the higher precipitation, higher seasonal variation in temperature, and lower fire frequency that characterizes the Sierra Nevada. The higher relative cover of R species in these sites may be related to attributes of this LHS related to drought tolerance and low fire frequency.

The list of R species consists mainly of scrub oaks (*Quercus dumosa, Quercus wislizenii*), *Cercocarpus betuloides,* and *Heteromeles arbutifolia*. These species have been classified as "drought avoiders" that exhibit behavioral (anisohydry), morphological (deep roots), and spatial (preference for moist sites) strategies for avoiding drought stress (Pratt et al. 2008; Ackerly 2004; Hanes 1971; Meentemeyer and Moody 2002). Additionally, R species have fire-independent seedling recruitment, meaning that their seedlings require long fire return intervals to establish in the understory (Keeley 1992). As a result, the success of the R life history strategy may be enhanced in areas with less predictable fire regimes characterized by long fire-free periods (Keeley et al. 2012).

Non-Sprouter Life History Strategy

Non-sprouters (NS) had low relative cover throughout the range of plots (Figure 4.2) and were completely absent in more plots than either F or R species. The NS model had the lowest overall r^2 of all models tested, presumably due to the aforementioned low relative cover and high absence in VTM plots. As a result, conclusions for NS species are more difficult to draw than those for F and R species. That being said, NS species did have higher relative cover in sites with high precipitation and low summer temperatures (Table 4.2), which may relate to the higher relative cover in northern California plots (Figure 4.2). The fire-only model did not provide any explanatory power, so climate-only and climate-fire models were essentially equivalent (AIC values within 2 units). Thus, there is no indication in these data of an effect of the fire layer on NS frequencies.

NS species are represented by *Ceanothus* and *Arctostaphylos spp.* that rely wholly on post-fire seed recruitment following stand-replacing crown fires. As with F species, the requirement of fire to reproduce is hypothesized to be advantageous in environments with highly predictable fire regimes (Keeley et al. 2012). However, NS species may also be sensitive to high frequency fire if fire return intervals are shorter than the time necessary to re-establish a belowground seedbank (Zedler et al. 1983; Jacobsen et al. 2004; Syphard et al. 2006). Furthermore, the advantage of the fire-recruitment strategy is thought to be greatest in areas where competition between post-fire seedlings and resprouts is reduced (Keeley et al. 2012). Vegetation communities with more open canopies and greater spacing between shrubs may reduce competition between seedlings and resprouts in the early post-fire environment, thus allowing the full benefits of the NS strategy to be realized. In our study we tried to focus on plots with higher densities of shrubs, eliminating the more open plots from analyses. Doing this may have eliminated some sites that are important for capturing the realized niche of NS species.

Climate Change Predictions

Climate change predictions for the next century include increases in temperature, changes in precipitation frequency and amount, and changes in fire regimes (Meehl et al. 2007; Westerling and Bryant 2008; Krawchuk et al. 2009). The distribution of shrub LHSs in our dataset illustrate that all three strategies are represented across the California landscape, although there are significant variations in the relative importance of each in different regions (Figure 4.2). This means that as climate and fire changes within these landscapes the relative importance of LHSs is also likely to change. Furthermore, the results of our multivariate models reveal significant patterns for the distribution of shrub LHSs in relation to minimum temperature, precipitation, and fire probability. Our models will serve as a foundation for testing various hypotheses related to future climate and other anthropogenic changes. Based on our results, we hypothesize that climate change trends toward warmer winter temperatures will favor F species. Increasing rainfall will favor NS and R, while reduced precipitation will favor F. Increasing fire probability will favor F species, while decreasing fire probability will favor R species. It is important to note that changes to climate and fire regimes are likely to occur at different rates, making simple predictions based on linear relationships between LHS and environmental variables difficult. However, our models can be combined with various scenarios for future climate and fire to tease out the more complex patterns of predicted change.

