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Geography of Plant Exposure to Global Change in the California Floristic Province

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Geography of Plant Exposure to Global Change in the California Floristic Province

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by

Miranda Brooke Rose

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Dedication

To my family, but especially to my grandmother, Mary Brooks Rose, who loved learning more than anyone I have ever known.

ABSTRACT OF THE DISSERTATION

Geography of Plant Exposure to Global Change in the California Floristic Province

by

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Global change is driving biodiversity loss globally and Mediterranean-type ecosystems, like those found in the California Floristic Province (CFP), are among the most diverse and threatened natural systems. Habitat loss due to climate and land use change amplifies species' extinction risks, with some species being more exposed than others due to their rarity as well as their geographic distributions. As we attempt to assess and model species' extinction risk, it is imperative to address and communicate the uncertainty introduced by each modeling component, especially as new approaches emerge, and assess this uncertainty spatially. While estimating species-level vulnerability is essential for prioritization, it is equally important to understand how habitat dynamics may vary across species ranges in response to global change. In this dissertation, I first assessed the relationships between species' rarity, geography, and exposure to climate and land use change for 106 plant species found in the CFP. I found that although small-ranged species in flat areas with high climate velocity tend to be the most exposed to climate change, those found at low elevations are at the highest risk of habitat loss via land use change. Next, I evaluated predictions of projected habitat suitability under different climate models, emissions scenarios, and species distribution modeling consensus (model averaging) approaches. Surprisingly, these results showed that vulnerability predictions made by different model averaging techniques can differ substantially, if the models are projected into geographic areas outside of species' ranges. Finally, I assessed how habitat suitability change varied across species ranges as a function of geographic features, including latitude, distance to coast, elevation, and topographic heterogeneity. I found substantial variation in the geography of species habitat change, with some, mostly montane species, showing potential refugia in high elevation areas regardless of climate model, while other species, such as those found in coastal sage scrub and chaparral, exhibited variability in the location of refugia depending on the magnitude and direction of climatic change. This dissertation emphasizes the spatial heterogeneity of global change in the CFP and the importance of conducting geographic assessments of species' vulnerability.

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Introduction

Human activities are causing rapid and widespread loss and redistribution of biodiversity globally (Ceballos et al., 2015; Pecl et al., 2017; Tilman et al., 2017; Tittensor et al., 2014). The conversion of natural habitat to urban and agricultural land, i.e., land use change, is estimated to have reduced the number of species in some habitats by over 75% (Newbold et al., 2015). Climate change, driven by carbon emissions, is predicted to further accelerate species loss as global temperatures continue to rise and precipitation patterns become increasingly variable (Urban, 2015). Anthropogenic impacts on natural systems are particularly severe in biodiversity hotspots (Myers et al., 2000), which are areas of high species richness that face disproportionate threats from human activities, both directly and indirectly (Trew and Maclean, 2021; Habel et al., 2019).

Mediterranean-type ecosystems (MTE), found in California, the Mediterranean Basin, the Cape Region of South Africa, Chile, and southern Australia, are among the most biodiverse and threatened ecosystems on earth (Myers et al., 2000). With over 2,000 endemic vascular plant species (Baldwin et al., 2012), the California Floristic Province (CFP), defined as that area of western North America with a MTE located almost entirely within California (Figure 1.1), is a geographically diverse biodiversity hotspot with high conservation importance (Burge et al., 2016). This region is also particularly vulnerable to the effects of climate change, agricultural expansion, and urbanization. These landscape transformations can significantly reduce the amount and alter the spatial distribution of species suitable habitat, often in ways that are geographically complex (Ackerly et al., 2010; Beltrán et al., 2014).

Identifying species that are most vulnerable to anthropogenic change, the characteristics that make them vulnerable, and the geographic locations where they face the highest risks are key goals of conservation science (Davidson et al., 2017). While multiple factors contribute to a species' vulnerability to environmental change, these factors can be grouped into three distinct categories: sensitivity, adaptive capacity, and exposure (Williams et al., 2008). Sensitivity reflects a species' physiological, ecological, and life history traits that determine its response to environmental change, e.g., species with low reproductive rates may be more sensitive to rising temperatures (Chessman, 2013). A species' adaptive capacity represents its ability to adapt in response to changing conditions and is influenced by factors such as genetic diversity, plasticity, and the potential for rapid evolutionary responses (Nicotra et al., 2015). Finally, exposure refers to the "the extent of climate change likely to be experienced by a species or locale" (Dawson et al., 2011). Exposure is often measured by the change in suitable habitat area for a given species (Serra-Diaz et al., 2014). Declines in species' habitat availability amplifies their risk of extinction, underscoring the significance of conducting exposure assessments as a critical step in comprehensively evaluating species' vulnerability to extinction in response to global change.

The risk of extinction is inherently higher for rare vs. common species due to their small range sizes, low abundances, and specific habitat requirements (Baillie et al., 2004; Leao et al., 2014; Ohlemüller et al., 2008; Staude et al., 2020). Of these factors, range size often plays the largest role in determining species extinction risk–with narrowly distributed species being much more vulnerable than wide-ranging taxa (Harnik et al., 2012). Despite this pattern, both small- and large-ranged plant species are projected to lose significant amounts of suitable habitat under global change scenarios (Thuiller et al., 2005) emphasizing the importance of exploring this pattern across a variety of species. In addition to rarity, species geographic position can also make species more or less vulnerable to the impacts of global change (Broennimann et al., 2006). For example, high elevation species may be especially exposed to climate change due to amplified increases in temperature in mountainous areas (Nogués-Bravo et al., 2007), while those at lower elevations, near human developments, may be the most vulnerable to habitat loss via land use change (Monteiro et al., 2011).

Furthermore, understanding the separate and additive effects of climate change and land use change on species vulnerability is crucial for effective conservation and management strategies (Santos et al., 2021). Some species may have characteristics that make them particularly vulnerable to one driver over the other, based on their rarity and geographic distributions. For example, species with narrow environmental tolerances may be especially susceptible to climate change (Thuiller et al., 2005), those that are found in future development zones are likely most vulnerable to urban expansion and agricultural development (Mendes & de Marco, 2018). By studying the combined influences of climate change and land use change on species vulnerability at broad spatial scales, researchers can identify the characteristics that make certain species more vulnerable. This knowledge can help prioritize species for protection and guide conservation action to mitigate the impacts of these change drivers on biodiversity.

Species distribution models (SDMs) are among the most widely used tools for predicting species' exposure to global change (Araújo et al., 2011; Thomas et al., 2004; Thuiller, 2004; Warren et al., 2018). These models relate species occurrences to a suite of environmental predictor variables, often using statistical and machine learning methods, to make empirical predictions about species' potential geographic range (Franklin, 2010). SDM outputs are especially useful for conservation prioritization and vulnerability assessments because they provide spatially explicit estimates of where a species is likely to occur or, conversely, which areas are likely to experience habitat reduction under future global change scenarios. However, different SDM algorithms, greenhouse gas concentration pathways, and climate models can produce vastly different spatial predictions of species' habitat suitability (Buisson et al., 2010; Conlisk et al., 2013; Syphard & Franklin, 2009). "Consensus" approaches that combine the outputs of multiple algorithms used to model species distributions through model averaging have emerged as a tool for addressing SDM-based uncertainty (Araújo & New, 2007). However, the influence of using different consensus approaches, e.g., median vs. performance weighted average, in predicting species' vulnerability to climate change has not been extensively studied.

Although species-level estimates of vulnerability provide useful information for prioritizing species for conservation and management efforts, exposure to global change will vary across species' ranges. However, in climate change vulnerability research that relies on SDM outputs, habitat suitability maps are often binarized to distinguish suitable vs. unsuitable areas, resulting in information loss (Guillera-Arroita et al., 2015). Though this is sometimes necessary for conservation prioritization and communication, exploring how continuous habitat suitability changes across species' ranges can elucidate which landscape features may be important for mitigating–or exacerbating–the influence of global change on species suitable habitat. Furthermore, understanding the potential dynamics of habitat suitability within species' ranges is critical for guiding conservation efforts that can target at-risk habitats while protecting those habitats that are predicted to remain relatively stable (Thorne et al., 2020).

The goals of this dissertation were to 1) identify the rarity and geographic traits that make plant species more (or less) vulnerable to climate and land use change, 2) quantify the sources of uncertainty when conducting spatial vulnerability assessments when using consensus-based species distribution models, and 3) assess the geographic characteristics of species-specific habitat refugia under climate change. The focal species of this work include a subset of endemic plants found in the California Floristic Province that range in their life history traits, growth forms, vegetation associations, and biogeographic characteristics. They range from the critically endangered Torrey pine (*Pinus torreyana*), a conifer that is found only in coastal San Diego County and Santa Rosa and San Miguel Islands, to California Blue Oak (*Quercus douglassii*), a tree that is widespread through the foothills of the Central Valley of California, North Coast Ranges, and San Francisco Bay Area.

Species are responding idiosyncratically to global change and predictive frameworks are needed to identify the characteristics that make species more (or less) vulnerable to extinction (Geppert et al., 2020; Gibson-Reinemer & Rahel, 2015). Furthermore, the inherent spatial heterogeneity of global change highlights the critical importance of conducting geographic assessments of species' vulnerability. This approach recognizes that vulnerability is not uniformly distributed across a landscape and emphasizes the need to consider geographic features that can either intensify or mitigate the impacts of global change on species populations. Exposure assessments, like the one presented in this dissertation, provide an opportunity to examine the relationship between species' characteristics and their range-wide exposure to climate and land use change. Additionally, this work allows for the evaluation of how different modeling components contribute to the uncertainty in estimating spatial vulnerability as well as how species' exposure may vary across their ranges – essential steps for targeted conservation and management strategies that address species' vulnerabilities within their spatial context.

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Chapter 1

Rarity, geography, and plant exposure to global change in the California Floristic Province

Abstract

Rarity and geographic aspects of species' distributions mediate their vulnerability to global change. We explore the relationships between species' rarity and geography and their exposure to climate and land use change in the California Floristic Province, a biodiversity hotspot. For 106 terrestrial plant species, we estimated four rarity traits: range size, niche breadth, number of habitat patches, and patch isolation; and three geographic traits: mean elevation, topographic heterogeneity, and distance to coast. We used species distribution models to measure species exposure – predicted change in continuous habitat suitability within currently occupied habitat –under climate and land use change scenarios. Using regression models, decision-tree models, and variance partitioning, we assessed the relationships between species' rarity, geography, and exposure to climate and land use change. Rarity, geography, and greenhouse gas emissions scenario explained >35% of variance in climate change exposure and >61% for land use change exposure. While rarity traits (range size and number of habitat patches) were most important for explaining species' exposure to climate change, geographic traits (elevation and topographic heterogeneity) were more strongly associated with species' exposure to land use change. Species with restricted range sizes and low topographic heterogeneity across their distributions were predicted to be the most exposed to climate change, while species at low elevations were the most exposed to habitat loss via land use change. However, even some broadly distributed species were projected to lose >70% of

their currently suitable habitat due to climate and land use change if they are in geographically vulnerable areas, emphasizing the need to consider both species' rarity traits and geography in vulnerability assessments.

Introduction

Human activity is driving rapid biodiversity loss, with current extinction rates at least 100 times greater than background rates for some taxa (Ceballos *et al.*, 2015). While land use change is the primary human activity driving species loss (Newbold *et al.*, 2015), anthropogenic climate change impacts on species geographic distributions have been observed globally (Chen *et al.*, 2011). Predictive frameworks for identifying vulnerable species are urgently needed in the face of rapid climate and land use change to anticipate where, and for which taxa, the most pressing needs for management and mitigation arise.

Spatially rare species generally face a greater risk of extinction across taxa and geographic locations than their more common counterparts (Ohlemüller *et al.*, 2008; Leão *et al.*, 2014; Staude *et al.*, 2020). The ecological and evolutionary mechanisms that produce spatial rarity vary, and to capture these nuances, Rabinowitz (1981) proposed a rarity framework based on three species characteristics: geographic range size, degree of habitat specificity (i.e., niche breadth), and local abundance. Although interrelated, each of these characteristics describes distinct features of a species' spatial rarity and may uniquely influence a species' vulnerability to environmental change. Range size has frequently been identified as one of the most important predictors of extinction risk (Payne & Finnegan, 2007; Leão *et al.*, 2014), with geographically restricted species often being associated with the highest extinction risks. In terms of spatial rarity and extinction vulnerability, small-ranged species with narrow niche breadths overwhelmingly face the highest vulnerability to environmental change (Johnson, 1998; Thuiller *et al.*, 2005; Payne & Finnegan, 2007).

Species persistence under global change also depends on the spatial configuration of habitat, including patch size and degree of isolation from other patches. Habitat patchiness, measured by the number of patches or the distance between patches, can protect or insulate species from the negative impacts of environmental change due to "risk-spreading", i.e., the risk of habitat loss is spread, and therefore diluted, across the landscape (Blowes & Connolly, 2012). This is especially true when the effect of a system perturbation is spatially "patchy," as is often the case with land use change and can be true for climate change in areas with complex terrain that modifies climate. However, habitat patchiness may reflect ongoing habitat loss due to changing climates (Petit *et al.*, 2003) and the conversion of natural land to urban or agriculture use, historical legacies that may make species more susceptible to continued habitat loss under future global change. Although not included in traditional rarity frameworks, aspects of fragmentation help describe the spatial rarity of suitable habitat across species' ranges and are considered rarity traits in this context.

Climate and land use change impacts are spatially structured, meaning that some species will be more vulnerable to their effects than others based on their geographic context. Distance to the coast, topography, and elevation are components of a species' physical environment that influence the magnitude of environmental change they will experience. However, the effect of a geographic factor on species' vulnerability can vary.

For example, while proximity to coastlines may offer the benefits of relatively stable or even cooling climates (Lebassi *et al.*, 2009), terrestrial species with suitable habitat projected to shift closer to the coast under climate change may be more vulnerable to range reductions than species projected to move inland (Broennimann *et al.*, 2006). Additionally, urban development is concentrated and projected to increase along coastlines in our focal study area—California, USA—making coastal species especially vulnerable to habitat loss via land use change.

Topographically complex landscapes can provide climatically stable refugia, e.g., north-facing slopes and cold air drainages, which may offer species refuge under rising temperatures (Serra-Diaz *et al.*, 2015), as they have during past climate change (Dobrowski, 2011), while also reducing climate velocities (Loarie et al. 2009). Furthermore, topographically complex areas are generally less likely to face urban and agricultural development than flatter areas (Syphard *et al.*, 2005), potentially reducing species' vulnerability to land use change in these areas. Additionally, elevational position influences species' vulnerability to environmental change. Interactions between declining water availability and rising temperatures in mountainous areas may exacerbate drought conditions and reduce suitable habitat for high-elevation species in water-limited Mediterranean-type climates, such as those found in the Sierra Nevada, California (McCullough *et al.*, 2016, Figure 1.1).

Exposure is a key component of species' vulnerability to global change that quantifies the magnitude of suitability change expected to be experienced by a species (Dawson *et al.*, 2011) and is often inferred from changes in species' environmentally suitable space

(Garcia *et al*. 2014a). Disentangling the relative importance of rarity and spatial context for determining species' exposure to global change is important for improving conservation decision-making, particularly if the relative contributions of these traits vary depending on the environmental change driver. In our research, we asked the following questions for a set of 106 plant species in the California Floristic Province (CFP): 1) *how do range-wide rarity and geographic traits relate to plant species' exposure to future climate and land use change?* and 2) *how do species' rarity and geographic traits interact to influence climate and land use change exposure?* In this study, we measured climate and land use change exposure as the total proportional loss of suitable habitat across species' currently occupied ranges (Garcia *et al.*, 2014b) because this metric does not rely on assumptions about dispersal capacity to reach new suitable areas outside the current range.

Methods

Study area and species

With >2,000 endemic vascular plant species (Baldwin *et al.*, 2012), the CFP, defined as the area of western North America with a Mediterranean-type ecosystem located almost entirely within California, is a topographically diverse biodiversity hotspot (Myers *et al.*, 2000). Stretching across 10 degrees of latitude and 4,000 meters of elevation, the California portion of the CFP (Figure 1.1) supports a wide variety of terrestrial vegetation systems. This region faces unique pressure from both climate and land use change, with temperatures projected to increase 2-7°C and developed land area projected to more than double between the late 20th-early 21st centuries and the year 2100

(Sleeter *et al.*, 2017; Pierce *et al.*, 2018). Our assessment was based on 106 plant species that are endemic to the CFP and that represent different life forms, range sizes (<200 to >300,00 km^2) and range locations (Serra-Diaz *et al.*, 2014). While not a random sample, these species include about 5% of the endemic flora and were selected to encompass the broad range of life histories and geographies found in the CFP (Supporting Information Appendix S1; Table S.1.1).

Species and environmental data

For 84 of 106 species, we compiled species presence-absence records from vegetation surveys (Hannah *et al*., 2008) and Calflora.org between 1980-2020. For the 22 species with too few presence-absence records from the vegetation surveys, we created a presence-only database using the Consortium of California Herbaria, the Global Biodiversity Information Facility (DOI: 10.15468/dl.nrdmke), the Integrated Digitized Biocollections, and the Botanical Information and Ecology Network. The number of presences available for modeling after filtering ranged from 12 to 4,646 across the 106 species (see Appendix Table S1.5 for data cleaning procedure; Table S1.2 for data sources). All occurrence data were restricted to the study extent (i.e., CFP).

We calibrated species distribution models (SDMs) using climatic, hydrologic, terrain, and soil predictors associated with plant distributions, especially in water limited ecosystems like California (Stephenson, 1998). Climatic and hydrologic predictors included climatic water deficit, actual evapotranspiration, minimum monthly temperature, and wet- and dry-season precipitation averaged from annual values for the years 1981-2010 at a 270 m spatial resolution. These variables are derived from the

California Basin Characterization Model (BCM), which uses fine-scale temperature interpolations and soil characteristics to capture the hydroclimatic effects of topography (Flint *et al.*, 2013; Hannah *et al.* 2014) and has been used in recent research to project the future distributions of plant species in California under climate change (Thorne *et al.*, 2017) (Table S1.3; Table S1.4).

Including edaphic variables as predictors in SDMs produces more comprehensive models based on factors limiting terrestrial plant distributions, especially when projecting models under climate change (Kueppers *et al.*, 2005; Velazco *et al.*, 2017). We obtained 10 m resolution soil pH, available water holding capacity, soil depth, and percent clay from gNATSGO (Soil Survey Staff, 2020). For species with >50 records, we included landform types (15) based on hillslope position and dominant soil formation processes (Theobald *et al.*, 2015), while topographic heterogeneity (continuous variation in elevation, obtained from a 90 m digital elevation model) was used instead for species with <50 records. We resampled the soil and terrain variables to match the spatial resolution of the climate data (270 m), using nearest neighbor resampling for the categorical landform data and bilinear approach for the continuous variables (Table S1.3). We also assumed that soil and landform conditions will remain constant through time and used them project models in space for both the current and future climatic conditions.

To assess climate change exposure for the period 2070-2099, we selected two Global Circulation Models (GCMs), CNRM-CM5 and HadGEM2-ES and two emissions representative concentration pathways (RCP), RCP 4.5 and 8.5 (IPCC 2013). The GCMs are among the ten recommended by California's Fourth Climate Change Assessment and encompass the variability in climate change projections for California (Pierce *et al.*, 2018), ranging from warm and wet (CNRM-CM5) to hot and dry (HadGEM2-ES), with a reduction in greenhouse gas emissions under the RCP 4.5 scenarios, and increasing greenhouse gas emissions ("business as usual") under the RCP 8.5 scenarios. All future climate data were produced by the BCM at a 270 m spatial resolution.

Land use data

To assess the impact of current and future land use, we used projections for the HadGEM2-ES RCP 4.5 and 8.5 scenarios from the Integrated Climate Land Use Scenario (ICLUS), which are based on a human demographic growth model and are consistent with the IPCC Special Report on Emission Scenarios (Theobald, 2005; Bierwagen *et al.*, 2010). These land use change scenarios predict increases in urban and exurban development and decreases in agricultural and forest lands (Figure 1.1). To simplify each land use category's impact on habitat suitability produced by the SDMs, we estimated that cells with natural land uses would have no impact on habitat suitability, cells within the exurban category would experience a 50% reduction in habitat suitability (e.g., an exurban grid cell with an initial suitability value of 0.75 is assigned a new value of 0.375), and cells classified as developed would become unsuitable (suitability value of zero) (Table S1.6).

Species distribution models

We selected eight SDM algorithms for ensemble predictions: generalized linear models, generalized additive models, boosted regression trees, random forests, artificial neural networks, support vector machines, maximum entropy, and gaussian process (Franklin, 2010). The last two algorithms were only used for presence-only models. Ensembles, in which predictions of individual algorithms are combined to produce a consensus distribution, can reduce model uncertainty and improve model transferability (Araújo & New, 2007). For each model, we applied the model-specific suitability value that maximized the sum of sensitivity and specificity as a threshold, retaining continuous suitability values above the threshold and assigning 0 suitability values to those cells below the threshold. This method removes areas with low habitat suitability while retaining variation in suitability within species' habitat (Muscatello *et al.*, 2021), and allowed us to later define discrete species' ranges from which to calculate the number of patches and patch isolation. The resulting continuous suitability values were averaged across all models to produce a "mean above threshold" ensemble. We produced 786 models (84 of presence-absence species * 7 algorithms/ensemble + 22 of presence-only species *9 algorithms/ensemble) with 3,144 projections (2 GCM's * 2 RCPs).

Our exposure analysis focused on the temporal dynamics of suitability within species currently occupied ranges. When a model is projected outside the calibration area, patches with high suitability may be predicted far from current species distribution, creating "overprediction" (Mendes *et al.*, 2020; Velazco *et al.*, 2020). Therefore, we constrained current and future model predictions by selecting only suitability patches (contiguous suitable pixels) that contained at least one occurrence (Mendes *et al.*, 2020). All SDMs were calibrated and evaluated using the *flexsdm* package in R (Velazco et al., 2022).

Rarity and geographic traits

We calculated four species-level rarity traits based on species occurrence data and currently occupied suitable habitat maps produced by the ensemble SDM procedure outlined previously. Rarity traits included range size, niche breadth, number of patches, and patch isolation. Range size was calculated as the area in km^2 encompassed by the minimum convex polygon that contained all species' occurrences used for modeling. We calculated niche breadth with the hydroclimatic and soil variables used to build SDMs, adapting methods developed by Vela Díaz *et al.* (2020) (Figure S1.2 & S1.3). We standardized all environmental variables across the extent of the CFP to z-scores (mean = 0, SD = 1) to account for differences in units of measurement and variance in the environmental variables. To reduce collinearity in the environmental data, we performed separate principal components analyses (PCAs) for 1) climate and 2) soil variables and selected the principal components that explained 95% of the variation in each (Figure S1.3). For each species, we calculated the sum of squared difference between the environmental value of each occurrence record and the environmental mean value of all occurrence records for that species. The niche breadth of a species represents the sum of this value across all environmental variables divided by the number of occurrence records for that species. To calculate the number of habitat patches and average patch isolation for each species' range, we first binarized currently occupied suitable habitat maps using the threshold that maximized the sum of model sensitivity and specificity. We then used functions from the *landscapemetrics* R package to calculate the number of habitat patches and the coefficient of variation of Euclidean nearest-neighbor distance between each patch (patch isolation) for each binarized habitat map (Hesselbarth *et al.*, 2019). Geographic traits included distance to coast, elevation, and topographic heterogeneity. We used a 90 m DEM to calculate topographic heterogeneity as the range in elevation values from a center cell and the three-cell neighborhood immediately surrounding it. These values were then converted to a 0-1 scale using the standard deviation of the range of values across the study area. To summarize species-level geographic traits, we averaged the values for each of these variables across all occurrences for each species. More information about the rarity and geographic traits and our predictions for the relationships between these traits and exposure are summarized in Table 1.1.

Calculating exposure to climate and land use change

We defined exposure in a 270 m grid cell within a species currently occupied range as habitat suitability change between the baseline (1980-2010) and future time period (2070-2099) based on SDM predictions and land use patterns:

$$Exposure_c = baseline\ habitat\ suitability_c - future\ habitat\ suitability_c \qquad (1)$$

In this framework, exposure varies continuously and is not dependent on binary thresholds, i.e., unsuitable vs. suitable (Guillera-Arroita *et al.*, 2015). To summarize species-level range exposure, we calculated habitat suitability as the sum of grid cells (c) across the total number of grid cells (n) in the spatial projections of species' occupied area (Leão *et al.*, 2021):

$$Habitat\ suitability_{sum} = \sum_{c=1}^{n}\ environmental\ suitability\ within\ occupied\ range_c \qquad (2)$$

Range exposure represents the sum of change in suitability values from the baseline and future time periods proportional to the baseline suitability averaged across the two GCMs for each RCP:

$$Range\ Exposure\ =\ \left(\frac{baseline\ \ habitat\ suitability_{sum} - future\ \ habitat\ suitability_{sum}}{baseline\ habitat\ suitability_{sum}}\right) \qquad (3)$$

We evaluated species' exposure to climate change only (CC), land use change only (LUC), and climate and land use change combined (CC + LUC) (Figure 1.2). Using this framework, range exposure values >0 correspond to a decrease in habitat suitability, while range exposure values <0 indicate an increase. A species projected to experience a complete loss of suitable habitat within its current range would have a range exposure value of 1.

Statistical analyses

Exploratory analyses revealed that our data demonstrated non-homogeneity of variance and skewed distributions (Figure S4.2), so we selected generalized additive models for location, scale, and shape (GAMLSS) as the regression framework to test our predictions about the relationships between individual species' spatial range traits and their exposure to climate and land use change (Table 1.1). GAMLSS is a flexible statistical modeling approach with a variety of distribution families and distribution parameters (location, scale, shape) (Rigby & Stasinopoulos, 2005) (see Appendix for modeling procedure).

Because of multicollinearity between two geographic traits, mean elevation and distance to coast, we first estimated the GAMLSS between exposure and each trait individually, including RCP scenario as an interaction term in each model to evaluate different relationships between spatial range traits and exposure under the two emissions scenarios, and species as a random intercept. While the GAMLSS approach allows us to assess the relationship between each species trait and exposure, we also wanted to quantify the unique and shared variance in exposure explained by rarity traits, geographic traits, and RCP. To do this, we performed variance partitioning via partial regression using the *vegan* R package (Oksanen *et al.*, 2021). Species are phylogenetically related, violating the assumption of data independence and can lead to overestimating degrees of freedom in approaches like GAMLSS. We examined Moran's I phylogenetic correlograms for the residuals of each GAMLSS using a phylogenetic tree created for California plant species (Thornhill *et al.*, 2017) (see Appendix for more details).

To explore interactions between species' traits and exposure, we also implemented a decision tree approach, which has been used to interpret extinction risk factors (Leão *et al.*, 2014). Decision trees iteratively partition data into subgroups based on values of predictor variables, with each resulting group being more homogenous in terms of the response variable, as measured by the Gini index (Breiman *et al.*, 1984). They can also handle multiple correlated predictor variables and rely on fewer assumptions than more traditional regression approaches, i.e., distribution of the response and predictor variables and data independence. Because the goal of our decision tree analysis is to understand how the interactions between multiple spatial range traits influence exposure, and not to make predictions, we did not apply any complexity costs to the final decision tree and present the "full grown trees" in our results. We evaluated how complexity influenced the error rate using 10-fold cross-validation (Figure S1.12).

Results

We modeled the spatial distributions and exposure of 106 species, including 48 shrubs, 32 trees, and 26 herbs. SDM's performed well across species and algorithm types (AUC: mean = 0.88± 0.06 *SD*; TSS: mean= 0.68± 0.14 *SD*; Boyce Index: mean = 0.87± 0.12 *SD*; Sorensen: mean = 0.58± 0.25 *SD*; FPB: mean = 0.92± 0.50 *SD*) (Figure S1.1).

Exposure to climate and land use change

Across all species and the two emissions scenarios, mean exposure was lowest for land use change alone (0.10), followed by climate change alone (0.27), and highest for the combined effect of both (0.34). As expected, species exposure was greater for the RCP 8.5 than the RCP 4.5 for climate change (mean .33 versus .21), land use change (.12 versus .07), and the combined effect of both (.41 versus .26) (Figure 1.3).

GAMLSS results

The univariate GAMLSS showed strong evidence that patch isolation, elevation, and distance to coast are each positively associated with exposure to climate change, while number of patches, and rarity trait niche breadth, are negatively associated with climate change exposure (Table 1.2). Range size showed evidence of quadratic relationships with exposure to climate change, where small-ranged and large-ranged species were the most exposed to climate change (Figure 1.4). There was no evidence of a relationship between mean topographic heterogeneity and climate change exposure in the overall model. However, we found a significant interaction between topographic heterogeneity and RCP emissions scenario, where topographic heterogeneity had no relationship with climate change exposure under RCP 4.5 but was negatively associated with exposure under RCP 8.5 (Figure 1.4). There was also evidence of an interaction between range size, number of habitat patches, topographic heterogeneity, and distance to coast and emissions scenario. R-squared values indicate that range size, along with RCP, explained the most variation in climate change exposure, followed by number of patches (Table 1.2).

We found strong evidence that niche breadth, patch isolation, elevation, and average topographic heterogeneity were negatively associated with land use change exposure. There was moderate evidence that average distance to coast is negatively associated with land use change exposure, as well (Table 1.2). Conversely, the number of habitat patches was positively associated with land use change exposure. In contrast to the results for climate change exposure, species with intermediate range sizes were the most exposed to land use change (Figure 1.3). Half of the model terms showed evidence of an interaction with RCP (Table 1.2). Generalized R-squared values showed that elevation explained the most variation in land use change exposure followed by number of patches and distance to coast (Table 1.2). The relationships between species' rarity and geographic traits and exposure to combined climate and land use change were similar to the patterns under climate change alone (Table S4.1, Figure S4.3). GAMLSS model residuals showed no evidence of phylogenetic autocorrelation (Figure S5.2), suggesting that our results were not affected by phylogenetic relatedness between species.

Variance partitioning

Overall, rarity traits, geographic traits, and RCP emissions scenario explained 35.2% and 61.9% of the variance in climate change and land use change exposure, respectively (Figure 1.5). While rarity traits explained the most variance in climate change exposure (14.1%), geographic traits were most important for explaining species' exposure to land use change (41.1%).

Decision tree analysis

Decision tree analysis revealed that range size was the most important predictor of climate change exposure under the RCP 8.5 emissions scenario, as indicated by the first tree split, with small-ranged species (<14,000 km^2) being more exposed than species with larger ranges (Figure 1.6). Subsequent splits indicated that species with higher mean topographic heterogeneity were less exposed to climate change than species in topographically homogenous areas. We observed a similar pattern for the number of patches, where species with more habitat patches were less exposed than species with fewer habitat patches across their ranges. Other splits indicated that species that were closer to the coast, had broader niches, or were at lower elevations tended to be less exposed than species far from the coast, at higher elevations, or that occupied narrow environmental niches. The least climate exposed groups of species (far left nodes, exposure = -0.051-0.012), were those with large range sizes, many habitat patches, and wide niche breadths, and that were located less than 46 km of the coast with high mean topographic heterogeneity (n = 26). However, the most exposed group of species (exposure = 0.78, n = 17), had small ranges and low mean topographic heterogeneity.