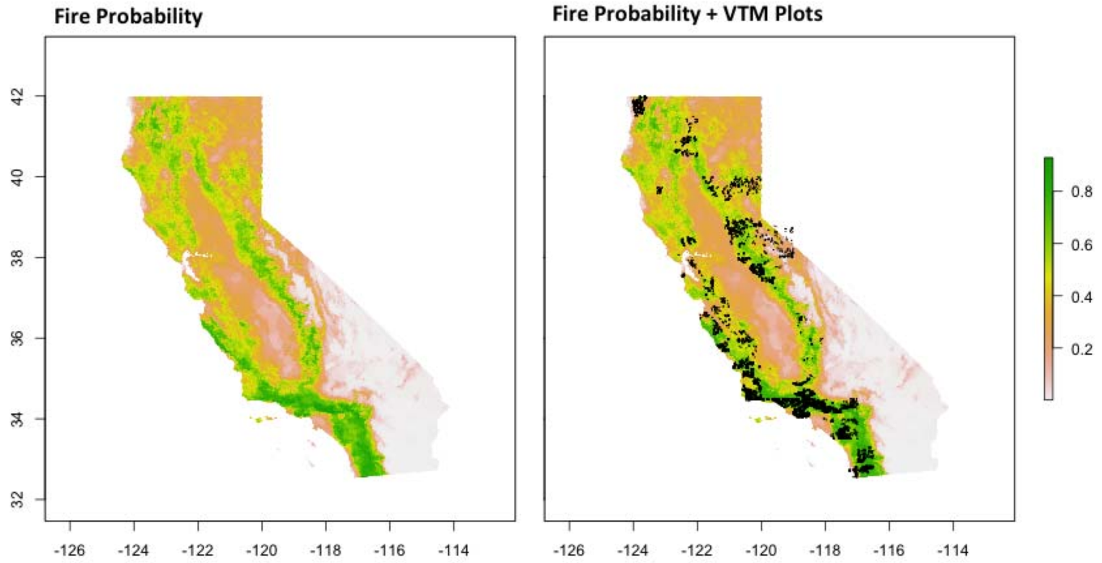


Figure 4.1. Map of Fire Proneness and Plots Used in Regression Analyses. The fire suitability map depicts the relative probability that fire will occur in a given location (Parisian and Moritz 2009) and geo-referenced plot locations of VTM plots used in multivariate analyses (see Methods).

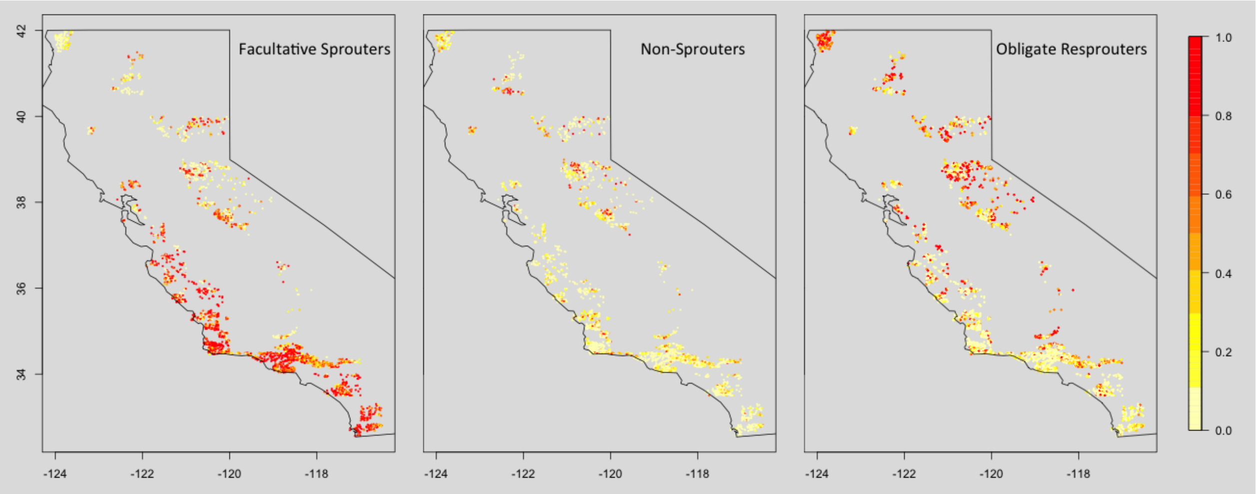


Figure 4.2. Relative Cover of Life-History Strategies in VTM Plots. Warmer colors indicate high relative cover. Facultative sprouting species have higher relative cover in plots in southern and central California coastal ranges. Non-sprouters have relatively low cover throughout the range but have higher relative cover in some Sierra Nevada plots. Resprouters have higher relative cover in Sierra Nevada and northern California plots.

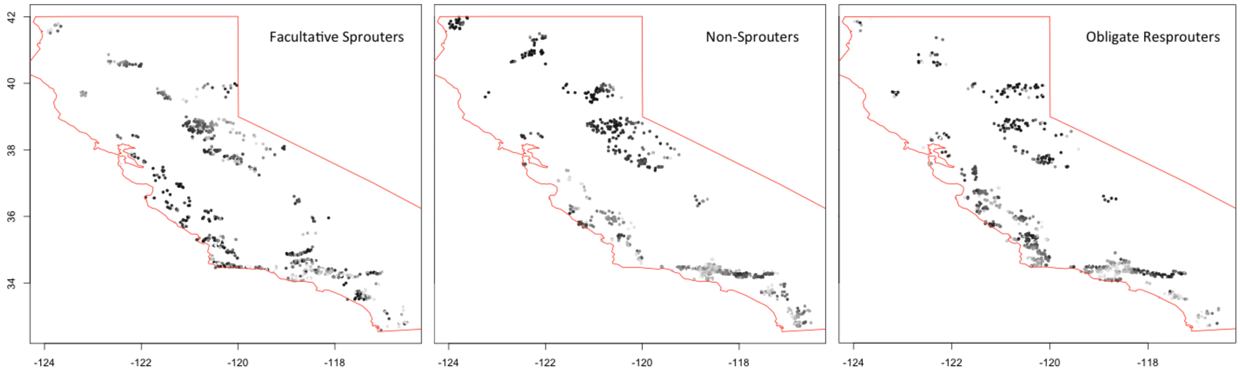
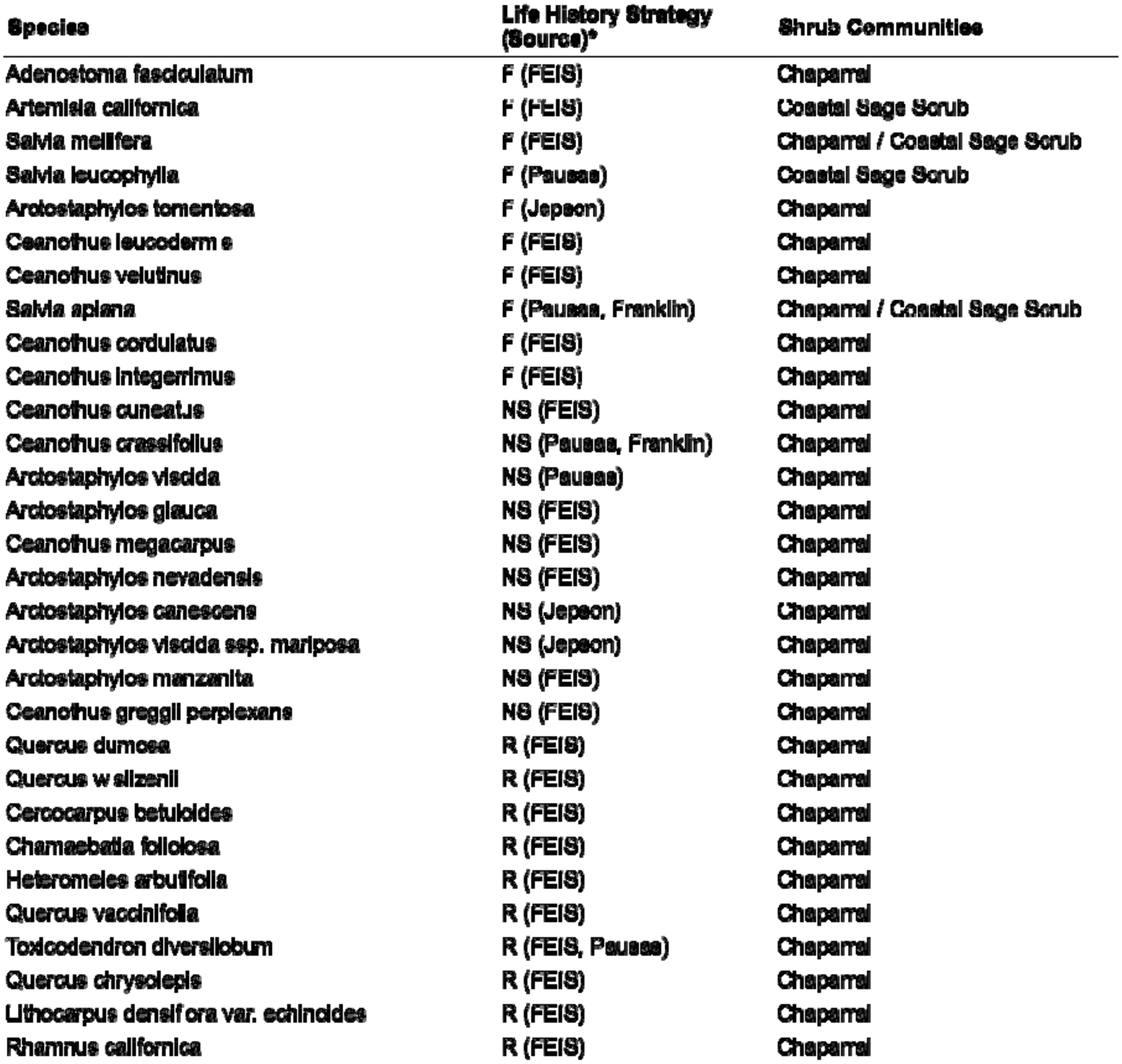