For land use change exposure under RCP 8.5, the first split is determined by the mean elevation of species' ranges, where species at higher elevations were less exposed to land use change than those at lower elevations. Species with higher mean topographic heterogeneity were less exposed than species in locations with lower average heterogeneity. Splits based on range size indicated that species with small range sizes were more exposed than widespread species. The least exposed group of species (exposure = 0.017-0.073, n = 35) were located at mean elevations greater than 771 m. However, the species that were predicted to be most vulnerable to land use change (exposure = 0.24, n = 17) were located at low elevations, in topographically homogenous areas, and had range sizes smaller than 71,000 km^2.

Discussion

In this study, we 1) measured exposure (change in habitat suitability within species' current geographic ranges) to climate and land use change for 106 plant species in the CFP, for two emissions scenarios for the time period 2070-2099, and 2) related rarity and geographic traits to species' range-wide exposure under future climate and land use change. We found that exposure to future climate and land use change varies among plant species in the CFP, with habitat suitability losses up to 100% for some species and gains up to 36% for others by the end of the 21st century. The average projected suitability loss ranged from 25% to 41% due to both climate and land use change, depending on emissions scenario. Rarity and geographic traits explained >35% of the variance in climate change exposure and >63% of variance in land use change exposure. Our results supported some but not all our predictions about the relationships between species' traits and their exposure to climate and land use change (Table 1.1).

Rarity traits and exposure

Species with small ranges were the most exposed to both climate and land use change, especially under the "business-as-usual" (RCP 8.5) higher emissions scenario (Figures 1.4 and 1.6). This finding is supported by past research that species with small range sizes face the highest extinction risks (Pearson *et al.*, 2014; Chichorro *et al.*, 2019), even when other aspects of rarity, i.e., habitat type and abundance, are considered (Harnik *et al.*, 2012). Species with small geographical ranges often occupy rare and/or cooler, relict climates that may disappear rapidly under climate change (Ohlemüller *et al.*, 2008). The heightened vulnerability of small-ranged species to both climate and land use change is particularly important in the CFP, where >60% of endemic plant species have range sizes <10,000 km^2 (Thorne *et al.*, 2009). However, we found that the relationship between range size and exposure was not linear or even monotonic. Our results indicate that widespread species may be more exposed to climate change than species with intermediate-sized ranges, a pattern that also found for European plant species (Thuiller *et al.*, 2005) but remains poorly understood. A closer look at the most exposed yet widely distributed species in our study system provides some insight into this complex pattern. Widespread species in the CFP that may face high levels of habitat decline due to both climate and land use change (>70% exposure) include California buckeye (*Aesculus californica*) and blue oak (*Quercus douglasii*), two tree species whose distributions are concentrated in the foothills of the Coast Ranges and the western Sierra Nevada regions that are predicted to face rapid climate change as well as exurban development during the next century (Figure 1.1). Furthermore, while species with large range sizes tend to have broader environmental niches, homogenous environmental conditions may be prevalent across a region and therefore contain widespread species with narrow environmental affinities (Meyer & Pie, 2018), as we found for both blue oak and California buckeye. This finding highlights that broad spatial distributions may not buffer species from the consequences of global change, especially if their ranges are in highly vulnerable areas.

Although niche breadth and range size were positively associated for our study species (r = 0.44; Figure S4.1) and across taxa in previous research (Slatyer *et al.*, 2013), they had different relationships with species' exposure, emphasizing the need to consider both when conducting vulnerability analyses based on species' traits. Species with broad niches tended to be the least exposed to both climate and land use change, though the relationships were highly variable (Figure 1.4). Anthropogenic change is already causing declines in habitat specialists, globally (Clavel *et al.*, 2011), and species with broad environmental tolerances may be more resilient to changing environmental conditions than specialist species (Broennimann *et al.*, 2006). Interestingly, our decision tree indicated that niche breadth was only important for predicting climate change exposure in specific biogeographic contexts. For species with intermediate to large range sizes, an intermediate number of habitat patches, near the coast, and in topographically heterogeneous areas, species with narrow niches were associated with higher climate change exposure (Figure 1.5). However, we found that some species with narrow niches defy this pattern and are predicted to face relatively low climate change exposure, including big pod ceanothus (*Ceanothus megacarpus*), California brittlebush (*Encelia californica*), purple sage (*Salvia leucophylla*), California goldenbush (*Ericameria* *ericoides*), alpine gooseberry (*Ribes lasianthum*). The first four species have relatively large range sizes concentrated along the coast of California, while alpine gooseberry's distribution is characterized by high topographic heterogeneity—all factors that may reduce species' vulnerability to global change. These instances highlight species for which geography may mediate the relationship between niche breadth and species' vulnerability to global change.

Regarding habitat configuration, species with fewer habitat patches and more dispersed ranges, i.e., higher patch isolation, were associated with higher levels of climate change exposure. Fewer habitat patches may indicate that a species occupies only a few, restricted habitat types, magnifying its climate change risk. We found that the number of habitat patches was positively, though not perfectly, related to range size (r =0.39; Figure S4.1), and this metric complemented range size as a determinant of climate change exposure in our decision tree. Among our study species, those with large range sizes (>=14,000 km^2) and many habitat patches (>= 6,213) were associated with the lowest levels of climate change exposure (5% average gain in habitat suitability, n = 11). Habitat dispersion, i.e., patch isolation, may reflect ongoing range disjunction due to past climate fluctuations (Petit *et al.*, 2003) and is predicted to increase as a result of anthropogenic climate change (Jackson *et al.*, 2015). While scattered distributions may have once reflected refugia during past climate change in California (Millar, 2012), we found that several species with isolated distributions, such as giant sequoia (*Sequoiadendron giganteum*), Parry pinyon (*Pinus quadrifolia*), and foxtail pine (*Pinus balfouriana*), were predicted to be highly exposed to climate change (>86% average habitat suitability loss under RCP 8.5). These findings suggest that climate change vulnerability assessments should consider aspects of habitat configuration alongside more commonly included traits such as range size and niche breadth.

For land use change exposure, we found that species with many habitat patches and low patch isolation were more exposed to land use change. Land use change in California is predicted to be patchy and concentrated in areas surrounding existing urban and agricultural centers as well as the foothills of the Central Valley (Sleeter *et al.*, 2017). Patchy spatial distributions may reflect that a species' range already overlaps with developed land that will expand in the future, as was the case for the riparian California sycamore (*Platanus racemosa*), which is distributed in human-dominated areas and was projected to lose >20% habitat suitability due to land use change alone. Because land development is predicted to be concentrated in specific regions in the CFP, species with aggregated spatial distributions will be at greater risk of habitat loss if their ranges overlap with centers of development, while species with dispersed ranges may benefit from "risk-spreading" if some of their habitat is far away.

Geographic traits and exposure

While past research suggests that montane species are among the most vulnerable to climate change globally (Dobrowski & Parks, 2016), others show that lowland species will also face significant habitat loss due to rapidly warming temperatures in the next century (Hülber *et al.*, 2020). Our findings support both paradigms in that high elevation species were disproportionately exposed to climate change; however, many low-elevation species were also highly susceptible to the consequences of climate change (Figure 1.4).

Complex topography is expected to provide suitable topoclimatic refugia that may facilitate species persistence under climate change (Ackerly *et al.*, 2020), as it has during past periods of environmental change (Dobrowski, 2011). Although we found that the range-wide measure of topographic heterogeneity explains the least amount of variation in climate change exposure among the rarity and geographic traits included in this analysis (Figure 1.4, Table 1.2), it was the most frequently included trait in the decision tree analysis, despite low importance (Figure 1; Figure S1.11). In every instance, higher average topographic heterogeneity was associated with reduced climate change exposure (Figure 5), suggesting that while it may not represent a robust lone predictor of species vulnerability to climate change at the spatial scale of this analysis, it is important in certain contexts. Notably, low topographic heterogeneity magnifies habitat loss (54% for higher vs. 78% for lower) for species with small range sizes, highlighting how traits can interact to increase species' exposure to global change.

Elevation, topographic heterogeneity, and distance to coast explained >40% of the variance in land use change exposure among our study species, emphasizing the importance of geographic context for predicting species' risk to habitat conversion. We found that species located at low elevations, in areas with low topographic heterogeneity, and near the coast were the most at-risk of habitat loss due to land use change. Projected land use patterns in the CFP support these findings, in that low-elevation, flat, and coastal regions will likely experience the greatest increases in urban and agricultural development by the year 2085 (Figure 1.7). In our study system, elevation was the most important factor in determining species' exposure to land use change, providing further evidence of the negative relationship between human impact and elevation that has been observed globally (Nogués-Bravo *et al.*, 2008).

Conclusions

Rarity and geographic traits are important determinants of species exposure to climate and land use change for plant species in the CFP. Our research highlights how complex interactions between these traits influence their exposure to global change and demonstrates the importance of analyzing the relationship between species' traits and vulnerability in multiple ways. While range size was an important predictor of species exposure to global change for our study species, it interacted with other aspects of species' spatial distributions, including habitat configuration, elevation, and topographic heterogeneity, to magnify or reduce species' vulnerability to habitat loss. Furthermore, we found that while species may be buffered from the consequences of one change driver, they may lose significant habitat under another, i.e., species with many habitat patches are predicted to fare well under climate change but were among the most exposed to land use change. Overall, this research emphasizes the usefulness of traits derived from simple occurrence records and distribution models in predicting species' exposure to future change and the importance of considering interactions between multiple traits in the context of climate and land use change.

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Tables and Figures

Table 1.1 Species' traits that are related to climate and land use change exposure (based on Pearson *et al.*, 2014; Franklin *et al.*, 2021) and predictions about how each traits is related to plant vulnerability to climate and land use change in the California Floristic Province (CFP).

	Attribute	Metrics	Predictions
Rarity traits	Range size	Area of minimum convex polygon around occurrences (km^2)	Smaller range size -- greater exposure to climate and land use change
	Niche breadth	Abiotic environmental tolerances based on climate, terrain, and soil variables (270 m resolution) extracted at species occurrences (Vela Díaz *et al.*, 2020)	Narrow niche breadth -- greater exposure to climate change
	Range fragmentation	Number of suitable habitat patches, average patch isolation -- based on ensemble SDM of currently occupied habitat (Hesselbarth *et al.*, 2019)	Higher range fragmentation -- less exposure to land use change (risk spreading) and greater climate change exposure
Geographic traits	Distance to coast	Average distance (km) from species' occurrences to the coastline NASA Earth Data	Closer to the coast -- less climate change exposure and greater land use change exposure
	Range topography	Average topographic heterogeneity* of species occurrences (0-1; 90 m) *Range in elevation values from a center cell and the three-cell radius immediately surrounding it, rescaled to 0-1 using the standard deviation of the range of values across the study area	Higher topographic complexity -- less exposure to climate and land use change
	Elevation	Average elevation (m) of species occurrences (90 m)	Higher elevation -- greater exposure to climate change and less exposure to land use change

Table 1.2 Results of GAMLSS models for species rarity and geographic traits (predictors) and response variables range-wide climate change and land use change exposure (crosses indicate variables that showed a significant interaction with RCP scenarios).

		Climate change exposure				**Land use change exposure**			
		R^2	Estimate	SE	p	R^2	Estimate	SE	p
Rarity Traits	Range size	0.31	-0.78^{+++}	0.009	**<.001**	0.39	1.2	0.27	**<.001**
	Range size^2		0.92^{+++}	0.12	**<.001**		-2.53	0.21	**<.001**
	Niche breadth	0.12	-0.02^{+++}	0.006	**0.001**	0.05	-0.19^{+++}	0.01	**<.001**
	Number of patches	0.29	-0.09^{+++}	0.008	**<.001**	0.57	0.36^{+++}	0.02	**<.001**
	Patch isolation	0.12	0.208	0.02	**<.001**	0.25	-1.85^{+++}	0.08	**<.001**
Geographic Traits	Elevation	0.17	0.0002	0.00001	**<.001**	0.80	-0.002	0.00005	**<.001**
	Topographic heterogeneity	0.10	-0.01^{+++}	0.04	0.75	0.32	-5.55	0.12	**<.001**
	Distance to coast	0.13	0.001	0.0001	**<.0001**	0.58	-0.02	0.0005	**<.0001**

R^2 indicates the proportion of variance in exposure explained by each rarity and geographic traits and RCP scenario. Exposure is based on the proportion of habitat suitability loss within species' currently occupied ranges, where 1 = 100% decrease. Estimates, standard errors, and p-values are based on individual GAMLSS between spatial traits and species exposure. (+) denote the significance of the interaction between each spatial range trait and RCP: $^{+++}P < 0.001$; $^{++}P < 0.01$; $^{+}P < 0.05$.

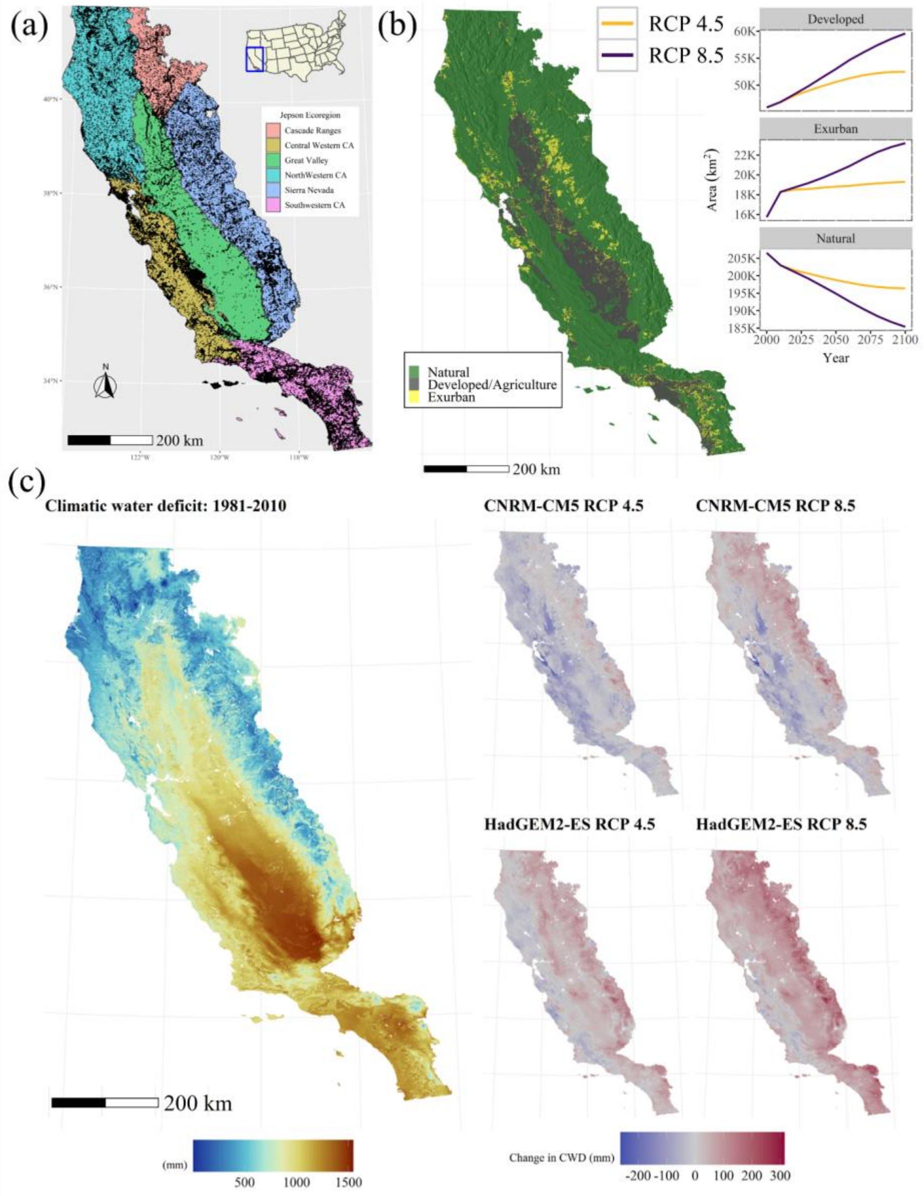

Figure 1.1 California Floristic Province (CFP) within California (a) Jepson Ecoregions and 76,266 survey locations for plant species presence-absence data. (b) Map of land use patterns in the CFP in the year 2000 and area trends for each land use class (natural, developed, and exurban) between 2000-2100 under two emissions scenarios: RCP 4.5 and RCP 8.5. (c) Climatic water deficit (the difference between potential and actual evapotranspiration) –an important driver of vegetation distributions in water-limited, Mediterranean type ecosystems– in the CFP for the historical period 1980-2010 and projected change for the period 2070-2099 under two climate models (CNRM-CM5 and HadGEM2-ES) and two emissions scenarios (RCP 4.5 and 8.5).

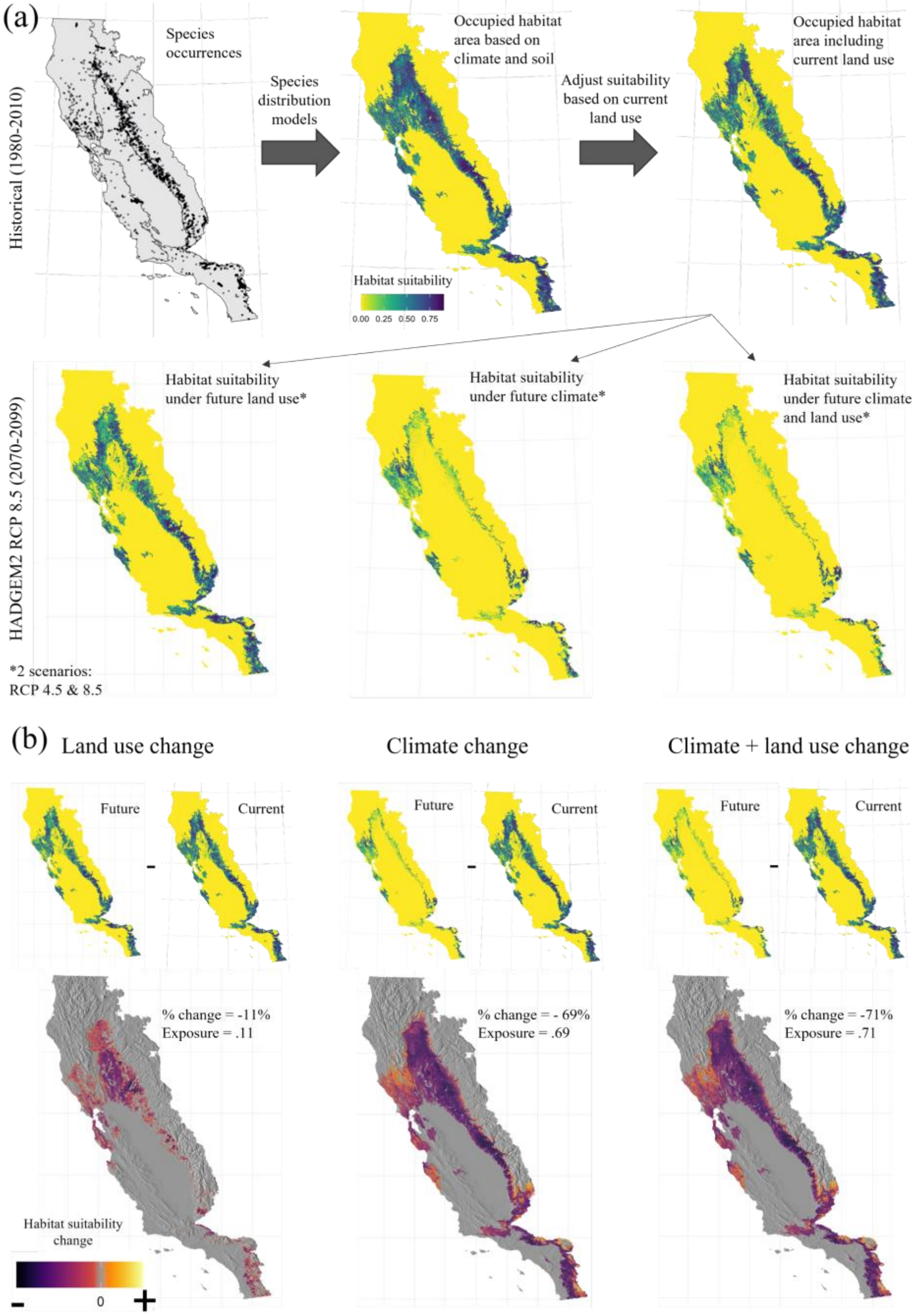

Figure 1.2 Framework for modeling species occupied suitable habitat during the baseline (1980-2010) and future time period (2070-2099) under climate and land use change (a) and estimating species' exposure to land use change, climate change (for each RCP), and climate and land use change overlaid on a DEM-derived hill shade for the study area (b). For our analysis, we averaged the exposure values from the two climate change GCM's (HadGEM2-ES and CNRM-CM5).

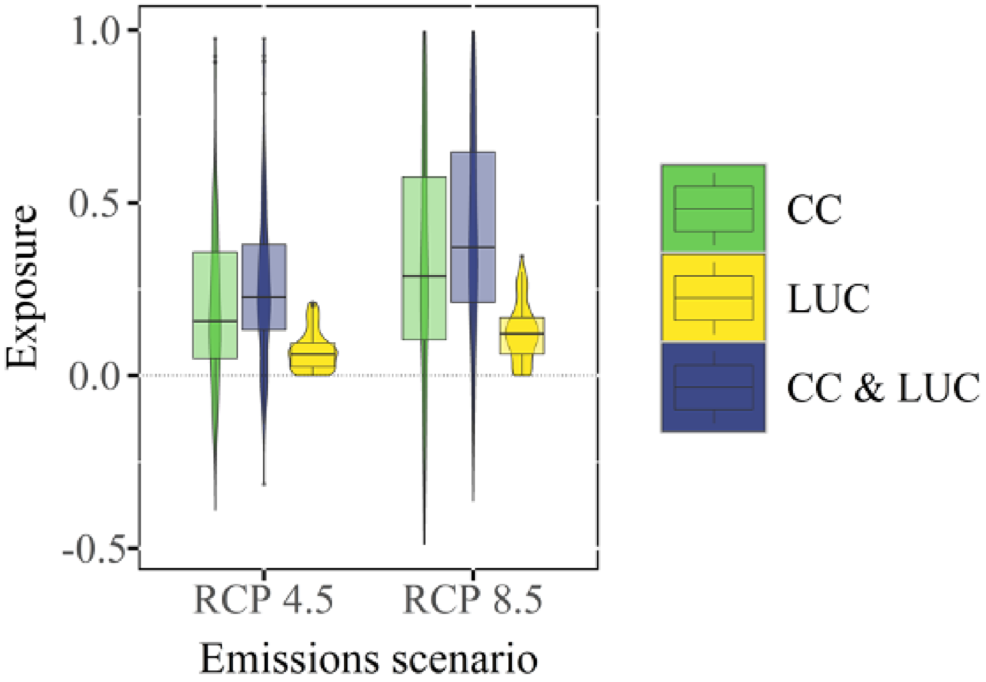

Figure 1.3 Boxplots summarizing species-level exposure under climate change (CC), land use change (LUC), and the combined effect of climate and land use change (CC & LUC) for each emissions scenario. Positive exposure values indicate a decrease of suitability. The boxplots show the median value along with the first (lower) and third (upper) quartiles (the 25th and 75th percentiles).

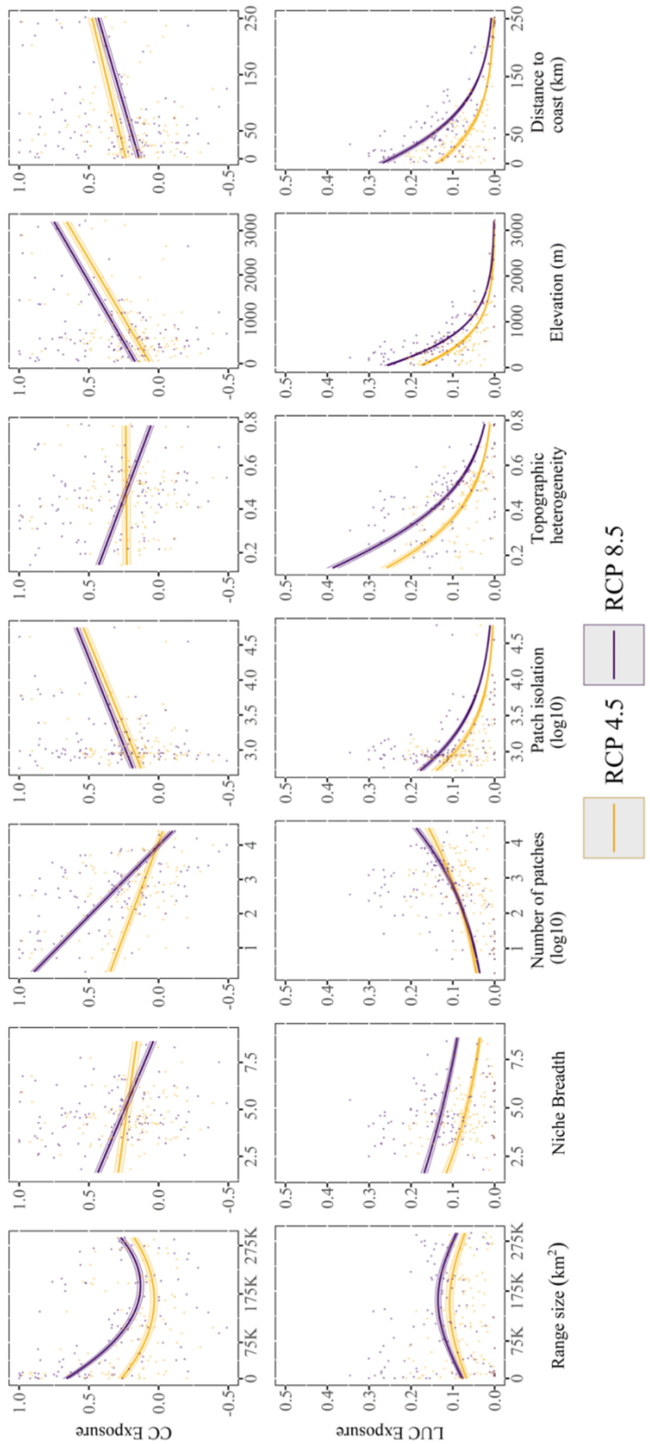

Figure 1.4 Fitted response curves for the GAMLSS relating rarity and geographic traits to climate change (CC) and land use change (LUC) exposure under emissions scenarios RCP 4.5 and 8.5. Upper and lower pointwise standard error curves are shown in each plot (shaded areas).

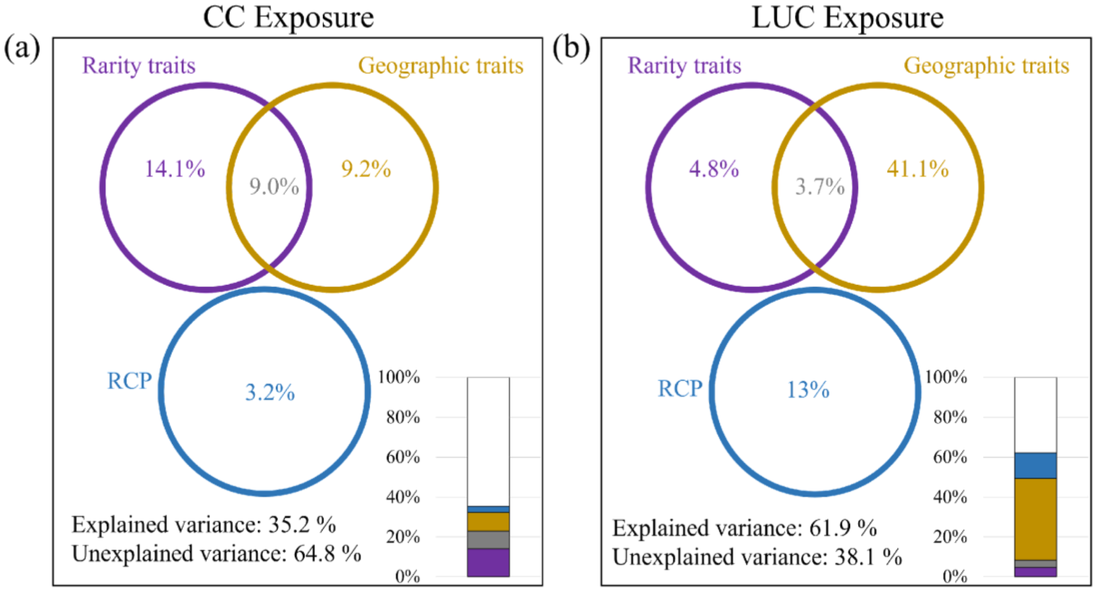

Figure 1.5 Proportion of variance in exposure to climate change (a) and land use change (b) explained by rarity traits (range size, niche breadth, number of habitat patches, and patch isolation), geographic traits (mean elevation, topographic heterogeneity, and distance to coast), and RCP emissions scenario. Overlapping areas indicate shared variance between traits, while non-overlapping areas indicate no shared variance.