Figure 4.3. Predicted vs. Actual Frequencies for Life-History Strategies in VTM Plots. Models used to produce predicted frequency values combine climate and fire variables (Table 4.2). Dark gray points represent model overprediction (modeled values higher than observed values), and light gray points represent underprediction.

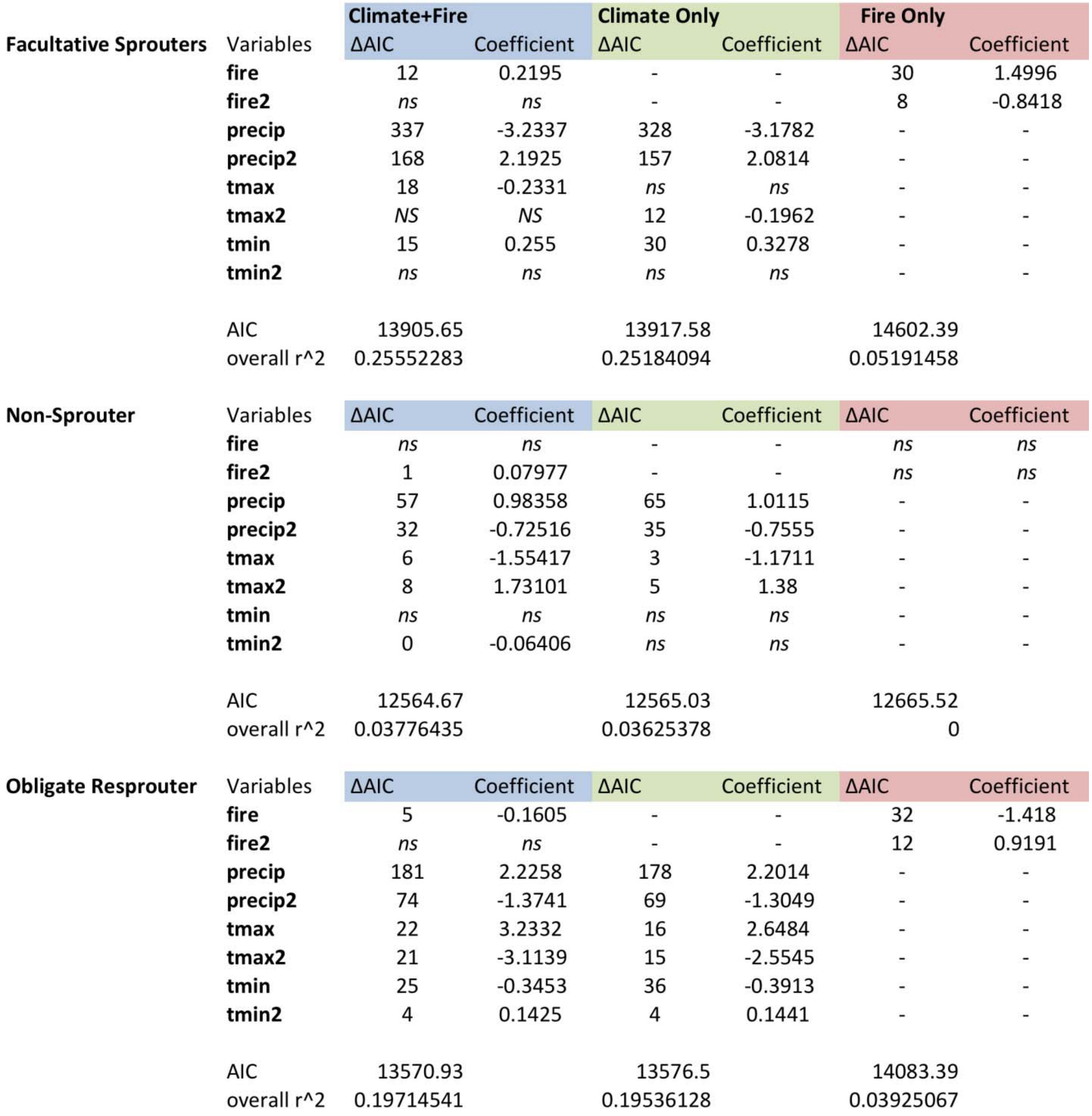
Table 4.1. List of 10 Most Common Species (Listed from Most to Least Common) from Each Life-History Strategy and the Shrub Communities in Which They Commonly Occur



Species	Life History Strategy (Source)*	Shrub Communities
Adenostoma fasciculatum	F (FEIS)	Chaparral
Artemisia californica	F (FEIS)	Coastal Sage Scrub
Salvia mellifera	F (FEIS)	Chaparral / Coastal Sage Scrub
Salvia leucophylla	F (Pausas)	Coastal Sage Scrub
Arctostaphylos tomentosa	F (Jepson)	Chaparral
Ceanothus leucodermis	F (FEIS)	Chaparral
Ceanothus velutinus	F (FEIS)	Chaparral
Salvia apiana	F (Pausas, Franklin)	Chaparral / Coastal Sage Scrub
Ceanothus cordulatus	F (FEIS)	Chaparral
Ceanothus integerrimus	F (FEIS)	Chaparral
Ceanothus cuneatus	NS (FEIS)	Chaparral
Ceanothus crassifolius	NS (Pausas, Franklin)	Chaparral
Arctostaphylos viscida	NS (Pausas)	Chaparral
Arctostaphylos glauca	NS (FEIS)	Chaparral
Ceanothus megacarpus	NS (FEIS)	Chaparral
Arctostaphylos nevadensis	NS (FEIS)	Chaparral
Arctostaphylos canescens	NS (Jepson)	Chaparral
Arctostaphylos viscida ssp. mariposa	NS (Jepson)	Chaparral
Arctostaphylos manzanita	NS (FEIS)	Chaparral
Ceanothus greggii perplexans	NS (FEIS)	Chaparral
Quercus dumosa	R (FEIS)	Chaparral
Quercus wislizenii	R (FEIS)	Chaparral
Cercocarpus betuloides	R (FEIS)	Chaparral
Chamaebatia foliolosa	R (FEIS)	Chaparral
Heteromeles arbutifolia	R (FEIS)	Chaparral
Quercus vaccinifolia	R (FEIS)	Chaparral
Toxicodendron diversilobum	R (FEIS, Pausas)	Chaparral
Quercus chrysolepis	R (FEIS)	Chaparral
Lithocarpus densiflora var. echinoides	R (FEIS)	Chaparral
Rhamnus californica	R (FEIS)	Chaparral

* FEIS = USDA Forest Service Fire Effects Information System: http://www.fs.fed.us/database/feis/; Jepson = The Jepson Manual, second edition; Pausas = Pausas et al. 2004; Franklin = Franklin et al. 2004

Table 4.2. Model Summaries for Multiple Regression Analyses. The best model for each life-history strategy incorporated linear + quadratic effects and logit transformed data (yellow). Overall, r^2 was used for model comparison and was calculated as: 1-Residual Deviance/Null Deviance (Menard 2000). *ns* denotes a non-significant result.