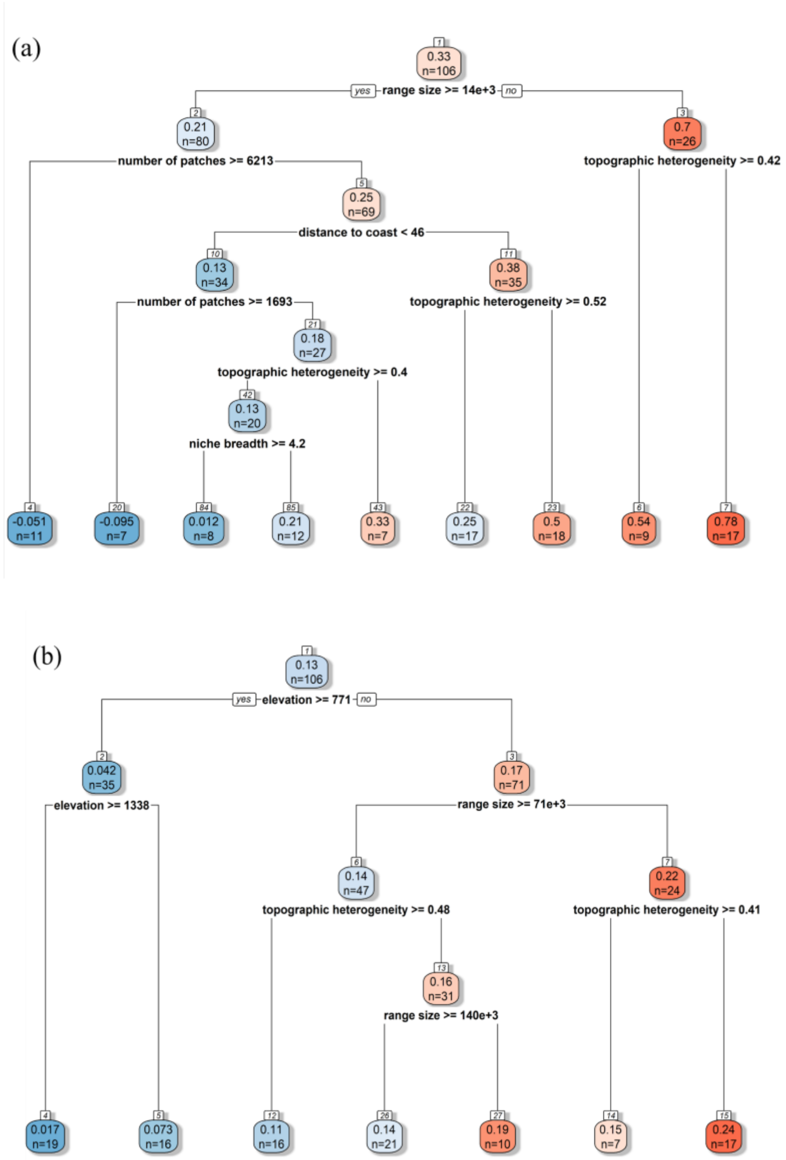

Figure 1.6 Decision tree showing exposure to (a) climate change and (b) land use change based on species' rarity and geographic traits under the RCP 8.5 emissions scenario (See Figure S6.3 for RCP 4.5). In each node, the top number indicates the average exposure of the species in that group, i.e., overall species had an average climate change exposure of .33 in RCP 8.5, and the second number (n=#) indicates the number of species in that group. The decision criteria are located below each node, where groups to the left meet that condition ("yes") and groups to the right do not ("no"). For example, all species grouped to the left of the first node in the first decision tree (a), have range sizes greater than 14,000 km^2, while those to the right have smaller range sizes. For each branch split, species to the right are more exposed than species to the left. Numbers at the top of each node correspond to the branch order, where gaps between numbers indicate branches that were pruned during model fitting.

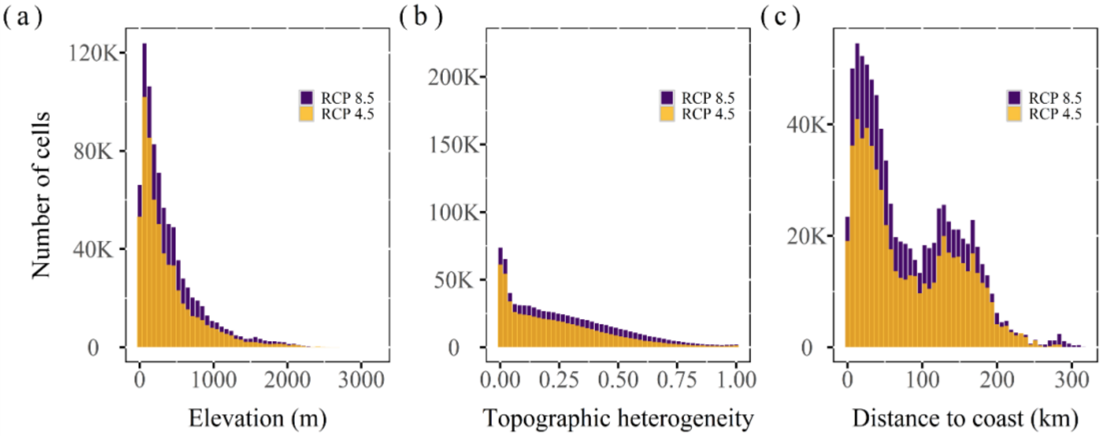

Figure 1.7 Frequency distribution of raster cells projected to become increasingly developed (natural to exurban/urban/agriculture or exurban to urban/agriculture) between 1995-2085 by elevation (m) (a), topographic heterogeneity (b), and distance to coast (km) (c) for emissions scenarios RCP 4.5 and RCP 8.5.

Chapter 2

Uncertainty in consensus predictions of plant species' vulnerability to climate change in the California Floristic Province

Abstract

Variation in spatial predictions made of species' ranges by various models has been recognized as a significant source of uncertainty for modeling species distributions. Consensus approaches that combine the results of multiple models have been employed to reduce uncertainty introduced by different algorithms. Our aim was to evaluate how estimates of habitat suitability change varied among different consensus methods, relative to the variation introduced by different climate change models and greenhouse gas emissions scenarios. Using six algorithms and five resulting consensus methods, we modeled the current and future potential distributions of 82 terrestrial plant species in the California Floristic Province. We explored model predictions under different combinations of global circulation models, emissions scenarios, time periods, dispersal assumptions, and the five consensus methods used to combine different species distribution modeling algorithms. We assessed how each of these factors contributed to the variability in future predictions of species habitat suitability change as well as aggregate measures of proportional species change. We also related variability in species-level habitat change to species characteristics. Assuming full dispersal capacity, variability between habitat predictions made by different consensus methods was higher than the variability introduced by different greenhouse gas concentration pathways and climate models. The relationships between species attributes and variability in future habitat predictions depended on the source of uncertainty and dispersal assumptions, though small-ranged species and those with low prevalence tended to be associated with high variability in range change forecasts. Our results support exploring the habitat suitability trajectories produced by multiple consensus approaches when considering habitat suitability change outside of species' current distributions, especially when projecting species with low prevalence and small range sizes, as these species tend to be of the greatest conservation concern yet produce highly variable model outputs. Differences in vulnerability between diverging emissions scenarios are most readily observed for end-of-century time periods and within species' currently occupied habitat (no dispersal).

Introduction

Species distribution models (SDMs) are among the most widely used tools for measuring and predicting species' responses to environmental change, i.e., forecasting species range shifts in response to climate change (Peterson et al. 2002, Thomas et al. 2004, Thuiller et al. 2005, Araújo and New 2007). These models relate species locations to environmental predictors to describe species' geographic and environmental distributions using statistical or machine learning methods, often to identify environmentally suitable areas for species persistence (Franklin 2010). A variety of modeling algorithms have been used for SDMs, ranging from statistical approaches like generalized linear models to machine learning tools such as random forest (Loyola 2012). Algorithms are a significant source of model uncertainty in describing species distributions (Elith et al. 2002, Thuiller 2004, Pearson et al. 2006, Qiao et al. 2015, Thuiller et al. 2019), as different modeling methods often produce different spatial predictions (Thuiller 2003, Syphard and Franklin 2009, Conlisk et al. 2013). SDMs are frequently used in applied conservation research, such as reserve design, species reintroductions, and identifying suitable habitat under changing climatic conditions, so addressing sources of uncertainty remains a key concern (Guisan et al. 2013, McShea 2014).

Consensus approaches combine an ensemble of habitat predictions made by individual algorithms and have emerged as a popular technique for reducing uncertainty introduced by algorithms, especially when these models are used to project habitat suitability under climate change (Araújo and New 2007, Thuiller et al. 2009, 2019). While there is some debate about whether consensus projections outperform individual algorithms (Marmion et al. 2009) or not (Crimmins et al. 2013, Zhu and Peterson 2017, Hao et al. 2020), consensus methods are frequently used for predicting species distributions under novel conditions and for conservation prioritization (Araújo et al. 2011). Various consensus approaches have been developed including, but not limited to, those based on basic mathematical functions: mean, performance-weighted mean (Zhang et al. 2015), median (Marmion et al. 2009; Peng et al. 2022), mean of the best models (Norberg et al. 2019), and mean of model outputs above a given threshold (Rose et al. 2023). Other approaches include committee averaging, which involves binarizing model probabilities based on a threshold and then averaging the binarized predictions across models (Thuiller et al., 2016) and median-based principal components analysis (Marmion et al., 2009; Zhang et al., 2015).

Past research has demonstrated that algorithm choice systematically influences estimates of future range change, e.g., the machine learning algorithm random forest was found to disproportionately predict extreme scenarios of habitat suitability loss when compared to other methods (Beaumont et al. 2016). However, the effect of different consensus approaches on predicted spatial distributions under climate change has not been extensively explored, though Zhang et al. (2015) found that while consensus methods generally agreed on the magnitude and direction of species' range change, they were spatially incongruent. Furthermore, different SDM consensus approaches produce distinct conservation prioritization schemes (Meller et al. 2014), which can impact the effectiveness of prioritization schemes. This phenomenon highlights the importance of comparing how these consensus approaches behave when predicting species' habitat suitability under climate change. Evaluating species susceptibility to extirpation as the result of anthropogenic change is a primary goal of modern conservation ecology and climate risk assessments that rely on SDM consensus outputs have the potential to shape conservation policy (Keith et al. 2014). We know that SDM algorithms often account for more variation in habitat predictions than predictions made by different global climate models (GCMs)—representations of the earth's climate system that vary in their predictions regarding the direction and magnitude of climate change— and representative concentration pathways (RCPs) – trajectories that reflect differences in potential greenhouse gas concentrations. However, we do not know the uncertainty between SDM consensus methods compares to differences in projected climatic change introduced by different climate models and under different GHG concentration pathways. Therefore, it is critical to assess each factor’s relative contribution to uncertainty of species’ vulnerability, even when we believe we have reduced that uncertainty via consensus forecasting.

Species’ attributes also influence uncertainty in projections of species range change under climate change by affecting the quality and quantity of available occurrence data or by influencing SDMs’ ability to capture the species-environment relationship (McPherson and Jetz 2007). Past research has found, for example, that future habitat predictions for fish species that occupy narrow elevational and thermal gradients or are widely distributed tend to be among the most consistent across SDM algorithms, climate models, and emissions scenarios (Buisson et al. 2010). On the other hand, a study on forest tree species suggests that spatial uncertainty among future habitat maps may be highest for species with high habitat specialization (Zhang et al. 2015). Aspects of species’ geographic distributions, such as elevational position and topographic heterogeneity, have strong effects on predictions of species’ vulnerability to climate change (Rose et al. 2023); and alternative approaches to characterizing the niche space and taxonomy of endangered species also lead to quite different predictions of potential range (Thorne et al. 2013). Such factors may influence uncertainty in future projections of habitat availability, although this relationship has not been tested.

Given that consensus methods are purported to reduce uncertainty in SDM projections, and that numerous SDM consensus methods exist to aggregate SDM projections, it is crucial to understand the degree of uncertainty found among these methods. To better understand how different consensus methods within an ensemble modeling framework influence estimates of species' range change under climate change and change in pixel-level species richness, we evaluated five consensus methods (Table 1) under climate change scenarios for 82 plant species native to California. We assessed model predictions under different combinations of global circulation models (GCMs), emissions scenarios (RCPs), time periods (mid-century and end-of-century), and dispersal assumptions (no and full dispersal). We asked the following research questions: i) What is the relative importance of each factor on the variability in species-level habitat suitability change and pixel-level change in species richness? ii) How do SDM consensus methods differ in their likelihood of predicting extreme changes in the extent of suitable habitat? and iii) How do species' rarity and geographic traits relate to uncertainty in species-level habitat suitability change?

Methods

Motivated by the need to assess climate change risk to floristic diversity in a plant diversity hotspot, we conducted this analysis for 82 terrestrial plant species in the California Floristic Province (CFP) (Figure S2.1). The CFP is a biodiversity hotspot characterized by a Mediterranean-type climate, rich flora, and high endemism (Myers et al. 2000). The 82 species represented heterogeneous range characteristics allowing us to relate aspects of their rarity and geography to uncertainty in habitat suitability change (question iii). Here we describe the species occurrence data collection and cleaning procedures, environmental data used as predictors, construction of SDMs, projection scenarios, measures of change in species' habitat suitability and richness used to assess uncertainty at the species level and across species, and analyses used to address the research questions.

Species records

Presence-absence records were compiled from vegetation surveys and Calflora between the years 1980-2020. Vegetation survey data were compiled by Dr. James Thorne (University of California Davis) and California Department of Fish and Wildlife and included two survey methods: rapids and relevés (Hannah et al. 2008). Rapid surveys were used as “presence-only’ data as these do not include full vegetation inventories and were part of various targeted surveying efforts (e.g., monitoring incidences of Sudden Oak Death). The relevé data included complete species lists and can be used as reliable absences if the species is not listed as present. We also included records from Calflora (www.calflora.org/) with medium or high location quality that were collected after 1980 as additional species presences. We only retained one presence or absence per 270 m raster grid cell. Among all 82 species, the number of presences available for modeling after filtering ranged from 22 to 4,854. The complete modeling workflow is described in the Overview, Data, Model, Assessment and Prediction (ODMAP) protocol (Zurell et al., 2020; Table S1.5 procedure for presence-absence species).

Current and future environmental data

We selected hydroclimatic, terrain, and soil predictors associated with plant distributions in water-limited ecosystems like California to build SDMs (Stephenson 1998, Kueppers et al. 2005, Dubuis et al. 2013). The hydroclimatic variables are derived from the California Basin Characterization Model (BCM) and include climatic water deficit, actual evapotranspiration, minimum monthly temperature, and wet- and dry-season precipitation averaged to ‘climate normals’ from annual values for the years 1981-2010 (Flint et al. 2013). These variables are available at 270 m spatial resolution and have been used to project plant species’ responses to various climate change scenarios in California (Ackerly et al. 2015, Thorne et al. 2017). For more details on the BCM, see Appendix S2.

Edaphic factors and landscape position also limit the spatial distributions of plants and including them as predictors in SDMs produces more reliable models than climate-alone (Kueppers et al. 2005, Coudun et al. 2006, Coudun and Gégout 2007, Dubuis et al. 2013, Velazco et al. 2017). Therefore, we also included soil pH, available water holding capacity, soil depth, percent clay (Gridded National Soil Survey Geographic Database, gNATSGO), and categorical landform types (n= 15) that reflect hillslope position and dominant soil formation processes (Theobald et al. 2015). In this study, we assumed that soil and landform conditions will remain constant between the baseline and future time periods (1980-2010, 2040-2069, and 2070-2099). All variables were resampled to 270 m using bilinear interpolation using the *terra* package in R (Hijams, 2022).

To assess variability in biodiversity scenarios due to different climate models and emissions pathways, we selected two global circulation models (GCMs), CNRM-CM5 (Voldoire et al. 2013) and HadGEM2-ES (Collins et al. 2011), and two emissions Representative Concentration Pathways (RCP), RCP 4.5 and 8.5 (van Vuuren et al. 2011). Predictions under the GCMs range from cooler, wetter (CNRM-CM5) to warmer, drier (HadGEM2-ES) relative to baseline, with moderate change projected under RCP

4.5, which assumes a reduction in greenhouse gas emissions required to stabilize radiative forcing, and “business-as-usual”, i.e., increasing greenhouse gas emissions, under RCP 8.5. These models and scenarios effectively capture the precipitation and temperature variability in climate change projections for California during the 21^{st} century (Pierce et al. 2018). BCM hydroclimatic variables projected using these GCMs and RCPs also were calculated based on 30-year climate normals for mid- and end-of-21st century (Table 2).

Species distribution models

We constructed SDMs with six commonly used algorithms: generalized linear models (GLM), generalized additive models (GAM), boosted regression trees (BRT), random forests (RAF), artificial neural networks (ANN), and support vector machines (SVM). SDMs built with default settings often do not perform as well as models built with species-specific hyperparameter tuning (Warren et al. 2014, Schratz et al. 2019), so we performed hyperparameter tuning for all machine learning methods (Table S1.7). We then combined individual algorithms with area under the receiver operating characteristic (AUC) > 0.7 using five consensus methods: 1) mean, 2) true skill statistic (TSS) weighted mean (meanw), 3) mean of models with higher-than-average TSS for a given species (meansup), 4) mean of suitability values above the threshold that maximizes sensitivity and suitability for each individual model (meanthr), and 5) median (Table 2.1). See Figure S2.2 for mapped outputs of the five different consensus methods under current climatic conditions for Engelmann oak (*Quercus engelmannii*), a rare tree species included in the current study.

Model calibration area affects predicted suitability patterns and can even inflate some model performance metrics (Acevedo et al., 2017; Lobo et al., 2008; VanDerWal et al., 2009), so the calibration area for each species was defined by the Jepson ecoregion(s) that contained occurrences. Including absence records in areas beyond a species range can distort model outputs, with predictions of high suitability in regions where a species is known not to occur, i.e., "naughty noughts" (Austin and Meyers 1996), and this distortion was mitigated by using occupied ecoregions to select absences. We used geographic cross-validation to partition species occurrences and evaluate how a model trained with data from one area performed on data in another area. This method is particularly useful for evaluating model transferability to new time periods or locations (Roberts et al. 2017, Santini et al. 2021). We tested 30 different block grid-sizes for species with ≥30 occurrences, blocks ranging from 13.5 km^2 to 81 km^2, and used to divide species presence and absence records into three to four spatially structured partitions that reduce spatial autocorrelation. For species with <30 occurrences, we tested between 3 and 30 latitudinal bands and partitioned species' records into only two partitions. For both approaches, the optimum partition selected was the one that equilibrated spatial autocorrelation (Moran's I), environmental similarity (Euclidean distance), and differences in the amount of data among partition groups (Standard Deviation - SD) (Velazco et al. 2019). We calculated three performance metrics for each SDM and consensus method: AUC, TSS, and the continuous Boyce index.

Habitat suitability change and species richness

Using each SDM projection under future scenarios (6,560 projections = 82 species * 5 consensus methods * 2 dispersal scenarios * 2 time periods * 2 RCPs * 2 GCMs; Table 2.2), we calculated species-level metrics of habitat suitability change (HSC) based on continuous habitat suitability values predicted under each model and scenario (Garcia et al. 2014). HSC measures the change in environmental suitability for a given species, model, and scenario relative to the currently occupied area based on the sum of suitability values across all grid cells (Equation 1). Occupied habitat included all suitable habitat patches for the baseline period (1980-2010) that contained at least one species occurrence (Mendes et al. 2020). For each species, we produced maps of currently occupied habitat for each consensus method that were then used as the baseline habitat suitability for the corresponding consensus predictions. Under the "no dispersal" assumption, we considered changes in habitat suitability within species' currently occupied area only (i.e., future habitat suitability was restricted to areas already occupied by the species), while the "full dispersal" scenario included all suitable areas projected outside of species' current distributions (i.e., whole study area –CFP). For each species, there were 80 estimates of habitat suitability change.

$$Habitat\ suitability\ change = \left(\frac{future\ \ habitat\ suitability_{sum} - baseline\ \ habitat\ suitability_{sum}}{baseline\ habitat\ suitability_{sum}}\right) \quad (1)$$

In addition to species-level HSC, we calculated a composite metric of projected biodiversity change, the relative change in suitability-weighted species richness at the pixel-level (270 m) (Thuiller et al. 2019) using all species' habitat suitability projections under future conditions. Here, species richness in a grid cell equals the sum of continuous habitat suitability values across all species. Relative change in species richness corresponds to the difference between future and baseline species richness divided by the baseline species richness in each grid cell. Our analysis produced 80 maps of relative change in species richness across the models and scenarios in Table 2.

Data analysis

i) Estimating the relative influence of each factor on future uncertainty

We used variance partitioning, represented by the percentage of explained deviance, to assess the importance of each factor (Table 2) in explaining the variance in predictions of change in habitat suitability (HSC) and species richness under future climate change, following methods presented by Thuiller et al. (2019). We partitioned the effects of SDM consensus methods, GCMs, and RCPs for each species (HSC) or pixel (change in species richness) using a nested ANOVA framework in which SDM consensus methods were the first level, followed by GCMs and RCPs. We did not include time period or dispersal assumption in the variance partitioning but showed how the variance explained by the other factors varies across the two time periods and dispersal scenarios. To visualize spatial patterns of uncertainty in species richness change, we calculated and mapped the standard deviation across all future projections and then for each uncertainty factor separately by first averaging predictions in species richness change across the other factors.

i) Likelihood of predicting extreme future habitat change

Habitat suitability change can be summarized based on the amount of stable habitat (current “in-situ” habitat that remains suitable) and habitat gain (the amount of habitat that becomes newly suitable “ex-situ” under a future scenario). To understand how SDM consensus methods differ in their likelihood of predicting change in the extent of suitable habitat, we considered four non-mutually exclusive categories of habitat suitability change, adapted from Beaumont, et al. 2016 (Figure 2.1). All categories are expressed as proportional to baseline habitat suitability within the currently occupied range and are based on calculations from either no dispersal or full assumptions, depending on the change category.

a) Low stability within current habitat (<40% of current in-situ habitat remains, no dispersal)
b) Low gain outside of current habitat (<40% gain outside of current habitat relative to current habitat, full dispersal)
c) High stability or gain within current habitat (>100% suitability increase within in-situ habitat, no dispersal)
d) High gain outside of current habitat (>100% increase in ex-situ habitat relative to current habitat, full dispersal)

Following Beaumont et al. (2016) methods, we used exact Chi-squared goodness-of-fit tests to evaluate the null hypothesis that the five SDM consensus methods would be equally represented in each extreme habitat suitability change category for the end-of-century (2070-2099). For example, in the case of low stability within current habitat, the null hypothesis is that each of the five consensus methods will be represented in 20% (⅕) of observed predictions of low habitat stability. Expected frequency was calculated as 0.2 multiplied by the total number of predictions within each extreme change category for each GCM, RCP, and time period and was compared to the observed proportional representation of each consensus method for each of the GCMs and RCPs. We examined the standardized residuals to explore which methods contributed most to the chi-square test results (standardized residuals > |2| are considered significantly different than expected by chance).

ii) Relating species' rarity and geographic traits to uncertainty

To investigate the relationship between species' characteristics and uncertainty in future projections of HSC, we first calculated three rarity traits based on species occurrences and environmental data used for modeling: prevalence, range size, and niche breadth. Sample prevalence was calculated as the number of species presences relative to absences. Range size was calculated as the area in km^2 encompassed by the minimum convex polygon that contained all species' occurrences used for modeling. We measured niche breadth with the hydroclimatic and soil variables used to build SDMs, as described in Rose et al. (2023), adapting methods developed by Vela Díaz et al. (2020). Additionally, we calculated four species-level geographic traits based on species occurrences and environmental datasets, including mean elevation, the range in elevation (difference between the average of the top and bottom 10%), mean topographic heterogeneity, and range in topographic heterogeneity.

To quantify uncertainty in HSC, we calculated the standard deviation of habitat suitability change values for each species across predictions made for the end-of-century period (2070-2099) (greater variability among HSC values representing greater uncertainty). To capture the variability in HSC introduced by each uncertainty component, we calculated the standard deviation in HSC between the modalities of one factor after averaging predictions across the modalities of the other two factors (Buisson et al. 2010). We estimated simple linear models for each rarity and geographic trait as the predictor and standard deviation in HSC as the response variable (results presented in Table S2.1, Figs. S2.3 and S2.4). Evaluating the correlation coefficients between all explanatory variables revealed relatively weak relationships (Pearson correlation coefficient ≤ 0.60, Figure S2.5). We then estimated multiple stepwise regression models for each uncertainty source and dispersal scenario (6 final models), including all rarity and geographic traits as predictors. The combination of simple and multiple regression models allowed us to explore both the individual influence of each rarity and geographic trait on HSC variability as well as which species' characteristics affected prediction uncertainty after accounting for other factors. For models relating species' rarity and geographic traits to HSC variability under full dispersal, we log-transformed the response variable so that the residuals more closely followed a normal distribution.

Results

Model performance

In total, we produced 902 SDMs (82 species * 11 SDMs - six algorithms and five consensus methods). Models performed well, overall (mean AUC = 0.88, mean TSS = 0.67, mean Boyce index = 0.86). The number of algorithms used in the consensus models ranged from three to six for each species. Consensus methods performed marginally better than individual algorithms across all performance metrics, except the meanthr consensus method (Figure S2.6).

Variance partitioning

i. Habitat suitability change

The relative influence of consensus methods, GCMs, and RCPs on projections of habitat suitability change varied depending on time period and dispersal assumptions (Figure 2.2). The choice of consensus methods explained the most deviance in habitat suitability change under full dispersal for the mid-century time period, with very high variability across species (mean = 59.0, sd = 30.1), followed by GCM (mean = 27.5, sd = 22.5) and RCP (mean = 13.5, sd = 11.9). For the end-of-century projections under full dispersal assumptions, choice of consensus methods still explained the most deviance in habitat suitability change (mean = 50.7, sd = 28.9) but was followed by RCPs (mean = 29.8, sd = 24.3) and then GCM (mean = 19.5, sd = 23.5). Under no dispersal, GCMs explained the most deviance in projections for 2055 (mean = 37, sd = 23.4), while RCPs were more important for habitat suitability change estimated for 2085 (mean = 44.6, sd = 24.5). No-dispersal estimates of habitat suitability change for both time periods were least affected by the choice of SDM consensus methods.

ii. Pixel-level change in species richness

The influence of consensus method, GCM, and RCP on uncertainty in changes in species richness at the pixel level varied only slightly under different dispersal assumptions and time periods (Figure 3). Across scenarios and time periods, percent explained deviance was highest due to SDM consensus method under full dispersal, end-of-century predictions (mean = 59.2, sd = 22). Consensus method ranked as the most important uncertainty factor, accounting for >50% of explained deviance under dispersal scenarios and time periods. As with the species-level HSC metrics, we found that RCP had a greater effect on end-of-century projections (% explained deviance mean = 25.1, sd = 20.6) than mid-century (mean =17, sd = 15), while GCM tended to matter more for mid-century (mean = 28.8, sd = 23.1) than end-of-century projections (mean = 18.1, sd = 17.9).

As demonstrated by the spread of the violin plots presented in Figure 2.3 and the large standard deviations in percent explained deviance, the relative influence of each investigated component (consensus method, GCM, and RCP) on predicted changes in species richness varied substantially at the pixel level. Furthermore, the variability in projected change in species richness depended on spatial region (Figure 2.4). Standard deviation in turnover across all projections ranged from 9.3% to 522.1%, and half of the study area had standard deviations > 65.0%. Standard deviation in predicted percent change in species richness for the 82 study species was highest in the southern portion of the Great Central Valley. Such a trend was found across all three investigated factors, with lower overall variability in the northern portion of the Great Central Valley, along the coast, and in southwestern California. Standard deviation due to time period, RCP, and GCM was relatively low (on average 7.5%, 6.9%, and 11.7%, respectively). Variability in changes in species richness was highest between dispersal scenarios (mean = 66.8%), followed by differences between consensus methods (mean = 21.6%).

Do consensus methods equally predict extreme habitat suitability change?

We evaluated the null hypothesis that five SDM consensus methods were equally likely to predict four categories of extreme habitat suitability change under climate change by the end of the century (2070-2099). Chi-squared test statistics ranged from 0.68 to 10.89 for the four habitat suitability change categories (Table 2.3). Overall, there was little evidence that consensus methods consistently differed significantly in the frequency with which they predicted extreme change, except low habitat suitability gain for the HadGEM2-ES GCM where there was strong evidence that consensus methods differed in their predictions of low habitat gain.

Low in-situ habitat stability (i.e., current habitat loss >40%) was the least frequently predicted extreme change category, representing 10.2% of all end-of-century predictions (Table S2.3). Although differences between consensus methods for this category were insignificant overall, the standardized residuals show that for GCM CNRM-CM5 RCP 8.5, the meanthr method was more likely to predict low levels of habitat stability than the other methods (Figure 2.5). For predictions of low habitat suitability gain outside of currently occupied habitat (24.7% of predictions), the median method was overrepresented in every climate change scenario, i.e., it was the method most likely to predict low levels of ex-situ habitat gain. All consensus methods were equally likely to predict scenarios of high habitat stability in-situ (35.5% of predictions) and high habitat suitability gain ex-situ (61.0% of predictions).

Relationship between species' attributes and uncertainty

The relationships between species characteristics and uncertainty in HSC differed substantially depending on dispersal assumptions (Figure 2.6). Under no dispersal assumptions, stepwise multiple regression models indicated that species with low prevalence and/or covering narrow ranges in topographic heterogeneity were associated with the highest uncertainty levels in HSC due to SDM consensus method. Similarly, species with small range sizes were associated with the greatest uncertainty in HSC due to GCM. Species with the greatest variation in predicted HSC under different RCP scenarios tended to be those located at high elevations, in areas with low topographic heterogeneity, and restricted ranges in elevation and topographic heterogeneity. Under full dispersal, uncertainty due to SDM consensus method was highest for species with low prevalence, small range sizes, and, to some degree, those occurring at low elevations. Species occurring over broad elevational gradients tended to have higher uncertainty due to SDM consensus methods. High uncertainty in HSC due to GCM was associated with small-ranged species and those located at lower elevation. Surprisingly, after accounting for the effects of range size, species with broader niche breadth were also associated with higher HSC uncertainty due to GCM. Finally, species with small range sizes were associated with the greatest uncertainty due to RCP scenario.

Discussion

In this study, we 1) assessed the relative contributions of different SDM consensus methods, climate models, and emissions scenarios to uncertainty in ensemble projections of plant species-level habitat suitability change and pixel-level plant species richness, 2) evaluated whether SDM consensus methods are equally likely to predict extreme changes in species habitat suitability, and 3) related species' rarity and geographic traits to uncertainty in projections of habitat suitability change. We found that differences between consensus methods contribute to >50% of explained deviance under full dispersal projections of future habitat change and that this contribution is reduced substantially under assumptions of no dispersal, where climate model and emissions scenario are more important. SDM consensus methods largely predicted extreme changes in habitat suitability with equal frequency, except for the median method which was the method most likely to predict low levels of ex-situ habitat gain. Finally, we found that measures of species' rarity and geography helped explain differences in the observed patterns of species' habitat suitability change. However, the importance of these characteristics depended on the source of uncertainty.

When using consensus methods in ensemble predictions of species vulnerability, which uncertainty factors matter most?

Consensus methods have long been proposed (Araújo and New 2007) to reduce the well-known uncertainty (variability) in model performance and spatial habitat predictions by different algorithms (Segurado and Araújo 2004, Syphard and Franklin 2009) – variation that is even greater when models are projected for other time periods (Thuiller 2004). However, we found considerable variation in habitat projections under climate change among consensus methods for many species. On average, variation in species-level habitat suitability change (HSC) calculated based on different consensus methods was greater than variability due to climate model or emissions scenario under full dispersal assumptions. Conversely, for in-situ (no dispersal) projections of habitat change within species' currently occupied area, variability between different emissions scenarios was higher than variability due to consensus method or climate model. Similarly, Thuiller et al. (2019) found that the influence of SDM method on uncertainty for species-level sensitivity metrics was much stronger under limited- than no-dispersal and that under no dispersal, uncertainty due to differences between RCP scenarios surpassed the variability introduced by SDM consensus methods or GCMs, especially for later time periods.