		Climate+Fire		**Climate Only**		**Fire Only**	
Facultative Sprouters	Variables	ΔAIC	Coefficient	ΔAIC	Coefficient	ΔAIC	Coefficient
	fire	12	0.2195	-	-	30	1.4996
	fire2	*ns*	*ns*	-	-	8	-0.8418
	precip	337	-3.2337	328	-3.1782	-	-
	precip2	168	2.1925	157	2.0814	-	-
	tmax	18	-0.2331	*ns*	*ns*	-	-
	tmax2	*NS*	*NS*	12	-0.1962	-	-
	tmin	15	0.255	30	0.3278	-	-
	tmin2	*ns*	*ns*	*ns*	*ns*	-	-
	AIC	13905.65		13917.58		14602.39	
	overall r^2	0.25552283		0.25184094		0.05191458	
Non-Sprouter	Variables	ΔAIC	Coefficient	ΔAIC	Coefficient	ΔAIC	Coefficient
	fire	*ns*	*ns*	-	-	*ns*	*ns*
	fire2	1	0.07977	-	-	*ns*	*ns*
	precip	57	0.98358	65	1.0115	-	-
	precip2	32	-0.72516	35	-0.7555	-	-
	tmax	6	-1.55417	3	-1.1711	-	-
	tmax2	8	1.73101	5	1.38	-	-
	tmin	*ns*	*ns*	*ns*	*ns*	-	-
	tmin2	0	-0.06406	*ns*	*ns*	-	-
	AIC	12564.67		12565.03		12665.52	
	overall r^2	0.03776435		0.03625378		0	
Obligate Resprouter	Variables	ΔAIC	Coefficient	ΔAIC	Coefficient	ΔAIC	Coefficient
	fire	5	-0.1605	-	-	32	-1.418
	fire2	*ns*	*ns*	-	-	12	0.9191
	precip	181	2.2258	178	2.2014	-	-
	precip2	74	-1.3741	69	-1.3049	-	-
	tmax	22	3.2332	16	2.6484	-	-
	tmax2	21	-3.1139	15	-2.5545	-	-
	tmin	25	-0.3453	36	-0.3913	-	-
	tmin2	4	0.1425	4	0.1441	-	-
	AIC	13570.93		13576.5		14083.39	
	overall r^2	0.19714541		0.19536128		0.03925067	

Conclusion

Our study examined data from extensive vegetation surveys of the California flora to ask the question: How does the distribution of native California shrub life-history strategies relate to climate and fire? By using life-history strategies as the unit of our analysis instead of individual species or broadly defined vegetation types, our study can provide information that is both more comprehensive and informative. The results of our multivariate models reveal that native California shrub distributions are significantly related to multiple features of the environment in ways that are consistent with prior studies of species physiology and landscape scale distributions. This analysis moves us closer to understanding what environmental variables are most important to California shrub distributions and provides a foundation for future models that can predict the impacts of climate change on these important components of the California landscape.

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Glossary

ACD	average conduit diameter
AIC	Akaike information criterion
AR4	Fourth assessment of the IPCC
BIC	Bayesian information criterion
DEM	digital elevation model
DJF	December, January, February
F	Facultative sprouters
FEIS	USDA Forest Service Fire Effects Information System
Fire	fire proneness
GFDL	Geophysical Fluid Dynamics Laboratory
IPCC	Intergovernmental Panel on Climate Change
glm	generalized linear model
JJA	June, July, August
LHS	life-history strategy
N	nitrogen
NRCS	Natural Resources Conservation Service
NS	Non-sprouters
PCM	parallel climate model
Precip	precipitation
PRISM	Parameter-elevation Regressions on Independent Slopes Model
PVM	probabilistic vegetation model
R	resprouters
SDM	species distribution model
SLA	specific leaf area
STATSGO	U.S. General Soil Map
Tmax	maximum summer temperature
Tmin	minimum winter temperature
USDA	United States Department of Agriculture
USGS	United States Geological Survey's
VTM	Weislander Vegetation Type Map