The influence of consensus methods was even more pronounced on variability in predictions of pixel-level changes in species richness and contributed more to the variability in these projections than GCM or RCP, on average. These findings emphasize that using an ensemble of projections from different algorithms is not a panacea for model uncertainty –different consensus methods can produce inconsistent projections of future habitat suitability. When evaluating the spatial distribution of uncertainty, we found that differences in biodiversity predictions made under different dispersal assumptions outweighed the differences observed due to other uncertainty components, followed by SDM consensus approach. The variation between dispersal scenarios, which dominates the variation due to all factors in biodiversity predictions, is pronounced in southern Great Central Valley which is predicted to become increasingly hot and dry under the HadGEM2 projections. The climate there is projected to become suitable for many species currently in the warmest parts of the CFP (disjunct from the southern portion of the Great Central Valley) and so allowing unlimited dispersal leads to highly variable predictions for that area, as some scenarios predict many range expansions, while others do not.

Likelihood of different consensus methods to predict extreme habitat suitability change

Summary measures of habitat suitability change predicted by SDMs, such as percent range change over time, are among the most common metrics used for assessing species' vulnerability to global change. Past research demonstrates that some algorithms, such as random forests, may be more likely to predict future habitat loss than others (Beaumont et al. 2016). Overall, consensus methods did not differ significantly in the frequency with which they predicted specific types of extreme habitat change, except that the median consensus method was more likely to predict low habitat gain outside of the current habitat than other methods. The median is less affected by outliers than the mean, and subsequently, less susceptible to one or two individual algorithms that predict high gains in habitat suitability outside a species' current range. This finding indicates that the median method may be especially useful for making conservative predictions of future habitat gain, though the patterns predicted by different consensus methods should be explored for other species groups.

It is important to note that although SDM consensus methods overall did not show a tendency to predict patterns of extreme habitat change, the variation in predictions of habitat suitability change between different consensus methods for a single species was often quite high. For example, for Torrey pine (*Pinus torreyana*), a critically endangered tree species restricted to coastal San Diego County, habitat suitability projections constructed from the five consensus methods under a single dispersal, climate model, and emissions scenario ranged from an 18% reduction in habitat to a 27% increase in suitable habitat. This example highlights the importance of considering the results of multiple SDM consensus approaches instead of relying on a single averaged output for conservation decision making. Meller et al. (2014) evaluated the implementation of different consensus methods for conservation prioritization, noting that decisions are highly sensitive to different summarizing approaches. When using SDM consensus approaches for conservation prioritization, we recommend that modelers carefully evaluate model performance using a variety of metrics and provide spatially explicit estimates of the variability observed between consensus methods.

How do rarity and geography relate to uncertainty in habitat suitability change?

Species characteristics, such as aspects of their rarity and geography, can influence their vulnerability to anthropogenic change and it is important to consider how they may influence the variability in range change predictions. While some research suggests that SDM-based habitat projections for specialist species tend to be more consistent than those produced for generalists (Buisson et al. 2010), others have found that consensus SDM methods produce more spatially congruent future range maps for generalist species (Zhang et al. 2015). We found that species with small range sizes were associated with the greatest variability in predicted habitat suitability change, especially under full dispersal assumptions. When species’ ranges are small in relation to the entire study area, it is very likely that many regions identified as suitable habitat are due to the range of environmental conditions used to build the models differing from those found in the projection data, i.e., extrapolation, even when those future projections are derived from consensus methods. Therefore, evaluating and addressing the severity of model extrapolation is essential when projections to novel time periods and areas are made (Elith et al., 2010; Rousseau and Betts 2022).

After accounting for the effect of range size, generalist species (those with broad niches) tended to have higher variability in habitat projections made under different GCMs given unlimited dispersal. We also found that species with high model accuracy tended to be those with the most consistent predictions of future habitat suitability change, with the notable exception of some small-ranged species with high model performance but high variability in predicted HSC (Figure S2.7). This pattern suggests that high model performance does not necessarily correspond to consistent predictions of future habitat because species with geographically restricted ranges are also often highly vulnerable to extinction (Staude et al. 2020). The finding that rare species tend to have more variable projections of habitat change, even when model performance is high, warrants careful model construction and consideration when making conservation decisions using SDM outputs.

Multiple algorithms, climate models, and emissions scenarios are often included in SDM research that focuses on predicting future habitat change (i.e., ensemble forecasting). Each of these components introduces unique variability to distribution maps and a summary measure of habitat change. Buisson et al. (2010) found similar relationships between species range characteristics and variability in range change due to different uncertainty components, with the exception that species with broader latitudinal, stream gradient, and elevation ranges were associated with greater range change variability under different climate models but lower variability due to other uncertainty components. The relationships between species attributes and the variability in future habitat projections varied depending on the source of variability and dispersal assumptions. For example, species prevalence, i.e., the ratio between presence and absence data used for modeling, was only related to variability in HSC projections due to SDM consensus method, where low prevalence was associated with high variability. Although prevalence can serve as an imperfect proxy for species rarity vs. commonness, it is also a data attribute that contributes to a model's ability (or inability) to successfully estimate the species-environment relationship (McPherson et al. 2004).

Species at high elevations, in regions with low topographic heterogeneity, and/or narrow elevational and topographic ranges were associated with the most variable predictions in habitat suitability change under no dispersal between RCPs. It is for these species that the ecological benefits of climate change mitigation will be greatest. This finding emphasizes the importance of geographic position regarding climate change under varying levels of greenhouse gas emissions – a component of uncertainty that heavily depends on human decisions to mitigate (or not) ongoing climatic change. The magnitude of climate change under different RCPs will be spatially structured in California, and the Sierra Nevada and surrounding foothills are expected to experience widely varying temperature changes and drought stress depending on the trajectory of greenhouse gas emissions (Pierce et al. 2018; Thorne et al. 2015). Our findings indicate that the variability in habitat projections made under different emissions scenarios is also spatially structured, leading to greater variability in future trajectories for species in certain geographic contexts. For example, of our study species, in-situ habitat for the emblematic giant sequoia (*Sequoiadendron giganteum*), a relict conifer endemic to the western slopes of the Sierra Nevada, is predicted to be the most impacted by increased greenhouse gas emissions (30% habitat reduction under RCP 4.5 vs. 85% reduction under RCP 8.5).

Conclusion

SDMs are among the most popular tools used for predicting the potential fate of species under global change. Our results support the common adage that ensemble forecasting, in which a variety of algorithms, climate models, and emissions scenarios are used to assess the range of possible futures for a particular species, is a necessity to better capture the variability introduced by these modeling components. Within ensemble forecasting, combining SDM algorithms using consensus methods may allow researchers to leverage multiple modeling techniques and reduce some uncertainty in SDM studies. However, the variability between future habitat predictions made by different consensus methods can be quite high, often outweighing the effects of different climate models and emissions scenarios. Furthermore, it has long been acknowledged that species characteristics should be considered when projecting the distribution of suitable habitat under novel conditions. We encourage SDM practitioners to consider multiple consensus approaches, evaluate their species-specific performance, and assess model extrapolation when considering habitat change outside of species' current distributions, especially when projecting species with low prevalence and small range sizes, which tend to be of greatest conservation concern yet produce highly variable model outputs.

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Tables and Figures

Table 2.1 Consensus SDM methods explored in this paper.

Consensus method	Definition/Description	Examples
Mean	Average suitability values of individual models	Predicting distribution of tree species in China under climate change (Zhang et al. 2015)
Performance weighted mean (meanw)	Average suitability values weighted by performance of individual models	European conservation areas under climate change (Araújo et al. 2011) Bird reserve network design (Meller et al. 2014)
Mean of best models (meansup)	Average suitability values of the highest performing model(s) (TSS, AUC, etc.)	Compare performance of different SDMs for a variety of organisms (birds, butterflies, plants, and vegetation types) (Norberg et al. 2019)
Mean of cells with suitability above a threshold (meanthr)	Average of suitability values for cells that are above a given threshold for all individual models	Bird reserve network design (Meller et al. 2014) - binary presence/absence predictions Plant exposure under climate and land use change (Rose et al. 2023)
Median	Median suitability values of individual models	Forecast spatial distribution of threatened plant species; assess ensemble model accuracy (Marmion et al. 2009) Climate and land use effects on Chinese woody flora (Peng et al. 2022)

Table 2.2 Models and scenarios evaluated for each species under future habitat projections.

Type	**Factor**	
Model	Ensemble model	Mean Meanw Meanthr Meansup Median
Scenario	Dispersal	No dispersal Full dispersal
	Time period of climate projections	2055 (2040-2069) 2085 (2070-2099)
	Global Circulation Model (GCM)	HadGEM2-ES (hot, dry) CNRM-CM5 (warm, wet)
	Representative Concentration Pathway (RCP)	RCP 4.5 (moderate emissions) RCP 8.5 (business-as-usual emissions)

Meanw = true skill statistic (TSS) weighted mean (meanw); meanthr = mean of suitability values above the threshold that maximizes sensitivity and suitability for each individual model; meansup = mean of superior models (models with higher-than-average TSS for a given species)

Table 2.3 Chi-square statistic for each extreme habitat suitability change category across all climate change scenarios for the end-of-century time period (2070-2099)

	χ^2			
Extreme change	**CNRM-CM5**		**HadGEM2-ES**	
	RCP 4.5	**RCP 8.5**	**RCP 4.5**	**RCP 8.5**
Low stability (a)	2.46	8.52	4.72	1.78
Low gain (b)	9.27	6.85	**10.31^{+}**	**10.89^{+}**
High stability (c)	0.67	3.97	3.42	5.12
High gain (d)	3.06	1.97	3.47	1.74

(+) denote the significance of the Chi-square statistic: $^{+}P < 0.05$.

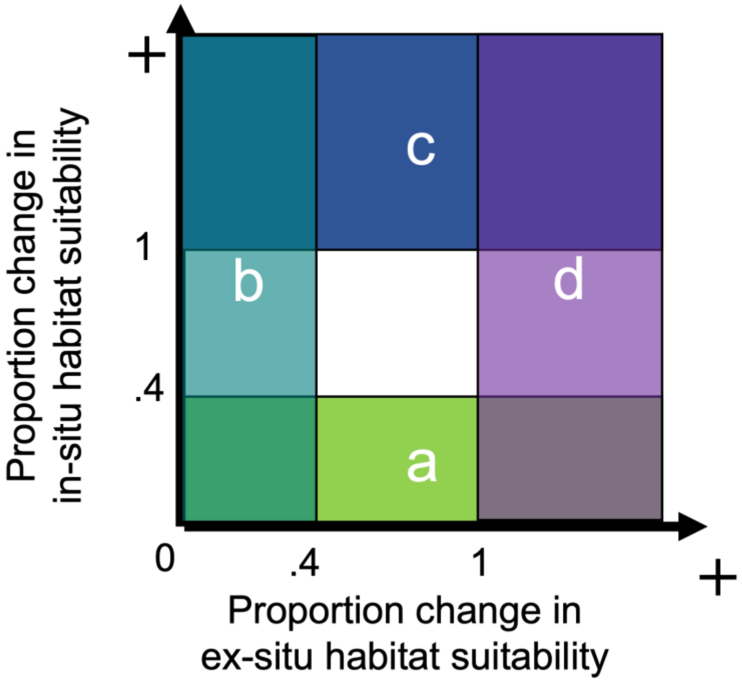

Figure 2.1 Projected habitat suitability change summarized along two axes: "Proportion change in ex-situ habitat suitability" and "Proportion change in in-situ habitat suitability". We calculated the number of predictions from five SDM consensus methods that were in the following "extreme" categories shown above: a) low stability within current habitat (<0.4 in-situ habitat remains), b) low gain outside of current habitat (prop. change ex-situ <0.4), c) high stability/gain within current habitat (prop. change in-situ >1), and d) high gain outside of current habitat (prop. change ex-situ >1).

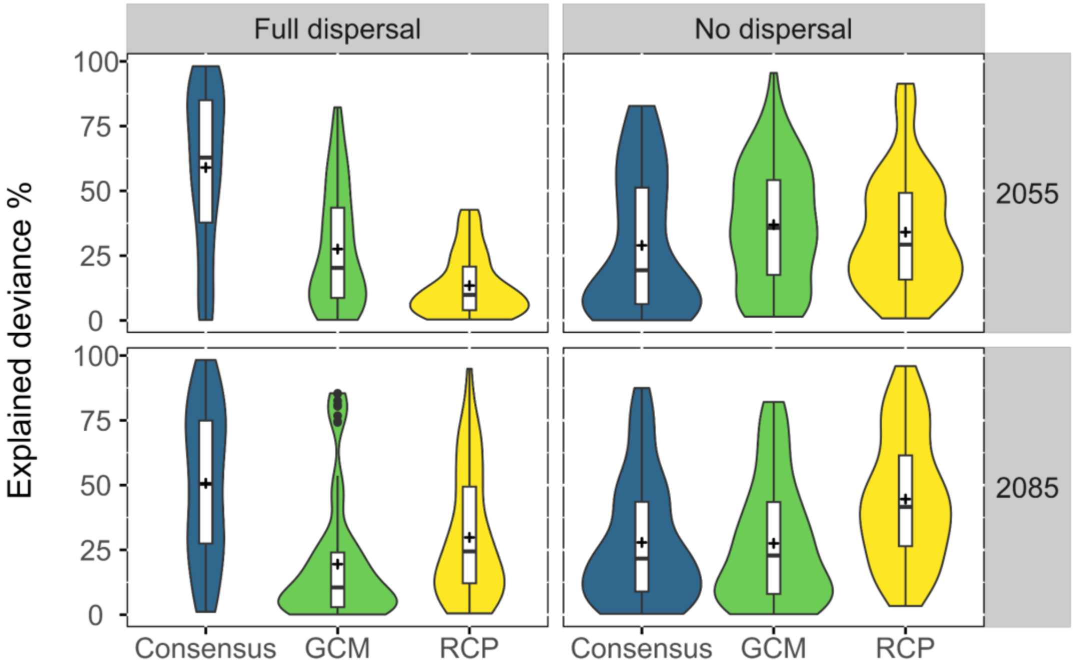

Figure 2.2 Percent explained deviance of uncertainty factors (SDM consensus method, GCM, and RCP) on projections of species' level habitat suitability change (HSC). Deviance was calculated across all species using a nested ANOVA and partitioning is represented by the percentage of explained deviance. Horizontal lines in the boxplots show the first quartile, median, and third quartile of the data and crosses denote the mean.

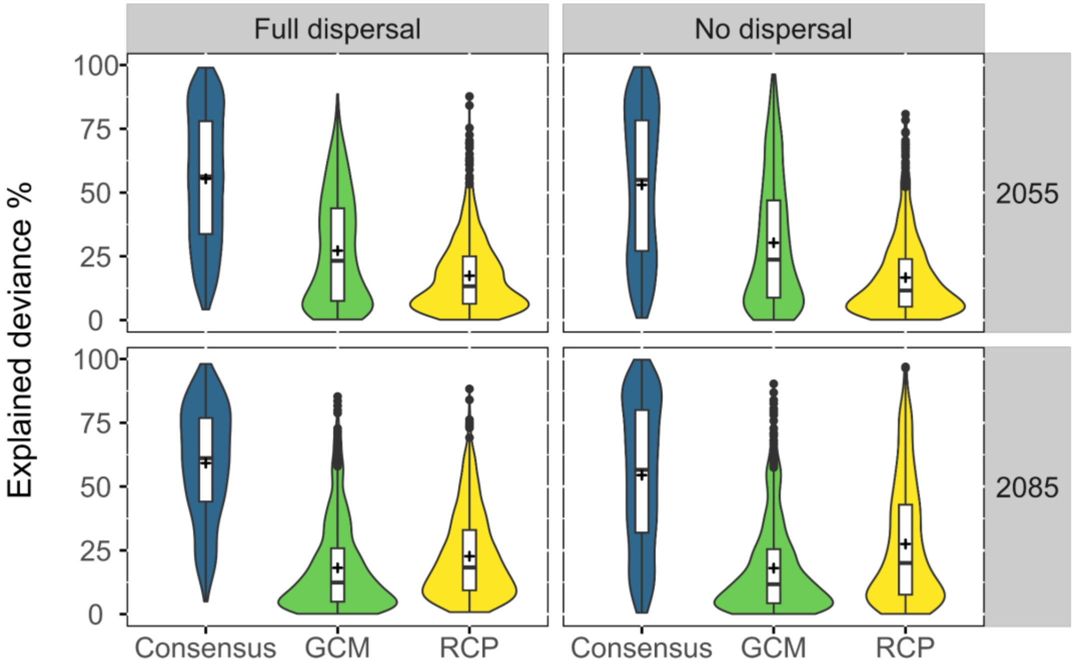

Figure 2.3 Percent explained deviance of uncertainty factors (SDM consensus method, GCM, and RCP) on projections of pixel-level percent change in species richness. Deviance was calculated across all pixels using a nested ANOVA and partitioning is represented by the percentage of explained deviance. Horizontal lines in the boxplots show the first quartile, median, and third quartile of the data and crosses denote the mean value.

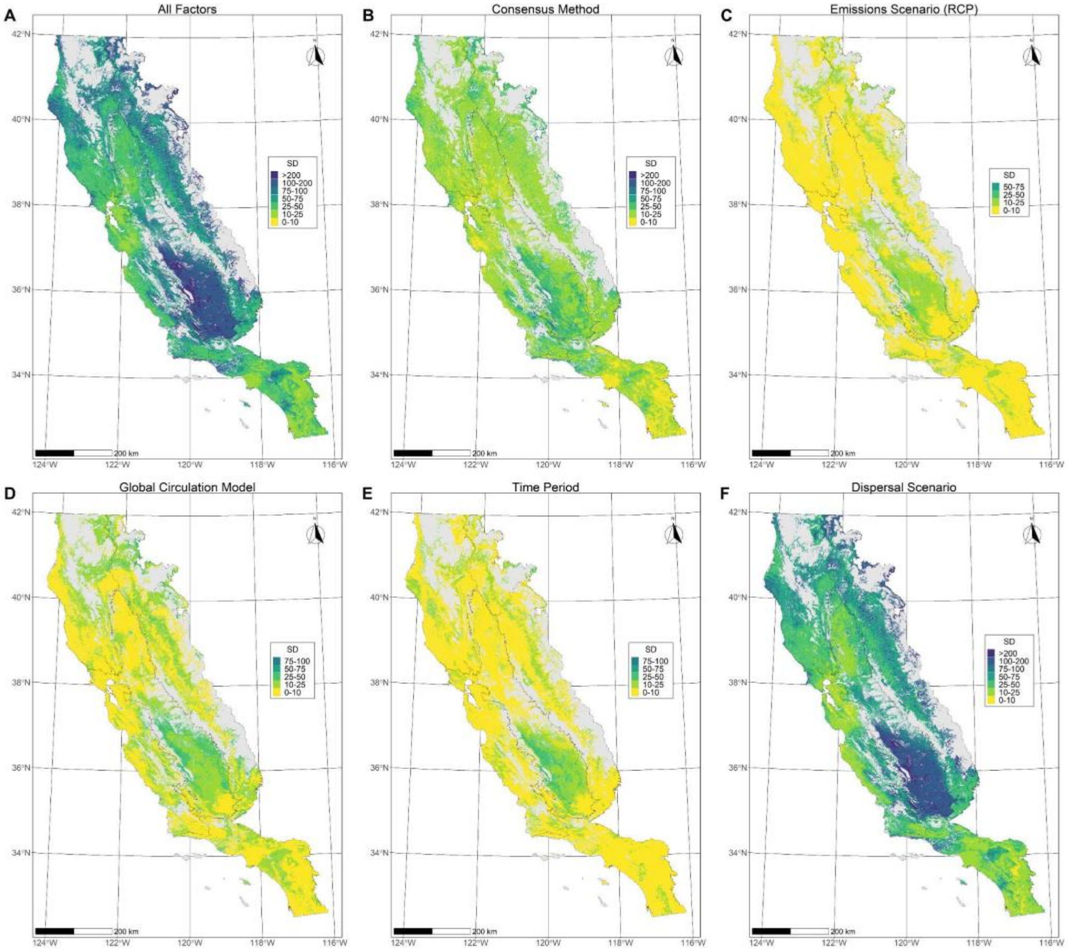

Figure 2.4 Standard deviation of change in species richness (%) across 80 future projections (A), due to consensus model method (B), global circulation model (GCM) (C), emissions scenario (RCP) (D), time period (E), and dispersal assumption (F).

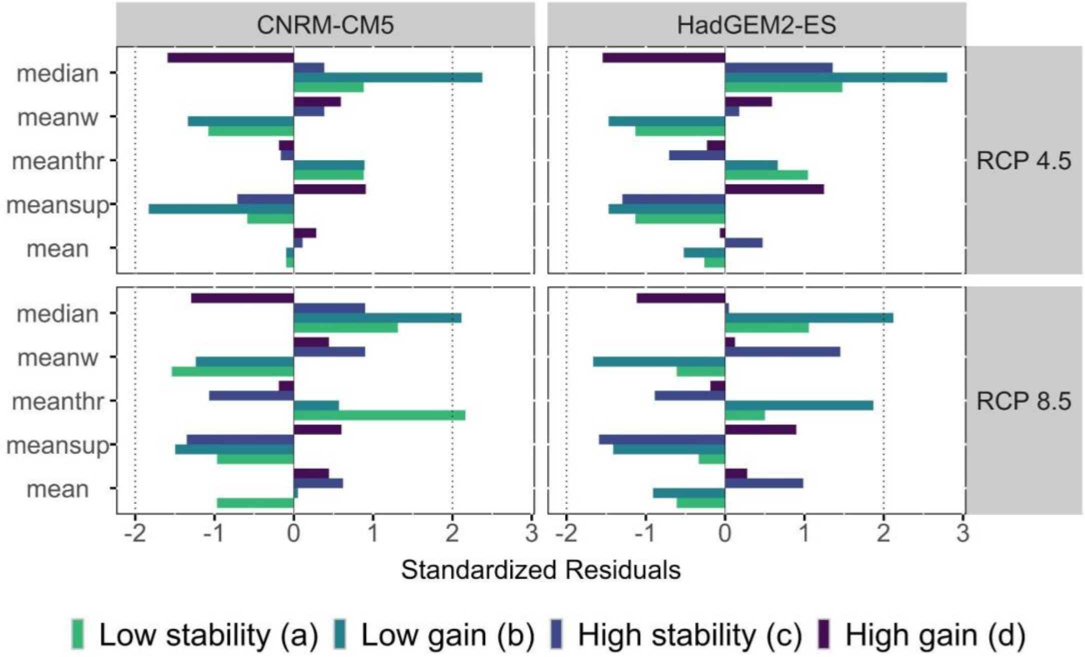

Figure 2.5 Standardized residuals from Chi-squared goodness-of-fit tests used to assess whether five consensus methods differ from one another in the frequency with which they predict four categories of change in habitat suitability for 82 plant species under two GCMs (CNRM-CM5) and RCPs (4.5 and 8.5). Standardized residuals can be used to identify which consensus method contributed most to the Chi-squared test results. The dotted lines indicate where residuals > |2| and represent instances where the observed frequency of the consensus methods differed significantly from the expected frequency for a given change category ($p < 0.05$).

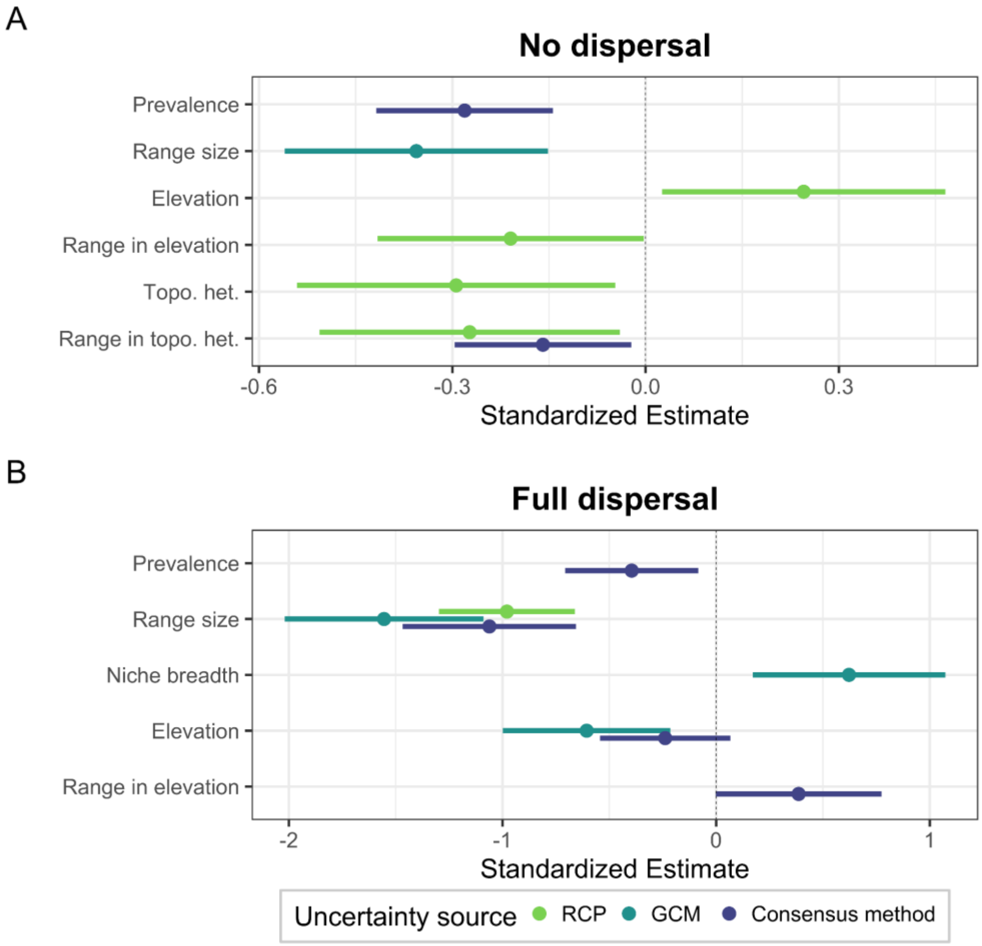

Figure 2.6 Results of six stepwise multiple linear regressions relating species' rarity and geographic traits to uncertainty due to SDM consensus method, GCM, and RCP as measured by the standard deviation in HSC due to each factor under no dispersal (A) and full dispersal (B). Predictor variables were scaled by subtracting the mean and dividing by the standard deviation (z-score).

Chapter 3

Geography of species-specific habitat dynamics under climate change

Abstract

Human activity drives species' loss and habitat degradation globally, especially in biodiversity hotspots, like the California Floristic Province (CFP), that are disproportionately threatened by climate change and habitat conversion. Although vulnerability assessments often focus on summary measures of species' range loss, such as percent range change, the effects of global change vary across species' ranges, impacting some populations and locations more than others. These variations may be mediated by geographic features at various spatial scales, such as latitude, distance to coast, elevation, and topographic heterogeneity. Understanding the within-range dynamics of habitat suitability change is imperative for conservation efforts that can target at-risk populations, as well as protecting those in areas with high habitat stability. Here, we assess the species-specific patterns in habitat suitability change for 82 plant species using species distribution models (SDMs) and projections of future global change in California. We found substantial variation in the geography of predicted habitat suitability change across species' ranges and under different climate models, depending on species' vegetation community and biogeographic characteristics. This work guides us toward a better understanding of how the physical environment and species' ecological tolerances interact to shape potential areas of refugia and vulnerability under global change.

Introduction

Anthropogenic climate change is widely recognized as one of the most significant threats to biodiversity on a global scale (Dawson et al., 2011). In the context of California, temperature projections indicate an expected increase of 2-7°C by the year 2100, while predictions of precipitation change vary widely across different climate models (Pierce et al., 2018). Furthermore, the magnitude of climatic change will vary geographically across the state, and some areas may act as climatic refugia based on their landscape position (Ackerly et al., 2010). Climatic refugia are areas generally characterized by stable temperature and precipitation conditions and are often influenced by landscape features such as latitude, continentality, elevation, and topographic diversity (Stewart et al., 2010; Stralberg et al., 2020). Identifying potential refugia from global change—potential havens where species can persist under changing environmental conditions—as well as those areas that are most vulnerable are key goals of conservation science (Keppel et al., 2012).

As temperatures rise and drought frequency increases, refugia for most species are expected to be located in relatively cool, wet areas (e.g., upward in elevation and poleward) as many species' abilities to survive in the drier, warmer, lower parts of their ranges are expected to decline (Allen & Breshears, 1998). For example, California blue oak (*Quercus douglasii*), a keystone species in the widespread foothill woodland ecosystem, has demonstrated elevated mortality on south-facing aspects, likely due to low moisture availability in the face of drought (Huesca et al., 2021). Past research predicts that most (but not all) California plant species are predicted to move upward in elevation and northward to track optimal conditions as lower elevation, southward populations experience increasingly warmer conditions (Loarie et al., 2008). Empirical observations in the Sierra Nevada have revealed extensive conifer die-backs in the Sierra Nevada at lower elevations (Fettig et al., 2019; Paz-Kagan et al., 2017), which may be partly driven by climate mismatches in these forests (Hill et al., 2023). Historical declines in pine abundance and increases in oak dominance have also been observed, consistent with increasing temperatures and water stress (McIntyre et al., 2015). However, suitable habitat for even currently adjacent species may diverge geographically under future warming as they track optimal environmental conditions within their ranges, with some species moving to higher elevations via a southward path and others moving to lower elevations, but toward the more maritime conditions near the coast.

Despite the general trend towards relatively wetter, cooler habitat, observed distribution shifts are often heterogeneous across species, with many taxa shifting in unexpected directions (e.g., downslope and towards the equator) (Lenoir et al., 2010). Downslope shifts by plant species have been observed across California (Crimmins et al., 2011; Kelly & Goulden, 2008; Madsen-Hepp et al., 2023). These surprising trends may partly be the result of species moving toward hydrologic refugia created by topographic features such as pole-facing slopes and cool air drainages, especially in water-limited ecosystems like those found throughout California. For example, research in the Sierra Nevada mountains suggest that bird species distributional shifts are characterized by opposing climatic forces. In this case, rising temperatures may be driving some species upward in elevation, while increasing water availability at lower elevations is pulling others downslope (Tingley et al., 2012). The idiosyncratic responses of species to climate change indicates that the location of potential refugia in California will be highly species-specific.

Identifying species-specific refugia may also highlight regions that are overlooked by approaches that rely solely on topographic diversity or regional climate patterns (Michalak & Stralberg, 2020; Serra-Diaz et al., 2014). Species' unique ecological tolerances along with "refugia-mediating" geographic features will determine the distribution and characteristics of species' refugia under changing climatic conditions. In addition to varying by species, the location of refugia will inevitably differ depending on the magnitude and direction of climatic change. While most global climate models (GCMs) generally agree that California will continue to warm over the next century (+4-7 °C), changes in precipitation will vary spatially and seasonally depending on GCM (Pierce et al., 2018). These uncertainties arise due to the different ways in which each model represents various atmospheric processes, rates and concentrations of greenhouse gases, and natural climatic variability, e.g., El Niño (Hawkins & Sutton, 2011). Uncertainty in biodiversity projections due to climate models must be considered when trying to identify species-specific climate refugia as species habitat predictions can diverge substantially under different GCMs (see Chapter 2).

Correlative species distribution models (SDMs) are popular tools for identifying species climatic refugia (Baumgartner et al., 2018; Brambilla et al., 2022; Tang et al., 2018), as they provide spatially explicit predictions of relative habitat suitability under various global change scenarios. These models relate species occurrence data to information about the climatic, soil, topographic and other environmental factors at those locations to make inferences about the limiting factors of species' distributions and they produce spatial predictions of species habitat suitability (Franklin, 2010). Although continuous mapped SDM outputs contain important information about relative habitat suitability (Guillera-Arroita et al., 2015), these maps are frequently binarized to distinguish refugia from non-refugia (or areas of vulnerability) -- delineations that can be necessary for conservation prioritization and land management. However, the magnitude of climate impacts on species habitat suitability will vary significantly across species ranges–patterns that are more readily observed from maps of continuous habitat suitability change (Figure 3.1a). Furthermore, retaining maps of continuous habitat change allows us to test which landscape features are most important for mediating species-specific refugia.

We assess how habitat suitability change varies within species ranges for a set of 82 plant species found in the California Floristic Province under two climate models using fine-scale bioclimatic predictors (Flint et al., 2013). Understanding the within-range dynamics of habitat suitability change is imperative for conservation efforts that can target at-risk populations, as well as protecting those in areas with high, persistent habitat stability. Because of the uncertainties associated with using SDMs to make predictions outside of species current distributions (Thuiller et al., 2019), the current research focuses on habitat dynamics within species current ranges (in-situ). We evaluate the species-specific relationships between predicted habitat suitability change and four geographic features: latitude, distance to coast (continentality), elevation, and topographic heterogeneity. In general, we expect species to be more vulnerable to climate warming at their southern range edges, inland, at lower elevations, and in areas with low topographic heterogeneity. However, we expect the relationship between habitat suitability change and geographic features within species' ranges to vary depending on species' vegetation type associations due to similar environmental conditions and biogeographic settings (see Figure 3.1c for example of diverging patterns between a montane conifer – *Abies magnifica*– and a coastal sage scrub shrub species– *Salvia leucophylla*). Although identifying species-specific refugia is data intensive, the results can be subdivided into habitat groups and potentially applied to species with similar environmental tolerances and geographic distributions.

Methods

Study area and species

Our study area included the Californian portion of the California Floristic Province (CFP) (~268,000 km^2) (Figure 3.1). While the full province extends north into the state of Oregon, east into Nevada, and south into Mexico, the fine spatial scale (270 m) hydroclimatic and soil variables we used to build species distribution models are only available for the state of California (Flint et al., 2013). This region has been identified as a biodiversity hotspot (Myers et al., 2000) that is uniquely threatened by pressure from climate change, urbanization, and fire regime shifts (Underwood et al., 2009; Franklin, Regan, and Syphard 2021). The 82 plant species represent a broad range of life history strategies, biogeographic affinities, and range characteristics and are predicted to vary in terms of their climate change responses (Rose et al., 2023) (Table S3.1).

Species data

Presence-absence records were compiled from vegetation surveys and Calflora between the years 1980-2020. Vegetation survey data were compiled by Dr. James Thorne (University of California Davis) and California Department of Fish and Wildlife and included two survey methods: rapids and relevés (Hannah et al. 2008). Rapid surveys were used as “presence-only’ data since they do not include full vegetation inventories and were part of targeted surveying efforts (e.g., monitoring incidences of Sudden Oak Death). The relevé data included complete species lists and can be used as reliable absences if the species is not listed as present. We also included records from Calflora (www.calflora.org/) with medium or high location quality that were collected after 1980 as additional species presences. We only retained one presence or absence per 270 m raster grid cell. Among the 82 study species, the number of presences available for modeling after filtering ranged from 22 to 4,854. The complete modeling workflow is described in the Overview, Data, Model, Assessment and Prediction (ODMAP) protocol (Zurell et al., 2020; Table S2.1).

Environmental data

To model the current and future spatial distribution of each species, we used a combination of hydroclimatic, soil, and landform variables (Table S1.4) that are known to drive plant distributions in water-limited ecosystems (Dubuis et al., 2013; Kueppers et al., 2005; Stephenson, 1998). We selected hydroclimate variables derived from the Basin Characterization Model (BCM) – a dataset specifically designed for California (Flint et al., 2013), including climatic water deficit, actual evapotranspiration, minimum monthly temperature, and wet- and dry-season precipitation. These variables are available at 270 m spatial resolution and have been used to project plant species' responses to various climate change scenarios in California (Ackerly et al. 2015, Thorne et al. 2017). Contemporary estimates of species distributions were based on averaged annual values of these predictors for the years 1981-2010.

Edaphic factors and landscape position also limit the spatial distributions of plants and including them as predictors in SDMs produces more reliable models than climate-alone (Kueppers et al. 2005, Coudun et al. 2006, Coudun and Gégout 2007, Dubuis et al. 2013, Velazco et al. 2017). Therefore, we also included soil pH, available water holding capacity, soil depth, percent clay (Gridded National Soil Survey Geographic Database, gNATSGO), and categorical landform types (n=14) that reflect hillslope position and dominant soil formation processes (Theobald et al. 2015). In this study, we assumed that soil and landform conditions will remain constant between the baseline and future time periods (1980-2010 and 2070-2099). All variables were resampled to 270 m using bilinear interpolation with the terra package in R (Hijams, 2022).

To project the impact of climate change on species' distributions, we used two Global Climate Models (GCMs): CNRM-CM5 (Voldoire et al., 2013) and HadGEM2-ES (Collins et al., 2011), and two emissions Representative Concentration Pathways (RCP), RCP 4.5 and 8.5 (IPCC 2013) for the time period 2070-2099. The projected change in climatic conditions under the GCM's range from warmer and wetter (CNRM-CM5) to hotter and drier (HadGEM2-ES), with moderate change (warming) under the RCP 4.5 emissions scenarios and greater change under the RCP 8.5 scenarios. While differences in

GCMs represent uncertainty between models of the Earth’s climate and its response to increasing greenhouse gas concentrations, differences in RCP scenarios represent varying levels of emissions, which will be determined by our ability to reduce emissions. RCP 4.5 represents a scenario where human societies effectively reduce emissions through investments in renewable energy and transportation, while RCP 8.5 assumes a “business-as-usual” future.

Species distribution models

We used species distribution models (SDMs) to estimate future and current habitat suitability for our study species at a 270-m spatial scale within the Californian portion of the California Floristic Province. The full procedure for building and evaluating the SDMs for our study species is detailed in Rose et al. (2023). In summary, the SDMs are based on a consensus of six commonly-used SDM algorithms: generalized linear models, generalized additive models, boosted regression trees, random forests, artificial neural networks, and support vector machines (Franklin, 2010). The consensus SDMs were based on the mean of raster cells with habitat suitability values above the thresholds that maximized the sum of sensitivity and specificity (“meanthr”), i.e., the true skill statistic (TSS), for each high performing algorithm (AUC > .7 for presence-absence). In total, we produced 1,008 models (84 of presence-absence species * 6 algorithms) with 2 projections (2 GCM’s* 1 RCP). Further details about model calibration, evaluation, and tuning can be found in the supporting information and in Rose et al., (2023).

Because of the uncertainty associated with predicting species' habitat dynamics outside of their current geographic ranges (Mendes et al., 2020; Thuiller et al., 2019; Velazco et al., 2020), we constrained all model predictions based on species' current range extents. Species' ranges were defined by suitable habitat patches that contain at least one occurrence record in the baseline time period 1980-2010. While this approach limits our ability to predict potential species' range shifts, it still allows us to characterize locations that are likely to become more or less suitable under future climate change. All SDMs were produced and evaluated using the *flexsdm* and *terra* packages in R (Velazco et al., 2022; Hijmans 2022).

Habitat suitability change and geographic features

Habitat suitability change was calculated as the difference between the mapped future (2070-2099) and current (1980-2010) SDM habitat predictions relative to current habitat suitability at the pixel level. Negative numbers indicate areas predicted to experience reduced habitat suitability while positive values correspond to areas predicted to increase in suitability for a given location (grid cell) and species. (Note: all pixels included in this analysis have non-zero current habitat suitability and are within species' currently suitable habitat (no cells can go from 0 to 1, but cells could theoretically go from 0.01 to 1 - however, this is unlikely).

To evaluate what factors might be related to how predicted habitat suitability change varies across species' geographic ranges, we considered four landscape features: latitude, elevation (m) derived from a 90-m digital elevation model (DEM; USGS), distance to coast (km) (https://oceancolor.gsfc.nasa.gov/docs/distfromcoast/), and topographic heterogeneity. Using the 90-m DEM, topographic heterogeneity was calculated as the range in elevation values from a center cell and the three-cell neighborhood immediately surrounding it. Values of topographic heterogeneity were converted to a 0-1 scale using the standard deviation of the range of values across the study extent.

Vegetation communities and biogeographic characteristics

To group species by vegetation community, we information from Calflora.org, the Manual of California Vegetation (CNPS 2023), and author's expert opinion to assign species to twelve broad categories: alpine, chaparral, closed-cone pine forest, coastal sage scrub, coastal strand, montane forest, pinyon-juniper woodland, redwood forest, salt marsh, valley and foothill woodland, valley grassland, wetland-riparian. The number of species per vegetation community ranged from 1-27 (Table S3.3).

We also assessed how a species' biogeographic characteristics, i.e., range size, average elevation, and distance from coast as well as vegetation community may influence the relationship between geography and habitat suitability change. Therefore, we used species occurrence records to calculate their mean elevation, distance to coast, and range extent–measured as the area of the minimum convex polygon that encompassed species occurrences.

Data analysis

To quantify the relationships between geographic features (distance to coast, elevation, topographic heterogeneity, and latitude) and habitat suitability change, we calculated the Pearson's correlation coefficient (r) between predicted habitat suitability change relative to current habitat suitability and each geographic feature under two climate models (warm/wet and hot/dry) for each species at the pixel level. Positive relationships between habitat suitability change and a geographic feature indicate that potential refugia (areas of relative habitat stability or gain within a species current range) are associated with higher levels of that feature, while negative relationships indicate potential refugia are associated with lower values (Figure 3.2). These results are organized by vegetation community. We then used simple, univariate linear regression to separately test the influence of species' biogeographic characteristics (range size, mean elevation, and mean distance to coast) on the relationships between predicted habitat suitability change each geographic feature, as measured by the correlation coefficient r. All analyses were conducted in R version 4.2.0 (R Core Team, 2022).

Results

Geography of habitat suitability change: general trends

The associations between geographic features and predicted change in habitat suitability were heterogeneous across our study species and the two climate models used in this analysis (Figure 3.3). Of the 82 study species, a little over half (56%) were projected to have decreasing habitat suitability as elevation increased under the warm, wet climate model (CNRM-CM5). Similarly, 61% of the species were predicted to experience reduced habitat suitability with higher levels of topographic heterogeneity, and 71% of species were expected to have reduced habitat suitability as latitude increased, corresponding to less suitable habitat in the northern portions of their ranges. Furthermore, 55% of the species were projected to have reduced habitat suitability in areas near the coast. These results indicate that for the majority of the study species, factors such as higher elevations, greater topographic heterogeneity, higher latitudes, and proximity to the coast were associated with habitat suitability loss.

In contrast, under the hot and dry climate model (HadGEM2-ES), most species were predicted to retain or gain suitable habitat at higher elevations (84%) and in areas with higher topographic complexity (60%) within their current ranges. More species were predicted to experience greater habitat loss at higher vs. low latitudes (56%) but greater habitat suitability at greater distances from the coast (70%). Notably, the strength and direction of these relationships varied substantially depending on the geographic feature and climate model.

Differences in the magnitude and geography of predicted habitat suitability change between vegetation associations

Pixel-level habitat suitability change under the two climate models varied widely between vegetation communities, species, and within species' ranges (Figures 3.4 and 3.5); however, some notable trends emerged. Of the study species, 4 wetland-riparian (100%), 10 valley and foothill woodland (62%), 4 montane forest (25%), 7 coastal sage scrub (70%), and 17 chaparral (63%) species were predicted to experience greater habitat suitability loss, on average, under the warm, wet vs. the hot, dry climate model (Figure 3.4, 73 species total). Of the nine species that were not included in these six vegetation communities, *Pinus attenuata*, *Pinus muricata*, *Umbellularia californica*, *Ericameria ericoides*, *Lupinus arboreus*, and *Pinus quadriolia* were also predicted to be relatively more vulnerable, overall, under the warm, wet model (Figure 3.5). Conversely, the other

~40% of study species were predicted to be more vulnerable to climatic change under the hot, dry model–including 75% of the montane forest species (n = 12) and the only alpine species included in this study (*Poa stebbinsii*). For most species, we predicted stability or increases in habitat suitability in some portion of their ranges (refugia) under both climate models. However, 16 species were predicted to experience varying levels of habitat suitability decline across their entire ranges: *Juncus balticus* (warm/wet only), *Delphinium hesperium*, *Pinus balfouriana*, *Ptilagrostis kingii* (hot/dry only), *Quecus sadleriana*, *Ribes lasianthum* (hot/dry), *Sequoiadendron giganteum*, *Opuntia littoralis* (warm/wet only), *Arctostaphylos pringlei*, *Arctostaphylos rudis*, *Ceanothus perplexans*, *Ceanothus verrucosus*, *Keckiella antirrhinoides* (warm/wet only), *Xylococcus bicolor* (hot/dry only), *Lupinus arboreus*, and *Pinus quadrifolia*.

We also found differences in the relationships between predicted habitat suitability change and each geographic feature across different vegetation communities (Figures 3.6 and 3.7). For all wetland-riparian species, habitat refugia were weakly to moderately correlated ($|r|$ = 0.05-0.50) with increasing distance from coast and decreasing latitude, while the influence of elevation was weak under both climate models. Refugia for *Salix lasiolepis* were moderately associated with flat areas under the warm/wet climate model.

The influence of distance to coast on habitat suitability change for valley and foothill woodland species was generally small and mostly negative--indicating a small tendency towards coastal refugia and habitat vulnerability inland. However, there were a few exceptions, notably the large, positive influence of distance to coast on habitat suitability change for *Quercus engelmannii* under the hot, dry model (*r* = 0.60). Refugia for valley and foothill woodland species were also often associated with increasing elevation, though the opposite trend was true for some species, especially under the warm, wet model. For example, *Quercus engelmannii* and *Quercus agrifolia* were predicted to be more vulnerable at high relative to low elevations under the wetter, warmer climate model projections. Seven of the species within the valley and foothill woodland community showed the strongest positive relationships between habitat suitability change and topographic heterogeneity among our study species under one or both climate models: *Aesculus californica* (hot/dry; *r* = 0.29), *Delphinium hesperium* (hot/dry; *r* = 0.37), *Dichelostemma capitatum* (warm/wet; *r* = 0.27), *Pinus sabiniana* (hot/dry; *r* = 0.37), *Quercus lobata* (hot/dry; *r* = 0.36), *Quercus douglasii* (*r* =0.29-0.33), and *Quercus wislizeni* (*r* =0.35-0.37).

Refugia for montane forest species, in general, were often linked to specific geographic features under both climate models. These features included increases in distance from the coast, elevation, latitude, and topographic heterogeneity. Exceptions included *Picea breweriana*, *Torreya californica*, *Quercus sadleriana*, *Chamaebatia foliolosa*, *Pinus coulteri*, and *Sequoiadendron giganteum*. For these species, relative refugia were found to be moderately to strongly associated with coastal areas, lower elevations, southern latitudes, and/or flat topography.

Species within the coastal sage scrub and chaparral vegetation types showed the most variability in geography-mediated habitat change patterns between the two climate models. For example, habitat suitability change for *Adenostoma sparsifolium* was moderately, negatively associated with elevation under the warm, wet model (*r* = -0.33) but strongly, positively associated with elevation under the hot, dry model (*r* = 0.56). Generally, refugia or areas of relatively low habitat loss for chaparral and coastal sage scrub species were associated with coastal, low-elevation, southern areas under the warm, wet climate model but inland, high elevation, and northern areas under the hot, dry model. Furthermore, consistently across the warm, wet climate model, refugia or areas of relatively low habitat loss for chaparral and coastal sage scrub species were often associated with topographically flat areas.

Among the eight species that were not included in the five major vegetation associations, *Sequoia sempervirens* and *Umbellularia californica* (both associated with redwood forests) showed similar geographic trends with respect to habitat change, where refugia tended to be located inland and towards northern latitudes under both climate models. However, refugia for both species were associated with low-elevation, flat areas under warmer, wetter conditions and somewhat higher elevations under the hot, dry model. *Pinus quadrifolia* was predicted to experience 100% habitat suitability loss under the warm, wet model, but lower levels of habitat loss under the hot, dry model were associated with inland areas, at high elevations, in areas with high topographic complexity, and towards the northern portion of its range. Interestingly, refugia for alpine *Poa stebbinsii* were strongly associated with high elevation areas but southern latitudes under the hot, dry model because higher elevation areas are located towards the southern portions of its range.

How do species' biogeographic characteristics influence the relationship between geography and habitat suitability change?

We found that species' average elevation, average distance to coast, and range size helped explain geographic patterns of predicted changes in habitat suitability, but that these relationships varied substantially between climate models (Figure 3.8). Species at higher elevations (and farther from the coast) were predicted to have stronger, positive associations between habitat stability and elevation and topographic heterogeneity under both climate models. Under the warm, wet model, high elevation species were also associated with refugia at northern latitudes and areas far from the coast, but these effects disappeared under the hotter, dryer projections. In terms of distance to coast, coastal species tended to be associated with coastal refugia under the warm, wet model only and low elevation refugia under both models, though there was more variability in this relationship under HadGEM2-ES. The influence of range size on geographic patterns of habitat suitability change were also dependent on the climate model. Under the warm, wet projection, species with small range sizes were more likely to retain suitable habitat near the coast and, to a lesser degree, in low elevation areas ($p = 0.073$). However, predictions under hotter, drier conditions showed the opposite pattern, where small-ranged species were somewhat more likely to exhibit high elevation refugia far from the coast.

Discussion

In this study we 1) predicted changes in habitat suitability within the current geographic ranges of 82 plant species spanning a variety of life histories and geographies in the CFP (California Floristic Province) under two alternative climate models for the time period 2070-2099, 2) quantified the relationships between predicted changes in habitat suitability within species' ranges and four geographic features that play a role in mediating climate refugia: distance to coast, elevation, latitude, and topographic heterogeneity, and 3) assessed how the geography of habitat suitability change varied across species with different biogeographic affinities and in different vegetation communities. We found substantial variation in the geographic patterns of habitat suitability change among the study species under the two climate models. Notably, there was greater variability in species-specific habitat change trends under the warm, wet climate model (CNRM-CM5) compared to the hot, dry model (HadGEM2-ES).

The geography of species-specific habitat change

There is a general expectation that species' refugia will be located at higher elevations due to cooler temperatures (Willmott & Matsuura, 1995), greater precipitation (Perry et al., 1994), and lower evaporative demand (Stephenson, 1998). However, these patterns vary depending on location, and observed patterns of recent climate change are highly variable with respect to elevation at a global scale (Pepin et al., 2022). Furthermore, documented range shifts in California indicate that downslope shifts in elevation are at least as common as shifts upslope (Crimmins et al., 2011; Rapacciuolo et al., 2014), and are likely driven by California's complex landscape and water availability at lower elevations. Similarly, the identification of "unexpected refugia" in this research supports previous work that species-based approaches may be uniquely suited for identifying flat regions that could serve as important refugia for certain species under climate change (Michalak & Stralberg, 2020). Generally, flat regions are not expected to serve as refugia, due to high velocities of climate change that may require long distance dispersal for a species to remain within its optimal thermal zone under warming climates (Loarie et al., 2009). Under both climate models included in this study, the way habitat suitability was predicted to change in relation to geographic features differed greatly among the 82 study species, with many species predicted to exhibit refugia in unexpected places, i.e., at lower elevations, in topographically flat areas, towards southern latitudes, and inland.

Differences in climate change predicted by the two models included in this research are geographically variable. Increases in 30-year averaged climatic water deficit and minimum temperature of the coldest month are much more pronounced under HadGEM2-ES than CNRM-CM5 across the CFP. Previous research on vegetation type exposure in California under the warm, wet model used here (CNRM-CM5) and an even more severe “hot-dry” GCM (MIROC ESM) showed that the warm, wet model predicted a higher proportion of California’s natural land area to become climatically marginal by end-of-century (Thorne et al., 2017).

Furthermore, the extent to which geography influenced predictions of habitat suitability also differed substantially among our study species, as evidenced by the variation in the correlation between habitat suitability change and geographic features (Figs. 3, 6, & 7). Habitat stability and the location of climatic refugia depend on the geographic and ecological characteristics of each species (Ashcroft, 2010). Overall, these results highlight the complexity of species' responses to environmental change as well as the challenges of predicting habitat refugia based on the physical landscape alone.

Differences between vegetation communities

While there was significant variability in the geographic patterns of habitat suitability change among our study species, we identified some patterns that were relatively consistent across species within certain vegetation communities. For example, we found that most coastal sage scrub (CSS) and chaparral species are predicted to be more vulnerable across their ranges under warmer, wetter conditions compared to an alternative hot and dry climate scenario. This vulnerability was particularly evident in high elevation areas characterized by complex topography. Although this finding may initially seem surprising, the warmer, wetter climate model predicts significant increases in precipitation that exceed historical values observed within the ranges of species within these vegetation communities, and so these higher values would be interpreted as exceeding the species' tolerance in the species distribution modeling framework. The anticipated patterns of increased precipitation under this model are expected to be especially notable in the coastal mountains where CSS and chaparral species are typically found.

The negative relationship between elevation and change in habitat suitability (where higher elevation corresponds to reduced suitability) for CSS and chaparral species under the warm, wet climate model is consistent climate change projections of potential drought in southern California. Previous research has shown that greater climate change exposure–defined as frequency of departure from historical range of variability in the climatic water deficit–at higher elevations in a southern California site based on predicted patterns of change in climate variables (independent of species-specific suitability) (McCullough et al., 2016). The consistency in this pattern of high elevation vulnerability in southern California underscores the need to consider the effects of elevation, precipitation changes, and species-specific habitat suitability, especially in CSS and chaparral systems.

Coastal sage scrub and chaparral species showed the greatest variation in habitat suitability dynamics between the two climate models. For example, predicted habitat suitability change for mission manzanita (*Xylococcus bicolor*) was negatively associated with distance to coast, elevation, latitude, and topographic heterogeneity under the warm, wet climate model, yet all these relationships were reversed under hotter, dryer conditions.

Although vegetation communities can be a useful way to organize species with similar ecological requirements and overlapping ranges, we found idiosyncratic habitat change and geographic relationships between species in the same community. For example, while the general trend for most montane forest species was for refugia to be found in areas away from the coast, at higher elevations, at more northern latitudes, and in areas with diverse topography, there were several montane species that deviated from this pattern. Instead, we predicted relative refugia in coastal areas, at lower elevations, southern latitudes, and in areas with relatively flat topography for *Picea breweriana*, *Torreya californica*, *Quercus sadleriana*, *Chamaebatia foliolosa*, *Pinus coulteri*, and *Sequoiadendron giganteum*. These results indicate that stable habitat may be found in unique and unexpected locations, even when compared to species with similar vegetation associations.

Effect of species' biogeographic characteristics on geographic trends in habitat suitability change

We found that average elevation, average distance to coast, and species' range size played a role in explaining the geographic patterns of predicted habitat suitability change. Under both climate models included in this study, species' that are currently found at higher elevations were consistently predicted to have higher relative habitat stability at high elevations and in areas with high topographic heterogeneity. This prediction is somewhat at odds with empirical evidence that lowland species are shifting upward in elevation more quickly than high elevation species (Mamantov & Gibson-Reinemer, 2021; Zu et al., 2023). For example, California plant species with higher optimum elevations have shown more pronounced downhill shifts (Crimmins et al., 2011), likely reflecting responses to 20th century climate change where, in California, warming has been somewhat offset by increases in precipitation leading to enhanced water availability. However, climate projections across multiple GCMs predict increases in climatic water deficit across California's mountainous regions (Thorne et al., 2015) -- which may drive more rapid shifts in the distributions of high elevation species as they track available water.

The influence of species' distance to coast and range size on the predicted geographic patterns of habitat suitability change varied by climate model. Specifically, we found that coastal species tended to exhibit refugia (or relatively low levels of vulnerability) at low elevations under both models, but that this trend was more pronounced under a warmer, wetter future. This finding is in line with the idea that species may shift their elevational distributions downslope when water is more available across the landscape. Finally, the predicted geographic patterns of habitat suitability change were more variable between climate models for small-ranged vs. widely distributed species (supported by results of Chapter 2), specifically regarding the elevational and coastal positioning of potential refugia. While hotter, drier conditions were predicted to drive habitat suitability upslope and away from the coast for narrowly distributed species, relative habitat suitability was highest for these species near the coast and at low elevations under wetter conditions. Small-ranged species may be the most vulnerable to future climate change (Vincent et al., 2020) and this vulnerability may be exacerbated by the uncertain location of potential refugia, which may shift dramatically depending on the direction and magnitude of climate change.

Conclusion

We found significant variation in the geography of predicted habitat suitability change across species' ranges, with distinct patterns between species and vegetation communities. The complex interactions between geography and species-specific habitat suitability change indicate that the spatial distribution of species-specific climatic refugia may occur in unexpected places, depending on the eventual magnitude and direction of temperature and precipitation changes. Finally, this research stresses the importance of conservation efforts that consider species' specific tolerances and vulnerability and how these factors play out across species' ranges to safeguard biodiversity in the face of uncertain climatic change.

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Figures

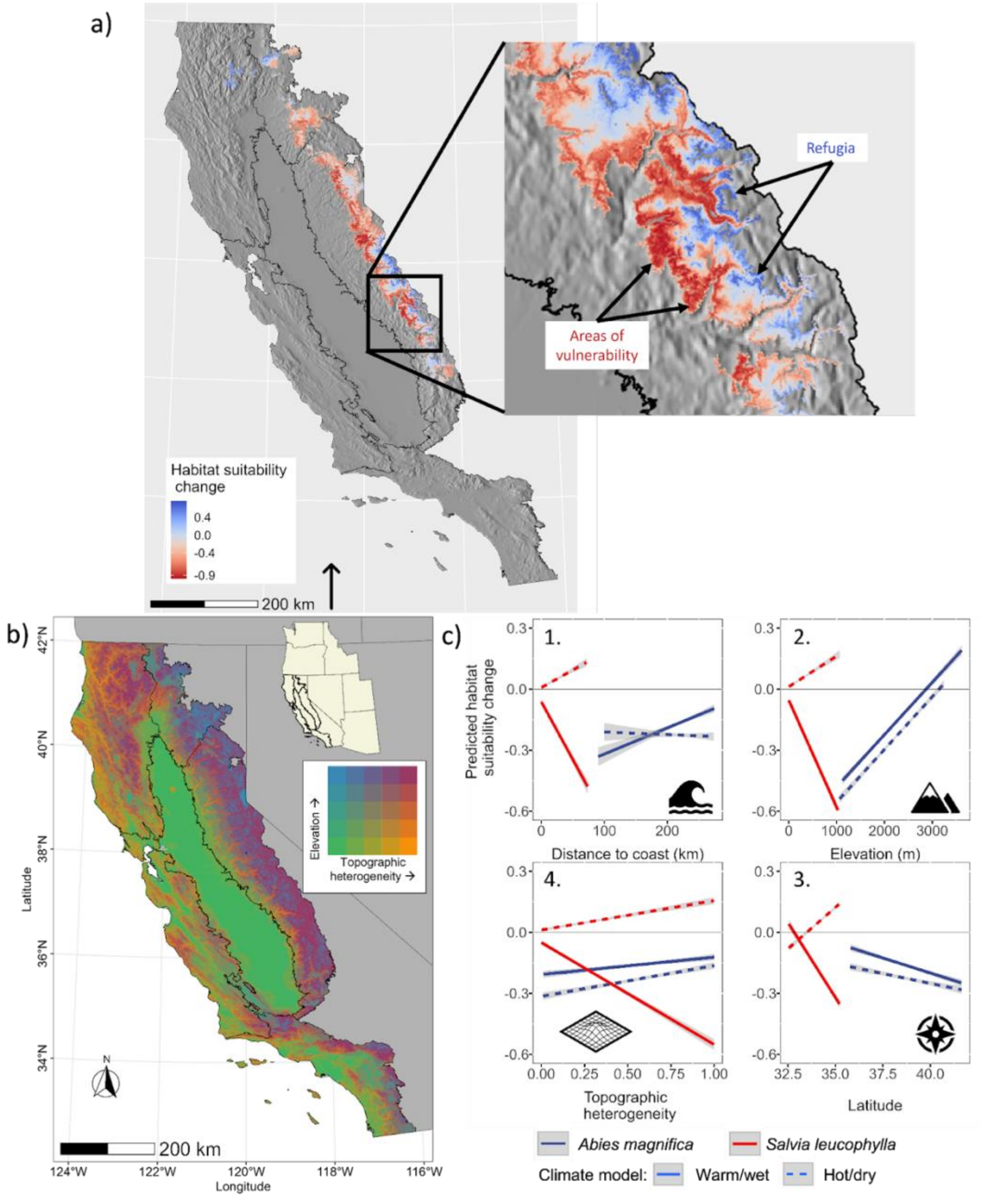
a)
Refugia
Areas of vulnerability
Habitat suitability change
0.4
0.0
-0.4
-0.9
200 km
b)
42°N
40°N
38°N
36°N
34°N
Latitude
124°W
122°W
120°W
118°W
116°W
Longitude
Elevation →
Topographic heterogeneity →
N
200 km
c)
1.
2.
3.
4.
Predicted habitat suitability change
0.3
0.0
-0.3
-0.6
0
100
200
Distance to coast (km)
0
1000
2000
3000
Elevation (m)
0.00
0.25
0.50
0.75
1.00
Topographic heterogeneity
32.5
35.0
37.5
40.0
Latitude
Abies magnifica
Salvia leucophylla
Climate model:
Warm/wet
Hot/dry

Figure 3.1 (a) Map showing the extent of habitat suitability change for *Abies magnifica* (red fir) under a hot, dry climate model and business-as-usual greenhouse gas concentration scenario, highlighting potential areas of refugia and vulnerability, (b) a map of the study area depicting the relationship between elevation and topographic heterogeneity in the portion of the California Floristic Province within the state of California (c) and trend lines showing the relationship between predicted continuous habitat suitability change for two species (purple sage– *Salvia leucophylla* and red fir– *Abies magnifica*) and four geographic features that are relevant to climatic refugia: 1.) distance to coast, 2.) elevation, 3.) topographic heterogeneity, and 4.) latitude under two global climate models (GCM). The solid lines indicate relationships under a relatively warm, wet model (CNRM-CM5), while the dashed line shows the predicted relationship under a hot, dry future (HadGEM2-ES). Importantly, the two species depicted have intermediate sized ranges yet occupy different regions within the CFP. While *Abies magnifica* is a high-elevation conifer tree species that is found in the montane forests of the Sierra Nevada, southern Cascade Range, Coast Ranges, and the Klamath Ranges, *Salvia leucophylla* is a small shrub distributed along the southern coast of California and Baja California (see Supporting Information for range map estimations).

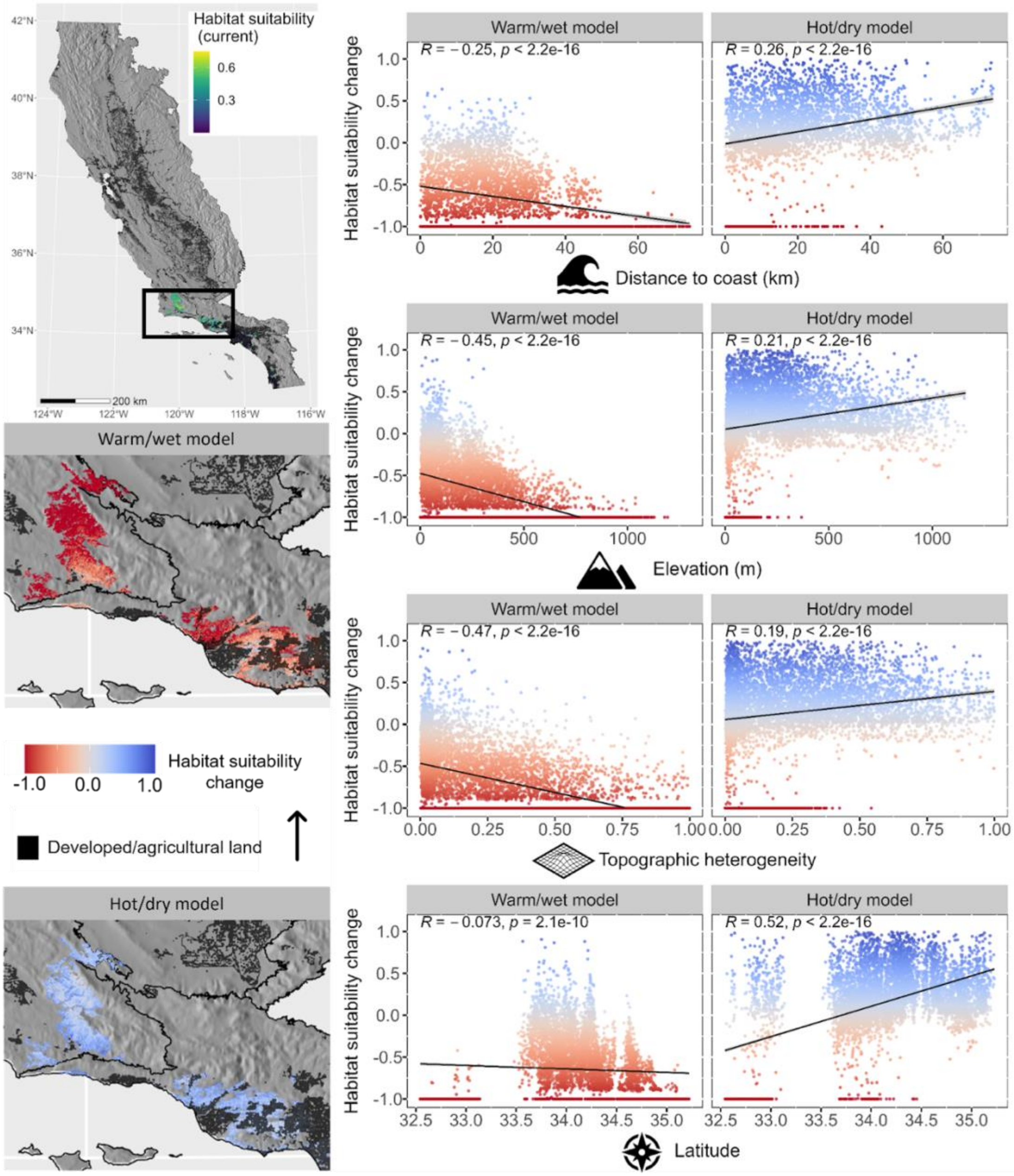

Figure 3.2 Predicted habitat suitability change for purple sage (Salvia leucophylla) under two climate models (warm/wet and hot/dry) along with scatterplots and smoothed trend lines showing the relationship between estimated habitat suitability change and each geographic feature at the pixel level. In both the maps and the scatterplots, color corresponds to habitat suitability change (relative to current habitat suitability), where red indicates areas of high habitat suitability loss and blue indicates increases in relative habitat suitability.

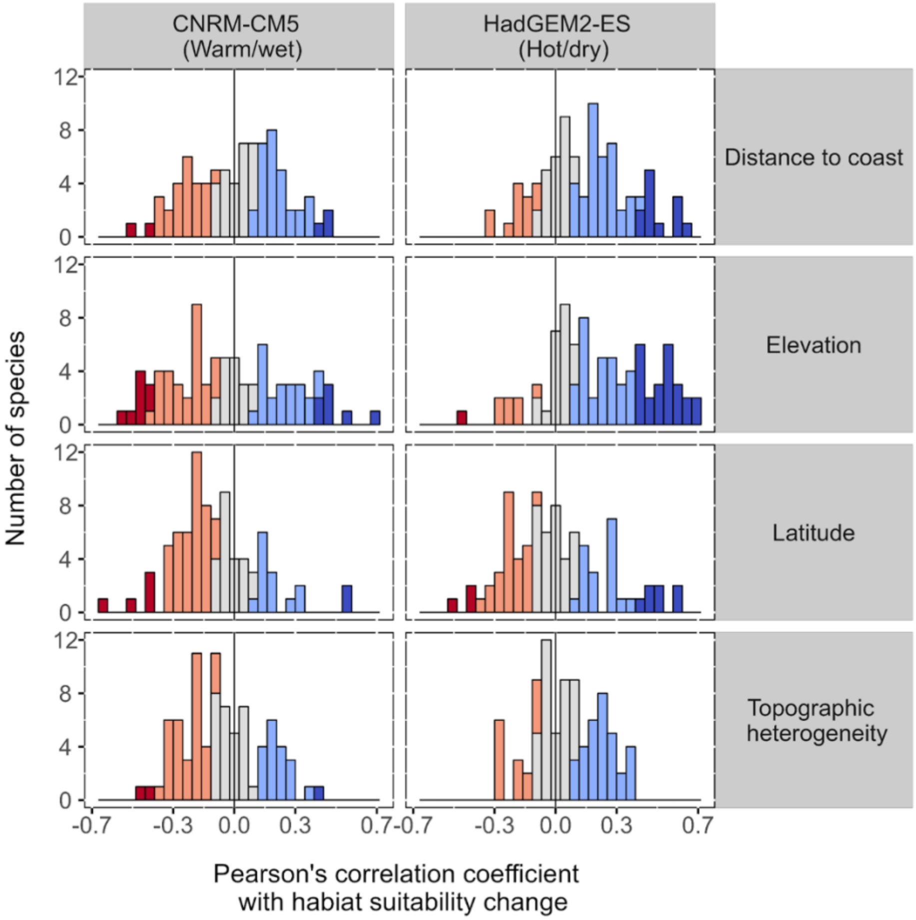

Figure 3.3 Frequency distributions of the Pearson correlation coefficients relating four geographic features to predicted habitat suitability change under two climate models for the time period 2070-2099. Colors indicate the strength and direction of the relationship between each geographic feature and predicted habitat suitability change, where dark red indicates strong negative correlations ($r < -0.4$) and dark blue corresponds to strongly positive correlations ($r > 0.4$). **Note:** Under the warm and wet climate model, all habitat for Pinus quadrifolia was reduced to 0 (relative habitat suitability change = -1) - making it impossible to relate habitat suitability change to any of the geographic features. Therefore, the 83 species are reported under the warm and wet climate model.

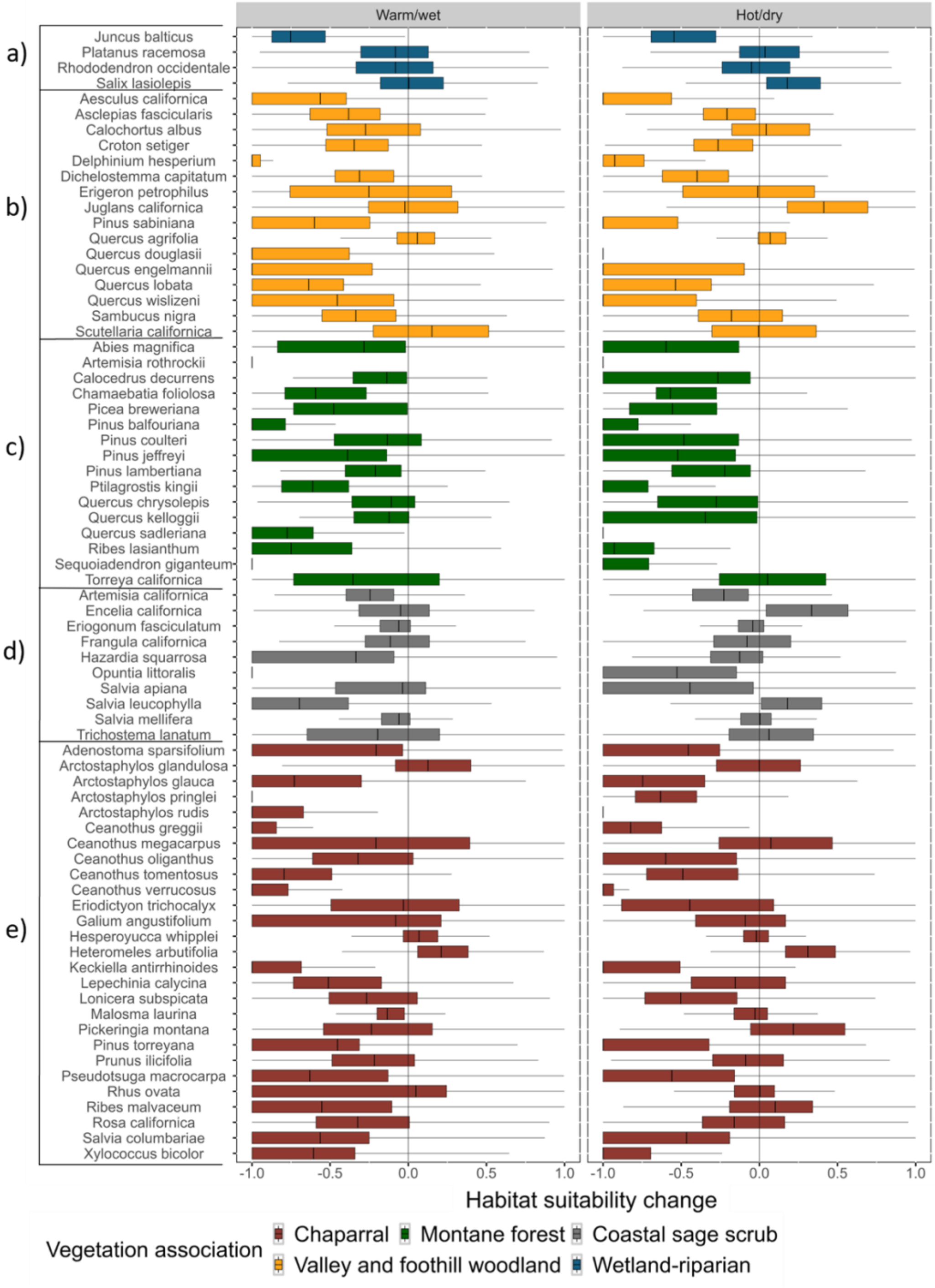
Warm/wet
Hot/dry
a)
b)
c)
d)
e)
Juncus balticus
Platanus racemosa
Rhododendron occidentale
Salix lasiolepis
Aesculus californica
Asclepias fascicularis
Calochortus albus
Croton setiger
Delphinium hesperium
Dichelostemma capitatum
Erigeron petrophilus
Juglans californica
Pinus sabiniana
Quercus agrifolia
Quercus douglasii
Quercus engelmannii
Quercus lobata
Quercus wislizeni
Sambucus nigra
Scutellaria californica
Abies magnifica
Artemisia rothrockii
Calocedrus decurrens
Chamaebatia foliolosa
Picea breweriana
Pinus balfouriana
Pinus coulteri
Pinus jeffreyi
Pinus lambertiana
Ptilagrostis kingii
Quercus chrysolepis
Quercus kelloggii
Quercus sadleriana
Ribes lasianthum
Sequoiadendron giganteum
Torreya californica
Artemisia californica
Encelia californica
Eriogonum fasciculatum
Frangula californica
Hazardia squarrosa
Opuntia littoralis
Salvia apiana
Salvia leucophylla
Salvia mellifera
Trichostema lanatum
Adenostoma sparsifolium
Arctostaphylos glandulosa
Arctostaphylos glauca
Arctostaphylos pringlei
Arctostaphylos rudis
Ceanothus greggii
Ceanothus megacarpus
Ceanothus oliganthus
Ceanothus tomentosus
Ceanothus verrucosus
Eriodictyon trichocalyx
Galium angustifolium
Hesperoyucca whipplei
Heteromeles arbutifolia
Keckiella antirrhinoides
Lepechinia calycina
Lonicera subspicata
Malosma laurina
Pickeringia montana
Pinus torreyana
Prunus ilicifolia
Pseudotsuga macrocarpa
Rhus ovata
Ribes malvaceum
Rosa californica
Salvia columbariae
Xylococcus bicolor
-1.0
-0.5
0.0
0.5
1.0
-1.0
-0.5
0.0
0.5
1.0
Habitat suitability change
Vegetation association
Chaparral
Montane forest
Coastal sage scrub
Valley and foothill woodland
Wetland-riparian

Figure 3.4 Boxplots showing the distribution of pixel-level habitat suitability change under the two climate models across species based on a 10% random sample of raster pixels for each species. Species are grouped by vegetation associations: (a) wetland-riparian, (b)valley and foothill woodland, (c) montane forest, (d) coastal sage scrub, and (e) chaparral. Color of box plots corresponds to vegetation association. Horizontal lines in the boxplots show the first quartile, median, and third quartile of the data.

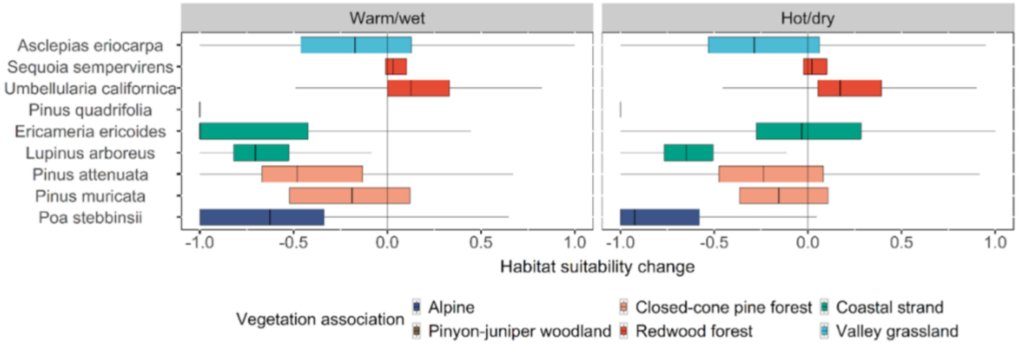

Figure 3.5 Boxplots showing the distribution of pixel-level habitat suitability change under the two climate models across species based on a 10% random sample of raster pixels for each species. Species are grouped by vegetation associations with only 1-2 species in each: valley grassland (Asclepias eriocarpa), redwood forest (Sequoia sempervirens and Umbellularia californica), pinyon-juniper woodland (Pinus quadrifolia,), closed-cone pine forest (Pinus attenuata, Pinus muricata), coastal strand (Ericameria ericoides, Lupinus arboreus), and alpine (Poa stebbensii). Horizontal lines in the boxplots show the first quartile, median, and third quartile of the data.

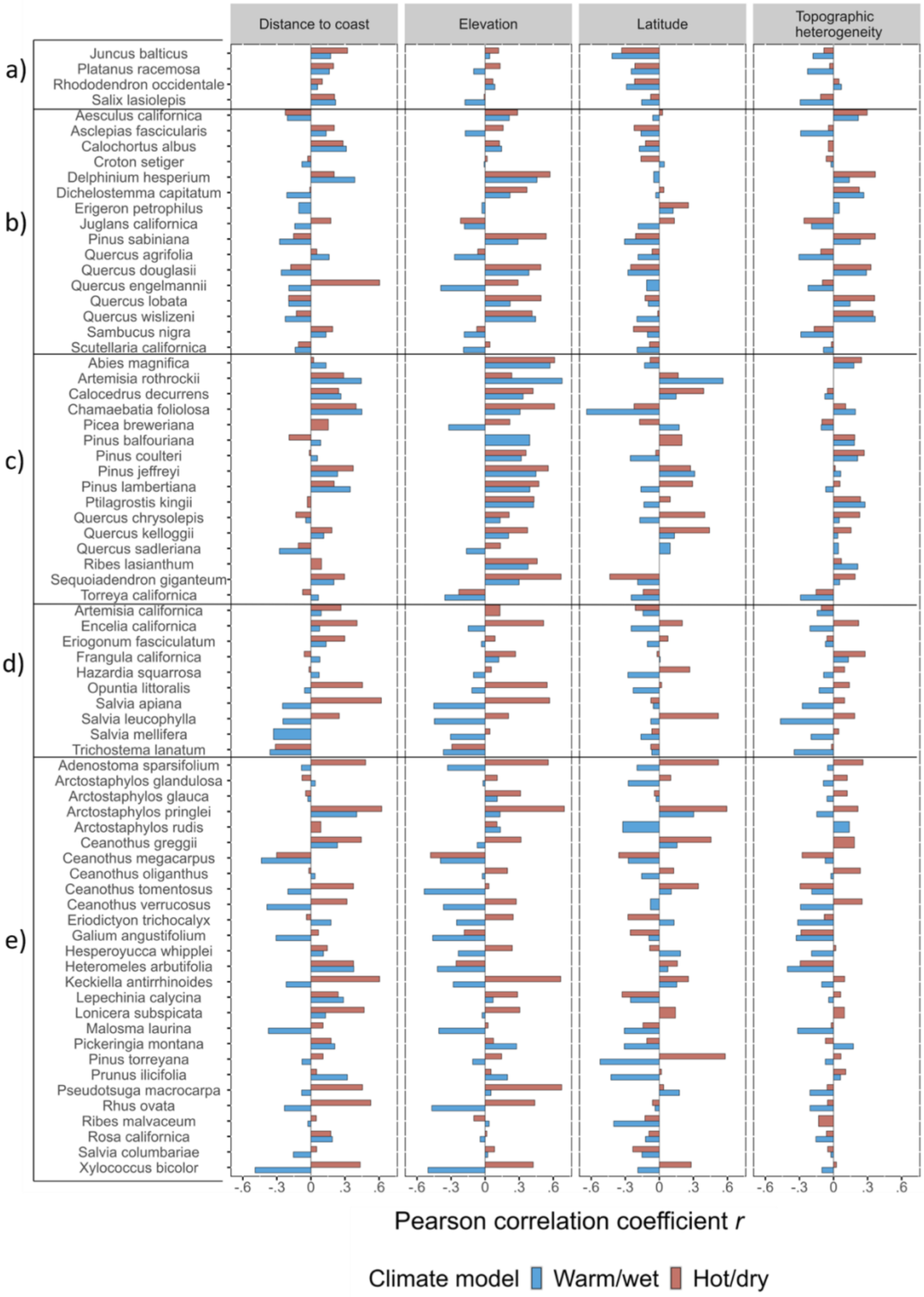
Distance to coast
Elevation
Latitude
Topographic heterogeneity
a)
Juncus balticus
Platanus racemosa
Rhododendron occidentale
Salix lasiolepis
b)
Aesculus californica
Asclepias fascicularis
Calochortus albus
Croton setiger
Delphinium hesperium
Dichelostemma capitatum
Erigeron petrophilus
Juglans californica
Pinus sabiniana
Quercus agrifolia
Quercus douglasii
Quercus engelmannii
Quercus lobata
Quercus wislizeni
Sambucus nigra
Scutellaria californica
c)
Abies magnifica
Artemisia rothrockii
Calocedrus decurrens
Chamaebatia foliolosa
Picea breweriana
Pinus balfouriana
Pinus coulteri
Pinus jeffreyi
Pinus lambertiana
Ptilagrostis kingii
Quercus chrysolepis
Quercus kelloggii
Quercus sadleriana
Ribes lasianthum
Sequoiadendron giganteum
Torreya californica
d)
Artemisia californica
Encelia californica
Eriogonum fasciculatum
Frangula californica
Hazardia squarrosa
Opuntia littoralis
Salvia apiana
Salvia leucophylla
Salvia mellifera
Trichostema lanatum
e)
Adenostoma sparsifolium
Arctostaphylos glandulosa
Arctostaphylos glauca
Arctostaphylos pringlei
Arctostaphylos rudis
Ceanothus greggii
Ceanothus megacarpus
Ceanothus oliganthus
Ceanothus tomentosus
Ceanothus verrucosus
Eriodictyon trichocalyx
Galium angustifolium
Hesperoyucca whipplei
Heteromeles arbutifolia
Keckiella antirrhinoides
Lepechinia calycina
Lonicera subspicata
Malosma laurina
Pickeringia montana
Pinus torreyana
Prunus ilicifolia
Pseudotsuga macrocarpa
Rhus ovata
Ribes malvaceum
Rosa californica
Salvia columbariae
Xylococcus bicolor
-.6 -.3 0 .3 .6
-.6 -.3 0 .3 .6
-.6 -.3 0 .3 .6
-.6 -.3 0 .3 .6
Pearson correlation coefficient *r*
Climate model
🟦 Warm/wet
🟥 Hot/dry

Figure 3.6 Species-specific correlations of habitat suitability change and geographic features: distance to coast, elevation, latitude, and topographic heterogeneity. Species are grouped by vegetation communities: (a) wetland-riparian, (b) valley and foothill woodland, (c) montane forest, (d) coastal sage scrub, and (e) chaparral. Only statistically significant ($p < 0.05$) correlations are shown. Blue bars correspond to correlations under the warm, wet climate model, while red bars indicate the correlation under the hot, dry climate model.

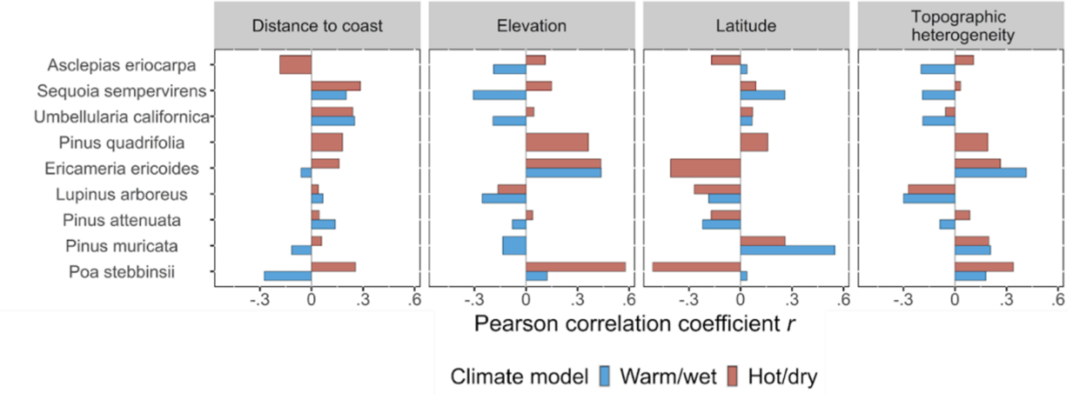

Figure 3.7 Species-specific correlations of habitat suitability change and geographic features: distance to coast, elevation, latitude, and topographic heterogeneity. Species are grouped by vegetation associations with only 1-2 species in each: valley grassland (*Asclepias eriocarpa*) redwood forest (*Sequoia sempervirens* and *Umbellularia californica*), pinyon-juniper woodland (*Pinus quadrifolia*,), closed-cone pine forest (*Pinus attenuata*, *Pinus muricata*), coastal strand (*Ericameria ericoides*, *Lupinus arboreus*), and alpine (*Poa stebbensii*). Only statistically significant ($p < 0.05$) correlations are shown. Blue bars correspond to correlations under the warm, wet climate model, while red bars indicate the correlation under the hot, dry climate model.

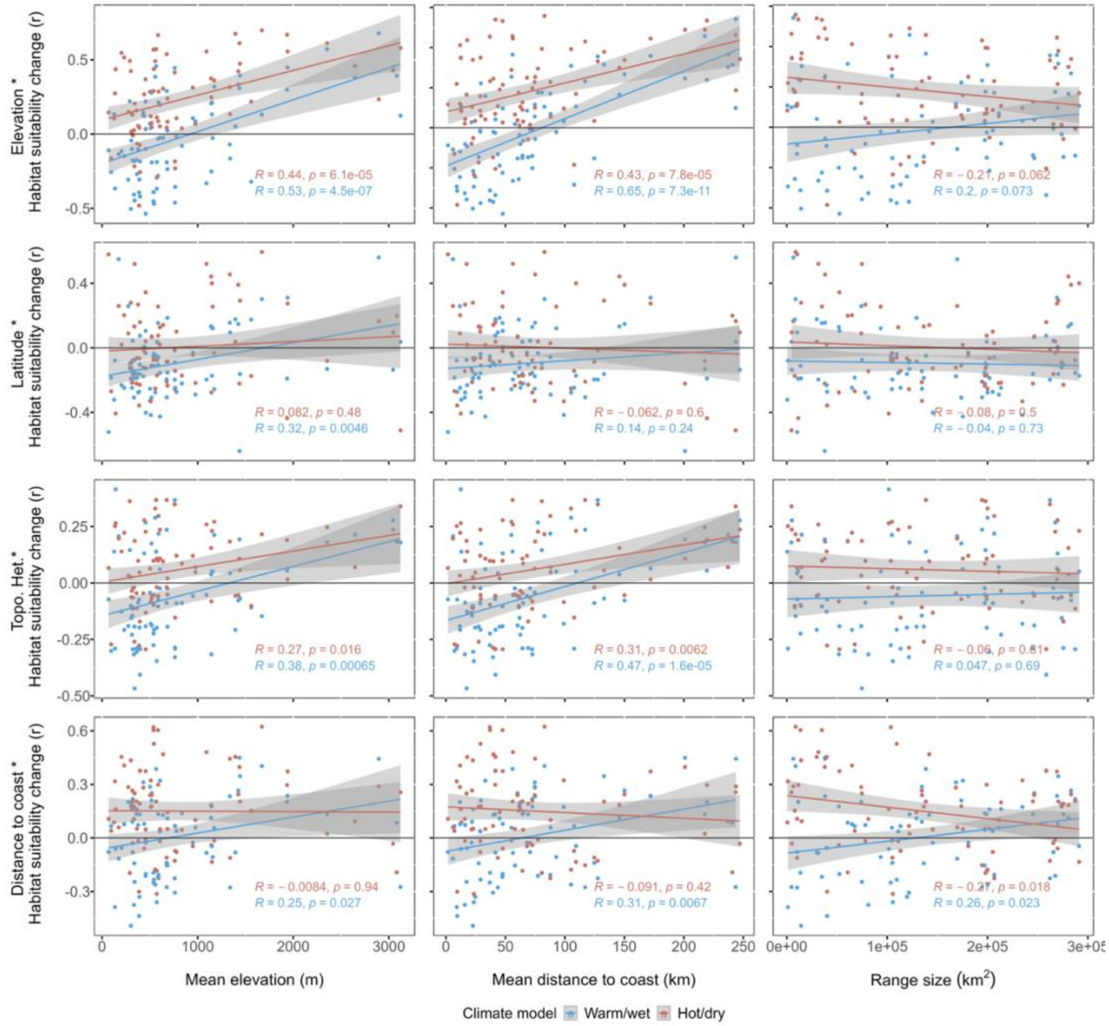

Figure 3.8 Scatter plots with linear regression fit and a 95% confidence interval for the relationships between species' biogeographic characteristics and the per-species geographic trends (correlation) in predicted habitat suitability change for elevation, latitude, topographic heterogeneity, and distance to coast.

Synthesis and Future Directions

My dissertation expands our understanding of the geographic factors that influence plant exposure to global change by identifying the spatial characteristics (e.g., range size, elevation, and topographic heterogeneity) that make plant species more (or less) vulnerable to climate and land use change, quantifying the sources of uncertainty (e.g., modeling consensus approach, climate model, and greenhouse gas concentrations) when conducting spatial vulnerability assessments using species distribution models (SDMs), and assessing the geographic characteristics of species-specific habitat refugia under climate change. Each chapter relied on a set of carefully constructed SDMs, incorporating best modeling practices, extensive vegetation survey data spanning decades, and fine spatial scale hydroclimatic predictors. These models were then used to investigate how predicted habitat suitability change (exposure) varied between species depending on their rarity and geographic characteristics (Chapter 1), under different modeling frameworks (Chapter 2), and across species ranges as a function of geographic features that can mediate potential climatic refugia (Chapter 3).

First, I assessed the relationships between species' rarity, geography, and exposure to climate and land use change for 106 plant species in the California Floristic Province. While aspects of species' rarity, such as range size and number of habitat patches, were most important for explaining species' exposure to climate change, their geographic associations, such as mean elevation and topographic heterogeneity across their ranges, were more strongly associated with species' exposure to land use change. Of the species included in this study, those that were narrowly distributed and occurred across relatively flat landscapes were predicted to be the most exposed to climate change. Conversely, low elevation species were predicted to be the most exposed to habitat loss via urban and agricultural expansion. Importantly, this research revealed that even some broadly distributed species—which are generally considered to be less exposed to the effects of global change (Ohlemüller et al., 2008) —were projected to lose significant portions of their current ranges (>70% habitat reduction). These broadly distributed yet vulnerable species were characterized by geographies with high climate velocities, like those found in flat and foothill areas, where current temperature and precipitation zones are predicted to shift rapidly across the landscape. The findings of this research emphasize the need to consider species' rarity traits as well as the physical geography of their ranges in vulnerability assessments.

Second, I evaluated predictions of projected habitat suitability under various combinations of global climate models, emissions scenarios, time periods, dispersal assumptions, and five SDM consensus methods. Although the variability in spatial predictions produced by different SDM algorithms has been long recognized (Elith et al., 2002), variability in habitat predictions between different consensus approaches has not been extensively investigated, despite their growing popularity as a means of reducing SDM uncertainty (Araújo et al., 2011). I found that the variability between species-level habitat predictions made using different consensus methods was greater than the variability between different greenhouse gas concentration pathways and climate models when "full dispersal" was assumed. Importantly, I also found that certain species, including those with few presence locations and with small range sizes, tended to produce highly variable spatial predictions of suitable habitat when the consensus SDMs were applied to locations outside of species' current ranges.

Lastly, I assessed how habitat suitability change varied across species ranges with respect to latitude, distance to coast, elevation, and topographic heterogeneity. These geographic features play a significant role in determining the extent of climatic change experienced by an organism and, therefore, they can act as mediators of potential refugia (Stewart et al., 2010; Stralberg et al., 2020). Among the 82 species included in this chapter, I found substantial variation in the geography of predicted habitat suitability change across species' ranges. These differences were due in part to variability in the magnitude and direction of climate change predicted by the two global climate models used in this research which reflect the general uncertainty regarding future climate change in California (Pierce et al., 2018). These results also suggest that warmer, wetter conditions might not be favorable for many plant species, particularly those that are adapted to drier conditions. I also found that while refugia for many inland, montane species tended to be in topographically complex, high elevation areas, the location of refugia for coastal species was highly dependent on the climate model used to project future environmental change.

My work assesses plant species geographic exposure to global change and the uncertainties associated with these predictions. However, while SDMs can be used to indirectly measure species' sensitivity to global change—how strongly a species may respond to environmental change due to physiological tolerances—, they do not incorporate factors that influence species' adaptive capacity, i.e., a species' ability to adapt to changing environmental conditions. Assessments that measure genetic variation and vulnerability across species ranges based on gene-environment relationships represent an exciting path forward in our attempt to identify vulnerable species and populations (Nielsen et al., 2021). Furthermore, biotic interactions strongly influence species’ distributions and are changing rapidly in response to human activity (Blois et al., 2013) but are not included in the current research. In the context of California, where landscapes are undergoing unprecedented transformations, considering the interactions between and impacts of fire, invasive species, climate change, and urbanization is of paramount importance (Keeley et al., 2011; Sandel & Dangremond, 2012; Seabloom et al., 2006; Syphared et al., 2007).

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Appendix

Chapter 1 Supporting Information

Appendix S1. Study species list, ecoregion, endemism, conservation status, and number of presence and absence records used for modeling.

Table S1.1 Selected species and their characteristics. Species modeled using a presence-only approach are denoted with (PO) after the number of presences used for modeling.

Species	Growth form	Primary ecoregion	Endemic to CFP/CA	Macrogroup/ Conservation Status	# of presences	# of absences
Abies bracteata	conifer broadleaf tree	Central Western	Yes	MG023 (p. 51); MG009 (p. 34)	83 (PO)	83
Abies magnifica	conifer broadleaf tree	Sierra Nevada	Yes	MG025 (p. 70)	2055	6265
Acanthomintha ilicifolia	annual herb	Southwestern	Yes	CRPR 1B.1 US T	92 (PO)	92
Adenostoma sparsifolium	evergreen shrub	Southwestern	Yes		531	3348
Aesculus californica	deciduous broadleaf tree	Central Western	Yes		3813	11045
Arctostaphylos glandulosa	evergreen shrub	Southwestern	Yes		756	6317
Arctostaphylos glauca	evergreen shrub	Central Western	Yes		1406	11012
Arctostaphylos mewukka	evergreen shrub	Sierra Nevada	Yes		101 (PO)	101
Arctostaphylos pringlei	evergreen shrub	Southwestern	Yes		106	2414
Arctostaphylos rainbowensis	evergreen shrub	Southwestern	Yes	CRPR 1B.1	114 (PO)	114
Arctostaphylos rudis	evergreen shrub	Central Western	Yes	CRPR 1B.2	66	1000
Artemisia californica	drought deciduous subshrub	Southwestern	Yes	MG044 (p. 124)	3875	2048

Artemisia cana bolanderi	evergreen shrub	Cascade Ranges	Core	MG096 (p. 240)	22 (PO)	22
Artemisia rothrockii	evergreen shrub	Sierra Nevada	Yes	MG096 (p. 240)	30	4045
Asclepias eriocarpa	perennial herb	Southwestern	Yes		431	11307
Asclepias fascicularis	perennial herb	Great Valley	Core		1040	11251
Calocedrus decurrens	conifer evergreen tree	Northwestern	Yes	MG009 (p. 33) MG023 (p. 51)	4854	8842
Calochortus albus	perennial herb	Central Western	Yes		572	8035
Calochortus obispoensis	perennial herb	Central Western	Yes	CRPR 1B.2	74 (PO)	74
Calochortus pulchellus	perennial herb	Great Valley	Yes	CRPR 1B.2	76 (PO)	76
Calochortus tiburonensis	perennial herb	Central Western	Yes	CRPR 1B.1 US T	50 (PO)	50
Ceanothus perplexans	evergreen shrub	Southwestern	Core		138	6639
Ceanothus megacarpus	evergreen shrub	Southwestern	Yes		659	3157
Ceanothus oliganthus	evergreen shrub	Southwestern	Yes		493	6304
Ceanothus tomentosus	evergreen shrub	Southwestern	Yes		165	6484
Ceanothus verrucosus	evergreen shrub	Southwestern	Yes	CRPR 2B.2	64	2431
Chamaebatia foliolosa	evergreen shrub	Sierra Nevada	Yes		687	6737
Chorizanthe orcuttiana	perennial herb	Southwestern	Yes	CRPR 1B.1 US E	19 (PO)	19
Corylus cornuta ssp. *californica*	deciduous shrub	Northwestern	Core	MG050 (p. 159)	97 (PO)	97

Croton setiger	annual herb	Great Valley	Core		1081	11289
Deinandra conjugens	annual herb	Southwestern	Yes	CRPR 1B.1 US E	81 (PO)	81
Delphinium hesperium	perennial herb	Central Western	Yes		142	11319
Dichelostemma capitatum	perennial herb	Great Valley	Core		2779	10459
Encelia californica	deciduous subshrub	Southwestern	Core		1190	2950
Ericameria ericoides	evergreen subshrub	Central Western	Yes		172	7481
Erigeron petrophilus	perennial herb	Central Western	Yes		83	8694
Eriodictyon trichocalyx	evergreen shrub	Southwestern	Core		198	7480
Eriogonum fasciculatum	evergreen subshrub	Southwestern	Core	MG044 (p. 121)	4235	9646
Eryngium aristulatum	perennial herb	Northwestern	Yes		67 (PO)	67
Frangula (Rhamnus) californica	evergreen shrub	Central Western	Core		955	11303
Frangula (Rhamnus) rubra	evergreen shrub	Cascade Ranges	Yes		442	10989
Galium angustifolium	perennial herb	Southwestern	Yes		928	3325
Hazardia squarrosa	drought deciduous shrub	Southwestern	Yes		1054	2925
Hesperocyparis forbesii	conifer evergreen tree	Southwestern	Yes	CRPR 1B.1	93 (PO)	93
Hesperocyparis sargentii	conifer evergreen tree	Northwestern	Yes		176 (PO)	176
Hesperocypari	conifer	Southwestern	Yes	CRPR 1B.1	30	30

s stephensonii	evergreen tree				(PO)	
Hesperoyucca whipplei	succulent shrub	Southwestern	Yes		3309	6635
Heteromeles arbutifolia	evergreen shrub	Central Western	Yes	MG043 (p. 114)	4293	10022
Juglans californica	deciduous broadleaf tree	Southwestern	Yes	CRPR 4.2	874	7321
Juncus balticus	perennial herb (graminoid)	Great Valley	Core	MG075 (p. 195)	284	11296
Keckiella antirrhinoides	evergreen shrub	Southwestern	Yes		257	3442
Lepechinia calycina	drought deciduous shrub	Central Western	Yes		278	11281
Lonicera subspicata	evergreen liana	Southwestern	Yes		601	7546
Lupinus arboreus	evergreen shrub	Central Western	Yes	MG058 (p. 177) CRPR 3.2	116	6449
Lupinus tidestromii	perennial herb	Central Western	Yes	CRPR 1B.1 US E	29 (PO)	29
Malosma laurina	evergreen shrub	Southwestern	Yes		2998	2250
Erythranthe (Mimulus) cardinalis	deciduous subshrub	Northwestern	Core		135 (PO)	135
Minuartia obtusiloba	perennial herb	Sierra Nevada	Yes	CRPR 4.3	16 (PO)	16
Opuntia littoralis	succulent shrub	Southwestern	Yes		691	2218
Phacelia insularis	annual herb	Central Western	Yes		23 (PO)	23
Picea breweriana	conifer evergreen tree	Northwestern	Yes		131	2931

Pickeringia montana	evergreen shrub	Central Western	Yes		274	10699
Pinus attenuata	conifer evergreen tree	Northwestern	Yes	MG009 (p. 33)	321	10431
Pinus balfouriana	conifer evergreen tree	Sierra Nevada	Yes	MG020 (p. 42)	527	6690
Pinus coulteri	conifer evergreen tree	Southwestern	Yes	MG009 (p. 33)	1258	3350
Pinus jeffreyi	conifer evergreen tree	Sierra Nevada	Yes	MG023 (p. 49)	3585	9560
Pinus lambertiana	conifer evergreen tree	Northwestern	Yes	MG023 (p. 49)	4307	8786
Pinus muricata	conifer evergreen tree	Northwestern	Yes	MG009 (p. 33)	267	6429
Pinus quadrifolia	conifer evergreen tree	Southwestern	Yes		61	2428
Pinus sabiniana	conifer evergreen tree	Central Western	Yes	MG009 (p. 33)	3103	10668
Pinus torreyana	conifer evergreen tree	Southwestern	Yes	CRPR 1B.2 (for subspecies)	22	2429
Platanus racemosa	deciduous broadleaf tree	Great Valley	Yes	MG036 (p. 105)	1921	11084
Poa stebbinsii	perennial herb (graminoid)	Sierra Nevada	Yes		49	4030
Potentilla anserina ssp. *anserina*	perennial herb	Sierra Nevada	Yes		12 (PO)	12
Potentilla anserina ssp.	perennial herb	Central Western	Core		121 (PO)	121

pacifica						
Prunus ilicifolia	evergreen shrub	Southwestern	Yes		1167	10111
Pseudotsuga macrocarpa	conifer tree	Southwestern	Yes	MG023 (p. 51)	1091	3459
Ptilagrostis (Stipa) kingii	perennial herb (gramminoid)	Sierra Nevada	Yes		59	4016
Quercus agrifolia	evergreen broadleaf tree	Central Western	Yes	MG009 (p. 33)	3398	5801
Quercus chrysolepis	evergreen broadleaf tree	Northwestern	Core	MG009 (p. 33)	4710	9167
Quercus douglasii	deciduous broadleaf tree	Central Western	Yes	MG009 (p. 33)	4516	10752
Quercus dumosa	evergreen shrub	Southwestern	Yes		233 (PO)	233
Quercus engelmannii	deciduous broadleaf tree	Southwestern	Yes	MG009 (p. 33)	181	2423
Quercus kelloggii	deciduous broadleaf tree	Northwestern	Yes	MG009 (p. 33)	4685	9658
Quercus lobata	deciduous broadleaf tree	Central Western	Yes	MG009 (p. 33)	3050	11179
Quercus sadleriana	evergreen shrub	Northwestern	Yes		472	2581
Quercus wislizeni	evergreen broadleaf tree	Sierra Nevada	Yes	MG009 (p. 33)	3111	11059
Rhododendron occidentale	deciduous shrub	Northwestern	Core		1281	2011
Rhus	evergreen	Southwestern	Yes		1960	2725

integrifolia	shrub					
Rhus ovata	evergreen shrub	Southwestern	Core		511	11256
Ribes lasianthum	evergreen shrub	Sierra Nevada	Yes		435	10555
Ribes malvaceum	deciduous shrub	Central Western	Yes		1067	11212
Rosa californica	deciduous shrub	Great Valley	Yes		1657	11070
Salix lasiolepis	deciduous broadleaf tree	Great Valley	Core	MG036 (p. 105)	1208	3310
Salvia apiana	deciduous subshrub	Southwestern	Yes		935	10496
Salvia columbariae	annual herb	Southwestern	Core		1214	2884
Salvia leucophylla	drought deciduous subshrub	Southwestern	Yes	MG044 (p. 123)	3075	2363
Salvia mellifera	drought deciduous subshrub	Southwestern	Yes	MG044 (p. 123)	1043	11312
Sambucus nigra ssp. caerulea	deciduous shrub	Great Valley	Core		97	8703
Scutellaria californica	perennial herb	Northwestern	Yes		968	4006
Sequoia sempervirens	conifer evergreen tree	Northwestern	Yes	MG024 p. 60)	2854	3977
Sequoiadendron giganteum	Conifer evergreen tree	Sierra Nevada	Yes		232	8655
Torreya californica	conifer evergreen tree	Northwestern	Yes		320	6371
Trichostema lanatum	evergreen shrub	Southwestern	Yes		3151	10630

Umbellularia californica	evergreen broadleaf tree	Northwestern	Core		138	138
Viguiera laciniata	drought deciduous shrub	Southwestern	Yes		338	2425
Xylococcus bicolor	evergreen shrub	Southwestern	Yes		116	6449

Species: accepted name according to calflora.org (6/1/2022)

Endemism: Yes = endemic to California or the California Floristic Province (CFP); Core = the core (most) of the species range is within the CFP although the range edges extend beyond. Endemism status and range from calflora.org, gbif.org, and Burge et al. (2016).

Macrogroup/Conservation Status: For species that are major species in California vegetation macrogroups, named or assessed in Thorne et al. (2016), the macrogroup number (MG###) they indicate or represent (and the page number) is shown. Species conservation status is listed, based on calflora.org. CRPR = California Rare Plant Rank. US indicates federal listing under the Endangered Species Act, E(ndangered) or T(hreatened)

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1. Species data

Vegetation survey data were provided by Dr. James Thorne (UC Davis) and California Department of Fish and Wildlife and included two survey methods: rapids and relevés (Hannah et al. 2008). Rapid surveys are used as "presence-only" data such as these do not include full vegetation inventories and were part of targeted surveying efforts (e.g., identifying incidences of Sudden Oak Death). The relevé data, on the other hand, include complete species lists and can be used as reliable absences if the species is not present. We also included records from CalFlora (www.calflora.org/) with medium or high location quality that were collected after 1980 as species presences. These species were modeled using a presence-absence framework because these models can more reliably estimate habitat suitability or probability of species occurrence(Guillera-Arroita et al. 2015). For presences-absence and presence-only records, we removed those records older than 1980 and 1950 respectively. For 22 species with few or no records in these databases, we acquired records from other biodiversity databases (Table S2.1).

To filter observations outside of species' natural habitat, we excluded occurrence records that included any of the following words in the "location description": "botanic", "botanical", "campus", "cultivated", "garden", "nursery", "square", and "zoo". We also removed data with missing or duplicate geographic coordinates, retaining only one presence or absence per raster 270 m cell. Species occurrences from the presence-absence and presences-only datasets were visually checked, and those records far outside the species known range were removed. For occurrences with location quality information, only those with high and medium precision were used.

Occurrences from non-systematic surveys, like those used in presence-only databases, usually are biased to locations near human infrastructure (e.g., roads or urban areas, McCarthy et al. 2012; Beck et al. 2014) where people tend to observe and record observations. Such bias negatively affects SDM predictions and performance (Beck et al., 2014). Therefore, we used an environmental filtering approach to correct this bias (Varela et al. 2014). A critical decision when implementing this approach is the number of data partitions used for defining the multivariate grid. For this reason, we used a procedure that consisted of testing 2-4 partition classes for each species and then calculated spatial autocorrelation based on the Moran's I index for each variable. Finally, the number of classes with the lowest average spatial autocorrelation between variables and with the highest number of occurrences was selected (Velazco et al. 2020).

2. Model calibration, evaluation, and tuning

All species were modeled with the same candidate environmental predictors (Table S1.3 and S1.4). Model calibration area for each species was defined by the Jepson ecoregion(s) (main text Figure 1) which contained occurrences. Calibration area can affect predicted suitability patterns and inflate some models' performance metrics (Acevedo et al., 2017; Lobo et al., 2008; VanDerWal et al., 2009). For presence-absence species, we only included absence records within the calibration area because including absence records in areas beyond a species range can distort model output, with predictions of high suitability in regions where a species is known to not occur, i.e. "naughty noughts" (Austin and Meyers 1996). For each presence-only species, we generated a number of pseudo-absences equal to the number of species occurrences. Such pseudo-absences were geographically constrained, i.e., they were sampled throughout the calibration area but not within 5 km of any occurrences (Barbet-Massin et al. 2012). For the MAX algorithm, we sampled 10,000 background points within the calibration area of each species. The number of pseudo-absences and background points were weighted by the number of occurrences in each geographical partition (bands or blocks, see Data partition, model evaluation, and tuning) to equally distribute the amount of data within each partition.

We used spatial block and band cross-validation to partition occurrence data and evaluate model performance. Spatial partitioning allows testing of model transferability by evaluating how well a model trained in one geographic block/band performs when tested in another block/band (Roberts *et al.*, 2017; Santini *et al.*, 2021). For species with ≥30 occurrences, we tested 30 different block grid-sizes, ranging from a resolution of 13.5 km^2 and 81 km^2, dividing species presence and absence records into three to four spatially structured partitions that reduce spatial autocorrelation. Similarly, for species with <30 occurrences, we tested between 3-30 latitudinal bands and partitioned species' records into two partitions. For both partition approaches, the selected partition was the one that equilibrated the spatial autocorrelation (measured by Moran's I), environmental similarity (Euclidean distance), and differences in the amount of data among partition groups (Standard Deviation - SD; Velazco et al. 2019).

To exclude less reliable models from our ensemble predictions, individual model predictions with an area under the receiver operating characteristic (AUC) < .7 for presence-absence models and a Boyce index < .5, F-measure on presence-background

(Fpb) < 1, or a Sorenson value < .7 for presence-only models were not included in the ensemble predictions.

Detail about SDM overview, data, modeling, and predictions are given in Table S1.5. Recent research on SDM parameterization indicates that the default settings often do not produce the best performing models and that species-specific hyperparameter tuning is an important step in building the best model for a given data set(Warren et al. 2014, Schratz et al. 2019). We performed model tuning based on a grid search approach of all possible combinations of hyperparameter values within a specific range of values (See Table S1.7 for further detail about hyperparameter values). The best hyperparameter values were based on the true skill statistic (TSS) and Sorensen metrics and the threshold that maximizes them for presence-absence and presence-only data, respectively. Spatial analyses were carried out using the *terra* package in R (Hijmans 2022).

Table S1.2 Occurrence record sources.

Source	**Site**
BIEN: Botanical Information and Ecology Network	bien.nceas.ucsb.edu/bien/
Calflora	www.calflora.org/
California Department of Fish and Wildlife	https://wildlife.ca.gov/
CCH: Consortium of California Herbaria	www.cch2.org/portal/
GBIF: Global Biodiversity Information Facility	www.gbif.org
iDigBio: Integrated Digitized Biocollections	www.idigbio.org/

Table S1.3 Environmental predictors used to build SDMs, quantify niche breadth, and summarize species' geographic traits.

Category	**Source**	**Variable**
Climate	Basin Characterization Model (Flint et al. 2013) 270 m spatial resolution	Actual evapotranspiration (mm) - aet
		Climatic water deficit (mm) - cwd
		Minimum monthly temperature (deg C) - tmin
		Winter (Dec-Feb) precipitation (mm) - ppt djf
		Summer (Jun-Aug) precipitation (mm) - ppt jja
Soil	Gridded National Soil Survey Geographic Database (gNATSGO) 10 m spatial resolution; resampled to 270 m	Soil pH
		Available water capacity (cm of water per cm of soil) - awc
		Soil depth (cm)
		Percent clay (%)
Terrain	Ecologically-relevant landforms (Theobald et al. 2015) 30 m spatial resolution; resampled to 270 m Topographic heterogeneity 90 m spatial resolution; resampled to 270 m	Geophysical landform/ Physiographic Diversity (15 categories) Topographic heterogeneity (0-1) – measures the range in elevation values from a center cell and the three-cell radius immediately surrounding it using the 90 m digital elevation model (DEM) from USGS. These values were then converted to a 0-1 scale using the standard deviation of the range of values across the study area. (Used as a predictor for species with <50 occurrences)

Location	NASA EarthData 90 m DEM of California, USA	Distance to coast (km) Elevation (m)

Table S1.4 Mean, minimum, and maximum values of the environmental variables used to quantify niche breadth and position across the California Floristic Province.

Environmental variables	Mean	Min	Max
Actual evapotranspiration (mm) - aet	364.6	0.0	1112.4
Climatic water deficit (mm) - cwd	847.7	0.0	1544.4
Minimum monthly temperature (deg C) - tmin	6.6	-8.2	15.0
Winter precipitation (mm) - ppt djf	141.5	19.5	674.4
Summer precipitation (mm) - ppt jja	6.8	0.4	49.3
Soil pH	6.0	0.0	10.3
Available water capacity (cm of water per cm of soil)	0.1	0.0	0.6
Soil depth (cm)	110.3	0.0	356.0
Percent clay (%)	20.1	0.0	65.2

Table S1.5 Details about SDM overview, data, modeling, and predictions (Zurell et al. 2020)

ODMAP element	Contents
Overview	
Authorship	● **Authors:** M. Brooke Rose, Santiago J.E. Velazco, Helen Regan, and Janet Franklin ● **Contact email:** mrose048@ucr.edu ● Title: Disentangling the effects of rarity and geography on plant exposure to global change in the California Floristic Province
Model objective	● **SDM objective:** mapping species occupied suitable area and predicting future suitability under climate and land use change to measure species exposure to each ● **Main target output:** continuous habitat suitability index (probability of species presence)
Taxon	● 106 terrestrial plant species native to California/ the California Floristic Province
Location	California Floristic Province
Scale of analysis	● Spatial extent (Lon/Lat): ○ California Floristic Province: Longitude 124.41° W-116.05° W, Latitude 32.53° N – 42.01° N ● Spatial resolution: 270m ● Temporal extent: period of climate normals (30-year average for 1980-2010) - used for model-building and delineating currently occupied habitat ● Temporal projection: 30-year average for 2070-2099 - used for model projections and estimating suitability loss and exposure
Biodiversity data overview	Observation type: field surveys compiled from multiple agencies and iNaturalist data (Calflora) – 76,266 records Response type: presence/absence & presence/pseudo-absence
Type of predictors	Climatic, edaphic, and topographic

Conceptual model/hypotheses	Hypothesis: Climate, soils, and landform are correlated with plant distributions.
Assumptions	We assumed that the species-environment relationship was in equilibrium and that all relevant predictor variables were included in our models.
SDM algorithms	**Model algorithms:** GLM (for species with more than 100 occurrences), GAM, BRT, SVM, RF, ANN (all species), Maxent and GAU (for presence-only models) **Model complexity:** The data determined model complexity in each case. BRT, SVM, RF, and ANN were tuned using a range of hyperparameters for each model. **Model averaging:** Average of cells above each model's threshold value for models with an AUC greater than or equal to .7.
Model workflow	*flexsdm* package (https://github.com/sjevelazco/flexsdm)
Software	Software: R Code availability: Available at Data availability: Available at
Data	
Biodiversity data	**Taxon**: 106 terrestrial plant species (see Appendix S1 of paper for table) **Taxonomic reference system**: Jepson Flora of California **Ecological level**: species and some subspecies **Data sources**: **Clipping:** presence and absence data were restricted to the California Floristic Province **Potential errors and biases:** Our presence-only data were collected from non-systematic surveys, so we used a procedure that consisted of testing for each species two, three, and four numbers and then calculated spatial autocorrelation based on the Moran's I index for each variable. Finally, the number of classes with the lowest average spatial autocorrelation between variables and with the highest number of occurrences was selected (Velazco et al. 2020)
Data cleaning	To filter observations outside of species' natural habitat, we excluded occurrence records that included any of the

	following words in the "location description": "botanic", "botanical", "zoo", "square", "campus", "cultivated". We also removed data with missing or duplicate geographic coordinates, retaining only one presence or absence per raster cell in our final model data for each species. Our final dataset consisted of 76,266 records plot records
Data Partitioning	We used spatial block and band cross-validation frameworks to partition occurrence data. For species with more than 30 occurrence records, we tested 30 different block grid-sizes, ranging from a resolution of 13.5 km^2 and 81 km^2, dividing species presence and absence records into three to four spatially structured partitions that reduce spatial autocorrelation. Similarly, for species with fewer than 30 occurrences, we tested between 3-30 latitudinal bands and partitioned species' records into two partitions for testing and training. For both partition approaches, the selection of the best partition was the one that split presences (and absence) data that equilibrate the spatial autocorrelation (measured by Moran's I), environmental similarity (Euclidean distance), and differences in the amount of data among partition groups (Standard Deviation - SD; Velazco et al., 2019, maybe cite flexsdm).
Predictor variables	● **Predictor variables:** climatic water deficit (cwd), actual evapotranspiration (aet), minimum monthly temperature (tmin), and wet- and dry-season precipitation (ppt djf and ppt jja), soil pH, available water holding capacity (awc), soil depth, percent clay, categorical landform data OR topographic heterogeneity. ● **Data sources:** Bioclimatic variables - Basin Characterization Model (Flint et al. 2013); Soil variables - Gridded National Soil Survey Geographic Database (gNATSGO); Categorical landforms - Ecologically-relevant landforms (Theobald et al. 2015); Topographic heterogeneity; Distance to coast (NASA Earth Data) ● **Data processing:** Masking and cropping the raster data to the extent of the study area (CFP) and resampling soil and terrain variables to match the spatial resolution of the bioclimatic variables (270m) ● **Spatial resolution of raw data:** 270m, 10m, 30m

	- **Projection:** NAD83 / California Albers
Model	
Variable pre-selection	Ecological relevance for plant species distributions
Multicollinearity	Several of our predictor variables were highly correlated; however, they are biologically meaningful to plant species in the CFP.
Model settings	See Table S1.7 for tuning parameters.
Threshold selection	The best hyperparameter values were based on the TSS and Sorensen metrics and the threshold that maximizes them for presence-absence and presence-only data, respectively
Assessment	
Performance statistic	In our ensembles, we excluded individual model predictions with an AUC < .7 for presence-absence models. For presence-only models, we excluded any models that had a Boyce index < .5, F-measure on presence-background (Fpb) < 1, or a Sorenson value < .7 from our ensemble (see Figure S1.1 for model performance summary)
Plausibility check	Habitat suitability maps were reviewed by Janet Franklin/expert botanist to assess the plausibility of the spatial projections.
Prediction	
Prediction output	- **Prediction unit:** probability of species presence/habitat suitability - **Post-processing:** ○ Current species distributions were restricted to suitable habitat patches that contain at least one species occurrence (occurrence-based restriction) (Mendes et al. 2020)

Table S1.6 ICLUS data reclassification scheme and impact on habitat suitability

New Class	Impact on suitability	Original Classes
Natural	No impact	Natural water, Reservoirs, Canals, Wetlands, Recreation, Conservation, Timber, Grazing, Institutional
Exurban	Reduce by 50%	Exurban: high and low density
Developed	Reduce by 100%	Pasture, Cropland, Mining, Barren land, Parks, Golf courses, Suburban, Urban, Commercial, Industrial, Transportation

Tables S1.7 Hyperparameters values used for tuning different algorithms and the total number of value combinations. In the Hyperparameters values column are the names of hyperparameters and the R codes used to create the sequence of values.

Algorithm	**Hyperparameter values**	**Number of combinations**
ANN	size = seq(2, 8, by = 1) decay = c(seq(0.01, 1, by = 0.05), 1, 3, 4, 5, 10))	175
BRT	n.trees = seq(10, 200, by = 10) shrinkage = seq(0.1, 2, by = 0.1) n.minobsinnode = seq(1, 15, by = 2)	3200
MAX	regmult = seq(0.1, 5, by = 0.2) classes = c("l", "lq", "lqh", "lqhp", "lqhpt")	125
RAF	mtry = seq(1, 8, by = 1)	8
SVM	C = seq(2, 80, by = 4) sigma = seq(0.001, 0.2, by = 0.002)	2000

MAX features classes: linear (l), quadratic (q), hinge (h), product (p), and threshold (t)

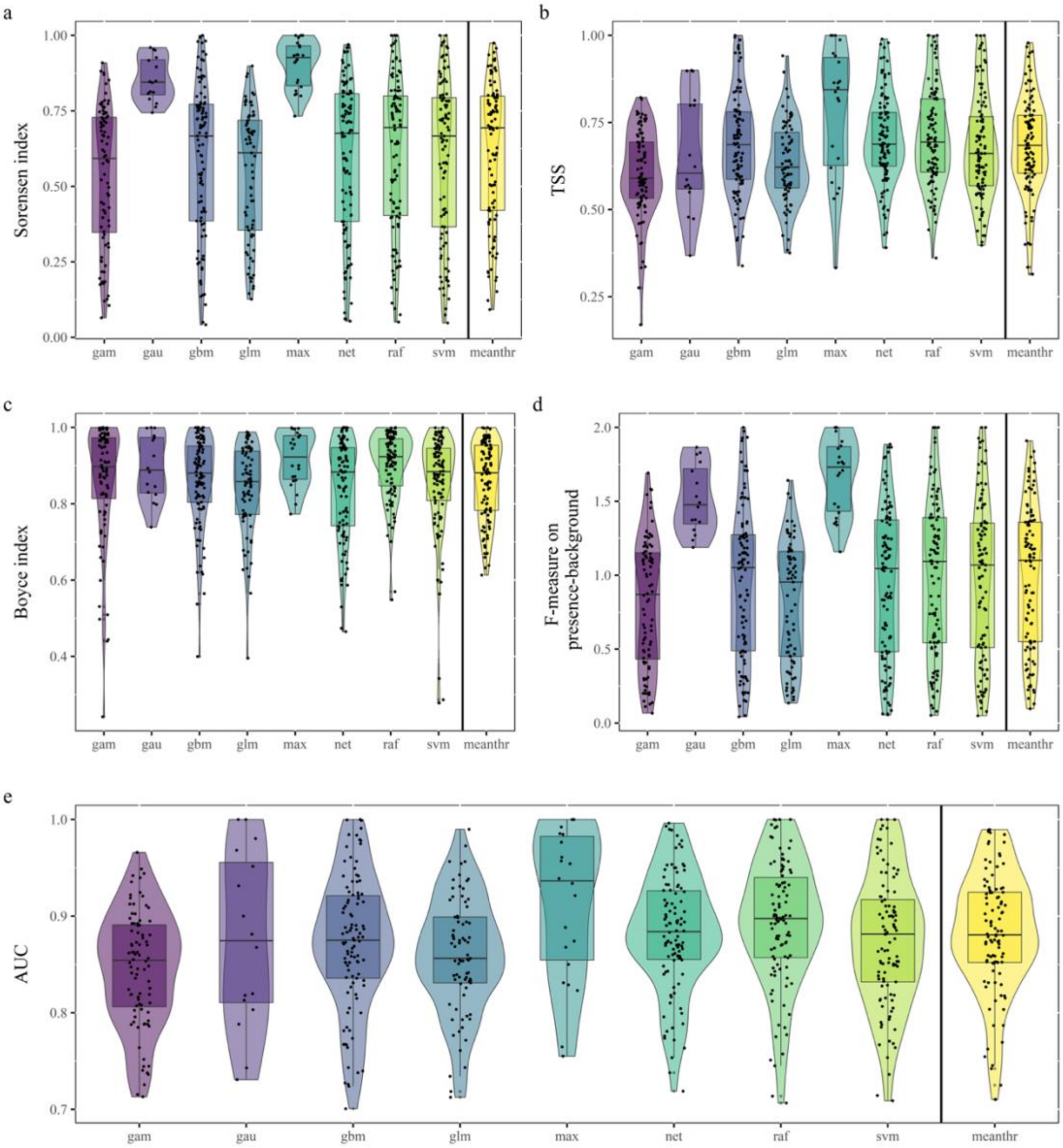

Figure S1.1 Model performance of the 106 plant species measured by a) Sorensen index, b) True Skill Statistic (TSS), c) Boyce index, d) F-measure on presence-background (FPB), and e) AUC for individual SDM algorithms and the ensemble model used in this analysis (meanthr).

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PCAs used to calculate niche breadth

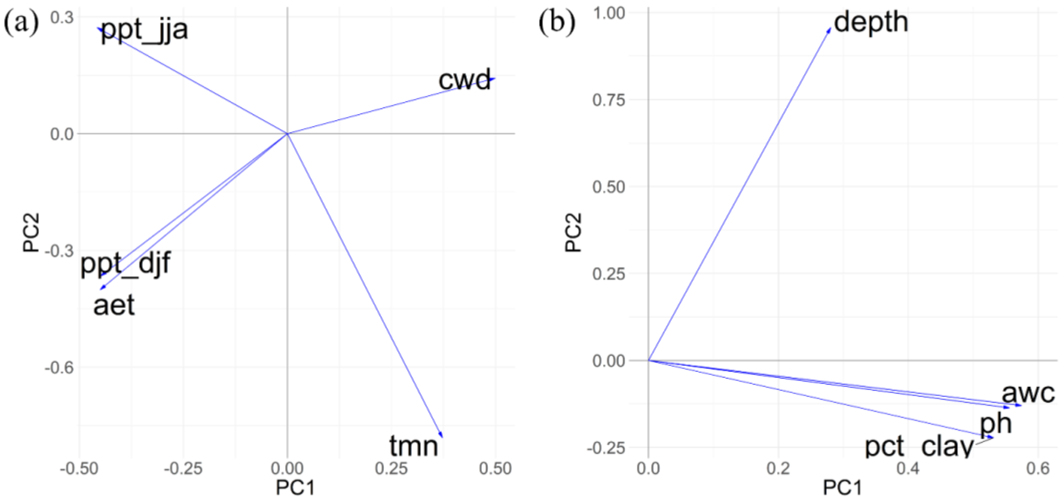
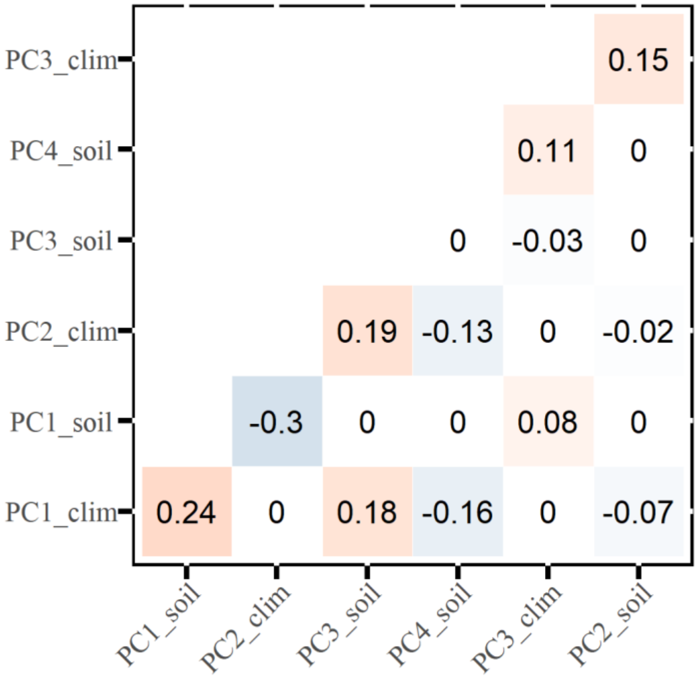


Figure S1.2 Ordination diagram for the first two axes of three PCAs conducted with climate variables (a) and the first two axes of the four PCAs conducted with soil variables (b) that explained 95% of the variation in each set of variables (De Marco and Nóbrega, 2018).



	PC1_soil	PC2_clim	PC3_soil	PC4_soil	PC3_clim	PC2_soil
PC3_clim						0.15
PC4_soil					0.11	0
PC3_soil				0	-0.03	0
PC2_clim			0.19	-0.13	0	-0.02
PC1_soil		-0.3	0	0	0.08	0
PC1_clim	0.24	0	0.18	-0.16	0	-0.07

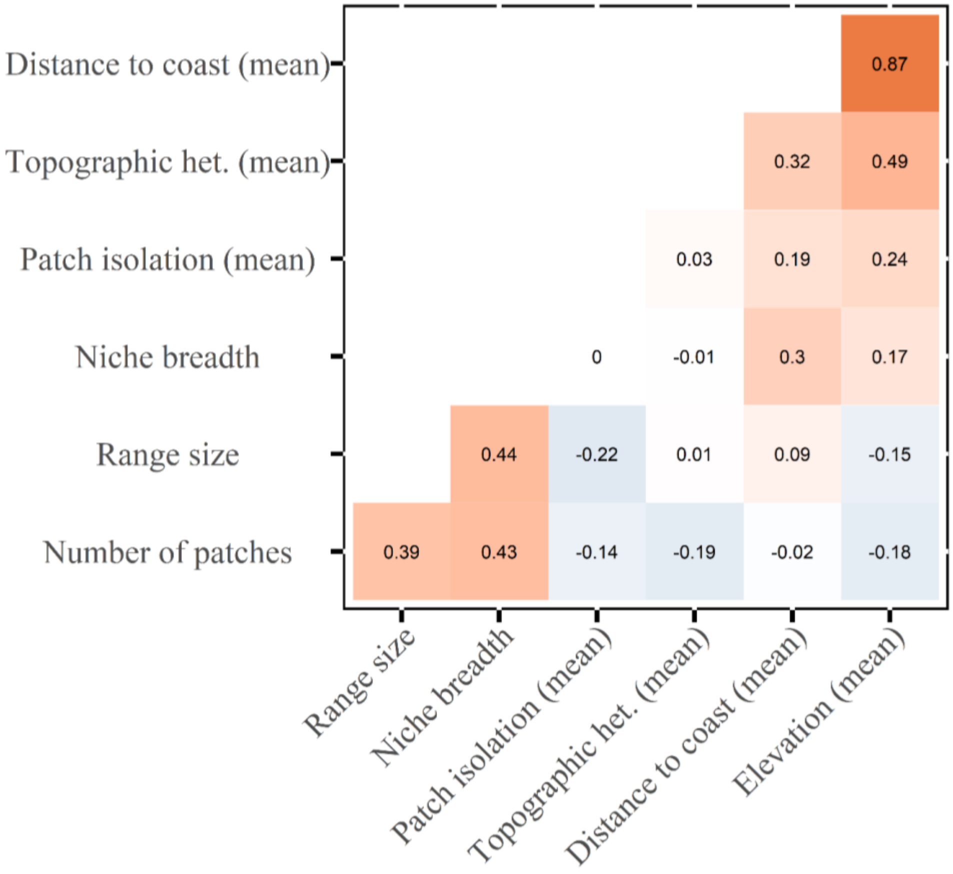
Figure S1.3 Pearson correlation matrix of the principal components produced from the climate and soil variables to quantify species niche breadth.

References

De Marco, P., Júnior & Nóbrega, C.C. (2018) Evaluating collinearity effects on species distribution models: An approach based on virtual species simulation. *PloS one*, **13**, e0202403.

GAMLSS modeling procedure

To estimate the relationship between spatial range traits and species exposure to climate and land use change, we fit univariate generalized additive models for scale, shape, and location (GAMLSS). Initial data exploration revealed several strong correlations between two of our predictor variables (Figure S4.1), i.e., distance to coast and elevation. Because we wanted to better understand the relationship between each spatial range trait and exposure, we chose to model exposure as a function of each spatial range trait individually.



	Range size	Niche breadth	Patch isolation (mean)	Topographic het. (mean)	Distance to coast (mean)	Elevation (mean)
Distance to coast (mean)						0.87
Topographic het. (mean)					0.32	0.49
Patch isolation (mean)				0.03	0.19	0.24
Niche breadth			0	-0.01	0.3	0.17
Range size		0.44	-0.22	0.01	0.09	-0.15
Number of patches	0.39	0.43	-0.14	-0.19	-0.02	-0.18

Figure S1.4 Pearson correlation matrix of spatial range traits.

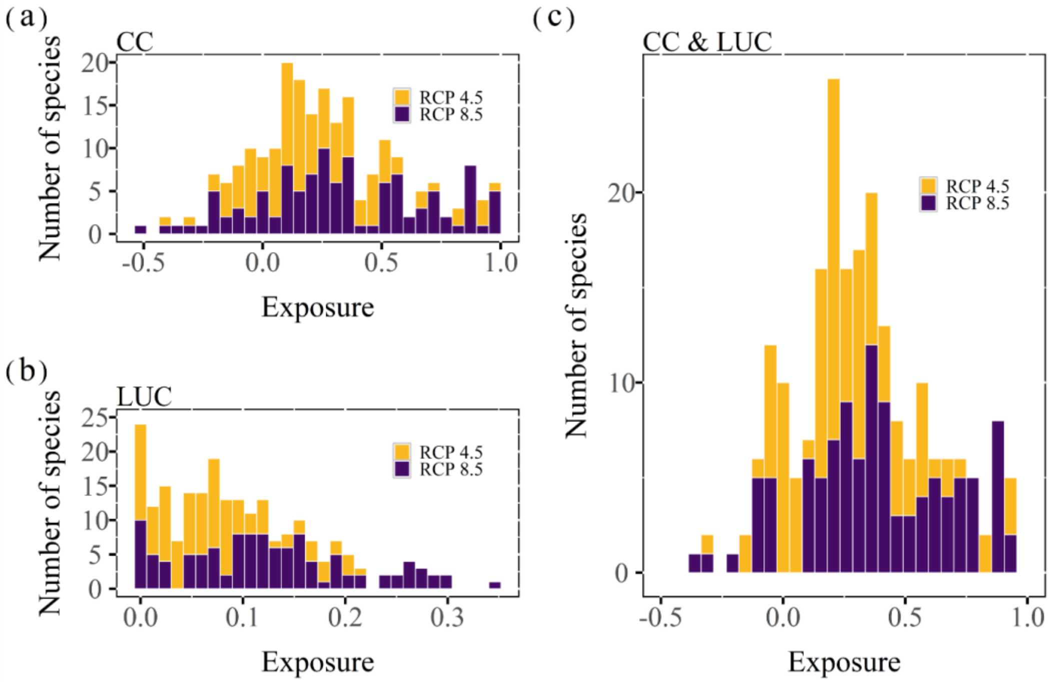


Figure S1.5 Frequency distribution of exposure values for climate change (a), land use change (b), and climate and land use change (c).

For climate change and climate and land use change, exposure values across species and RCP scenarios ranged from -0.5 to 1.0 (Figure S4.2), while exposure values for land use change alone ranged from 0 to 0.35. Therefore, we used different distribution families included in the gamlss R package to model the relationship between exposure to the different drivers and spatial range traits (Rigby and Stasinopoulos 2005; Stasinopoulos *et al.*, 2017; Rigby *et al.*, 2019). For climate change and climate and land use change exposure, we compared models with the normal (NO), Skew Normal Type 1 (SN1), Skew Normal Type 2 (SN2), and sinh-arcsinh original 2 (SHASHO2) distributions. We selected the SN1, which is designed to fit skewed response variables that range from $-\infty$ to ∞. However, land use change exposure values were all 0 because it was impossible for a species to experience increases in habitat suitability under land use change within our framework, so we tested the beta inflated at 0 (BEINFO), zero-adjusted GA (ZAGA), and the Pareto 2 original (PARETO2o) distributions. We selected the Beta inflated 0 distribution (BEINF0), which is suitable for nonnegative response variables. For all our models, we tested different location, scale, and shape parameters based on combinations of RCP and the spatial range trait being tested. All distribution and parameter selection tested for a given model were evaluated based on Akaike information criterion (AIC) and a visual inspection of the model residuals assumption of normality and homoscedasticity.

Table S1.8 Results for GAMLSS models for species traits and exposure for climate and land use change exposure combined.

Climate and land use change exposure				
	R^2	Estimate	SE	p
Range size	0.34	-1.14^{+++}	0.11	**<.001**
Range size^2		1.07	0.11	**<.001**
Niche breadth	0.14	-0.03^{+++}	0.006	**0.007**
Number of patches	0.28	-0.10^{+++}	0.01	**<.001**
Patch isolation	0.15	0.12	0.03	**<.001**
Elevation	0.16	0.00008	0.00001	**<.001**
Topographic heterogeneity	0.16	-0.15^{+++}	0.05	**0.005**
Distance to coast	0.14	0.0005	0.0001	**<.001**

(+) denote the significance of the interaction between each spatial range trait and RCP: $^{+++}$P < 0.001; $^{++}$P < 0.01; $^{+}$P < 0.05.

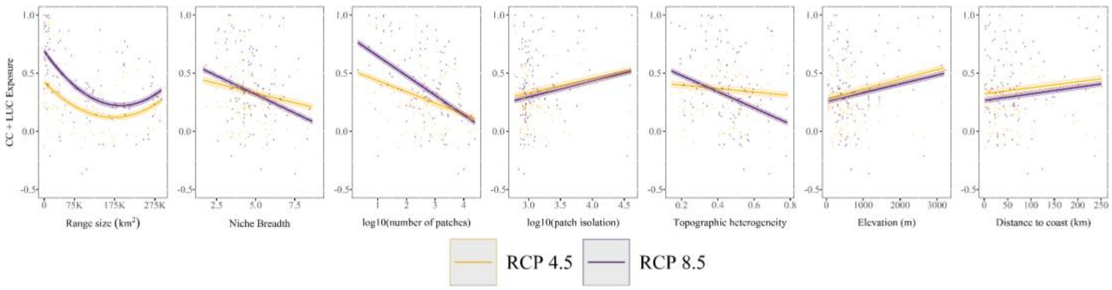


Figure S1.6 Fitted response curves for the GAMLSS relating rarity and geographic traits to the combined effect of climate change and land use change exposure under RCP 4.5 and 8.5.

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Phylogenetic tree and tests for phylogenetic dependence

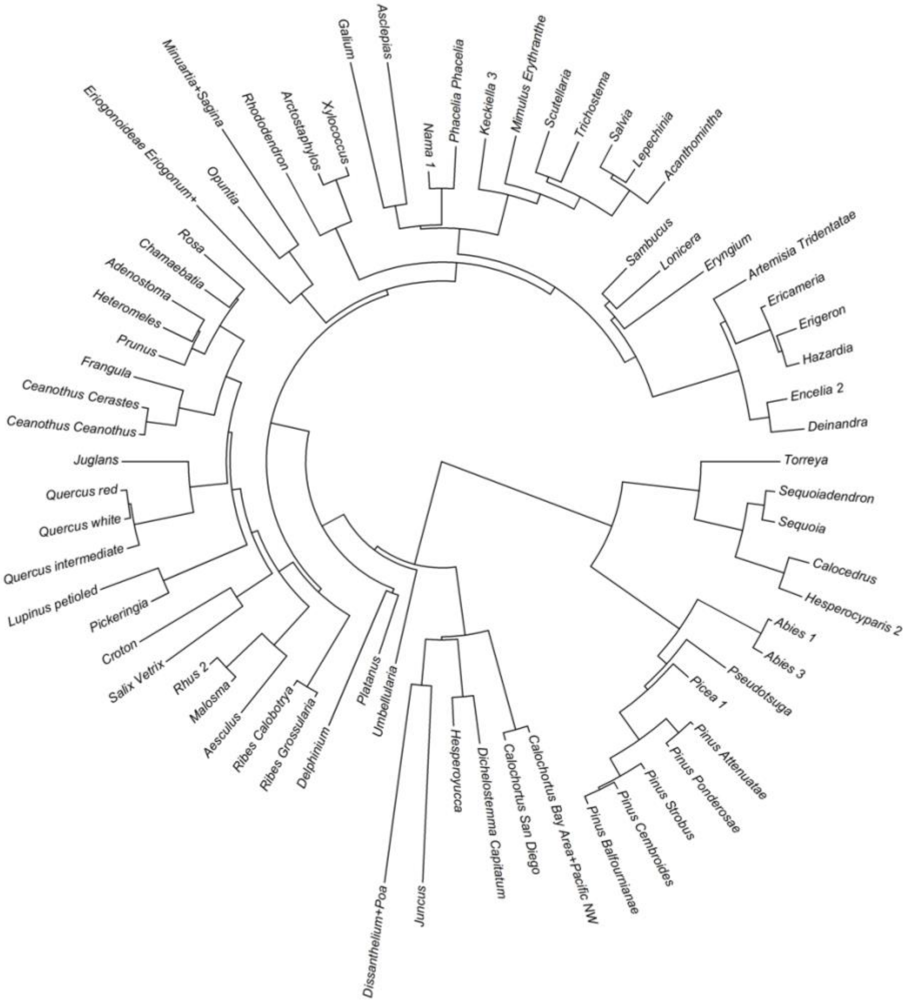
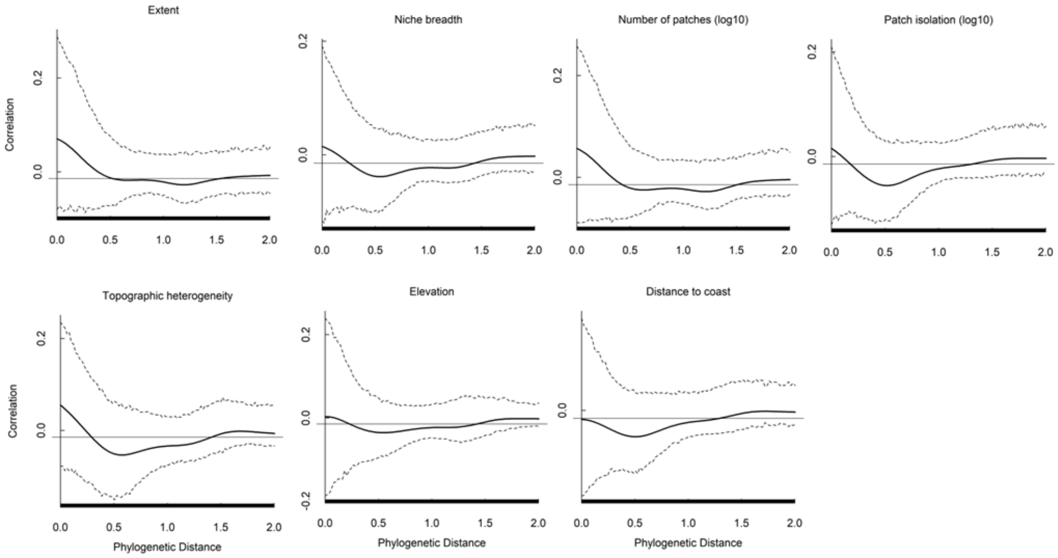


Figure S1.7 Phylogenetic tree for study species produced by Thornhill et al. (2017).

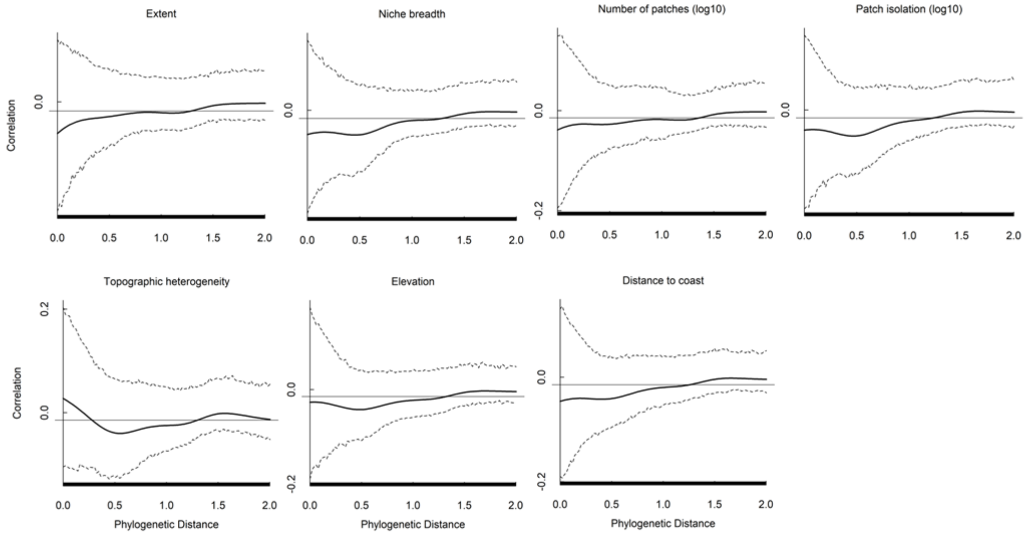
Moran’s I Phylogenetic Correlograms of GAMLSS Model Residuals

We examined Moran’s I phylogenetic correlograms for the residuals of each GAMLSS relating species traits to exposure using the *phylosignal* package (Keck et al., 2016). Overall, the residuals did not show any significant phylogenetic structure, except small amounts for models relating land use change exposure to rarity and geographic traits under RCP 8.5 (Figure S5.1).

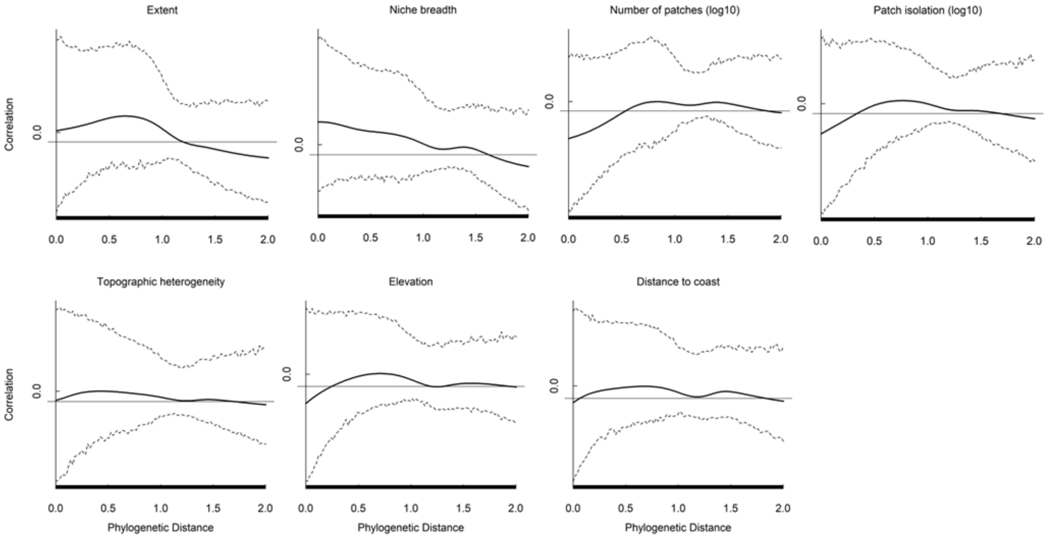
(a) Climate change (RCP 4.5)



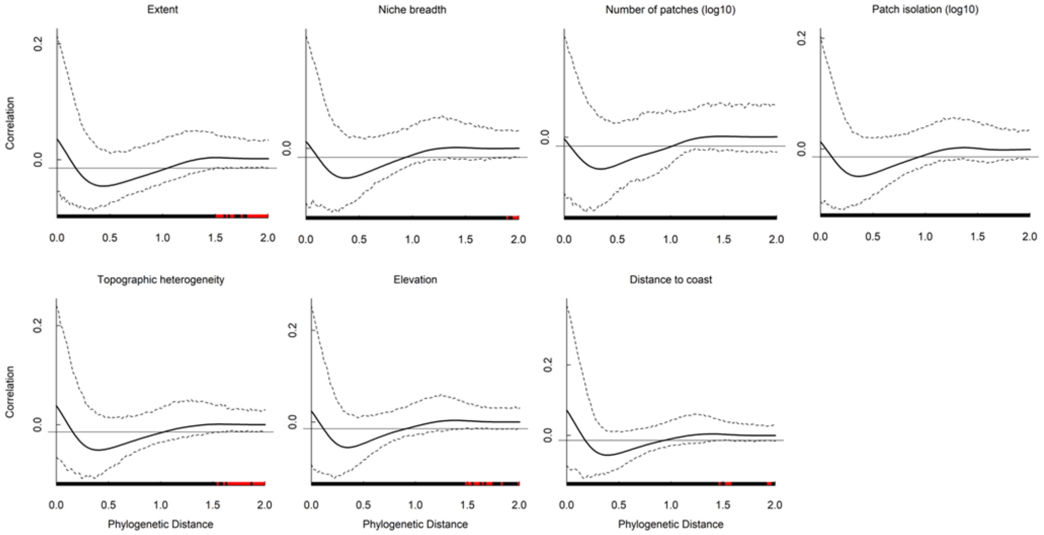
(b) Climate change (RCP 8.5)



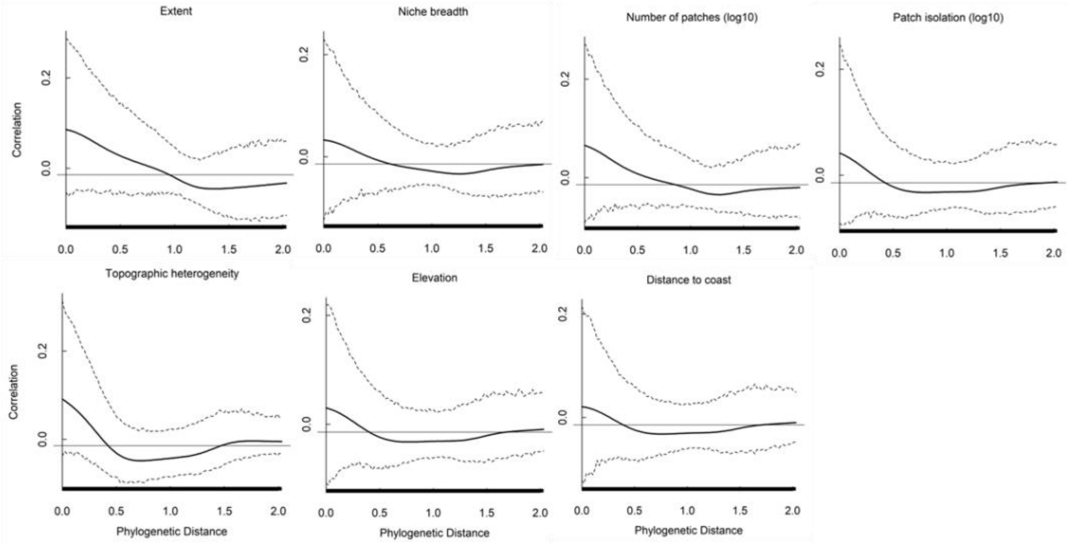
(c) Land use change (RCP 4.5)



(d) Land use change (RCP 8.5)



(e) CC + LUC (RCP 4.5)



(f) CC + LUC (RCP 8.5)

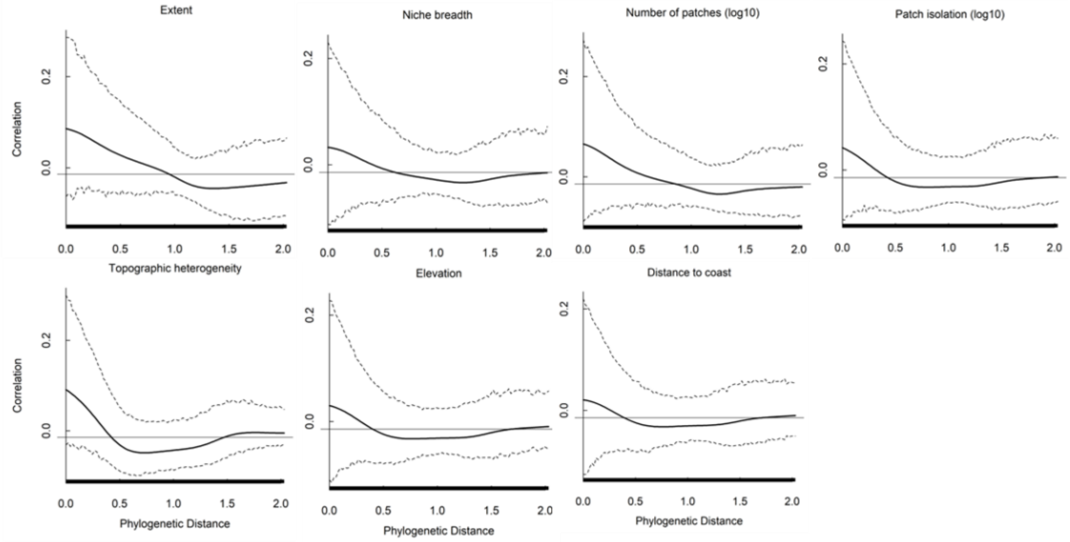


Figure S1.8 Phylogenetic correlograms for the residuals of the GAMLSS relating species traits to exposure under climate change RCP 4.5 (a) and RCP 8.5 (b), land use change RCP 4.5 (c) and RCP 8.5 (d) and the combined effects of both RCP 4.5 (e) and RCP 8.5 (f). The solid black lines represent the Moran’s I index of autocorrelation, and the dashed black lines represent the lower and upper confidence intervals (95%). The bars at the bottom show whether the autocorrelation is significant, where black indicates nonsignificant autocorrelation and red indicates significant positive autocorrelation.

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Thornhill, A.H., Baldwin, B.G., Freyman, W.A., Nosratinia, S., Kling, M.M., Morueta-Holme, N., Madsen, T.P., Ackerly, D.D. & Mishler, B.D. (2017) Spatial phylogenetics of the native California flora. *BMC biology*, **15**, 96.

Decision tree analysis

We used functions in the *rpart* and *rpart.plot* packages in R to build and plot regression tree models (Therneau *et al.*, 2010; Milborrow, 2021).

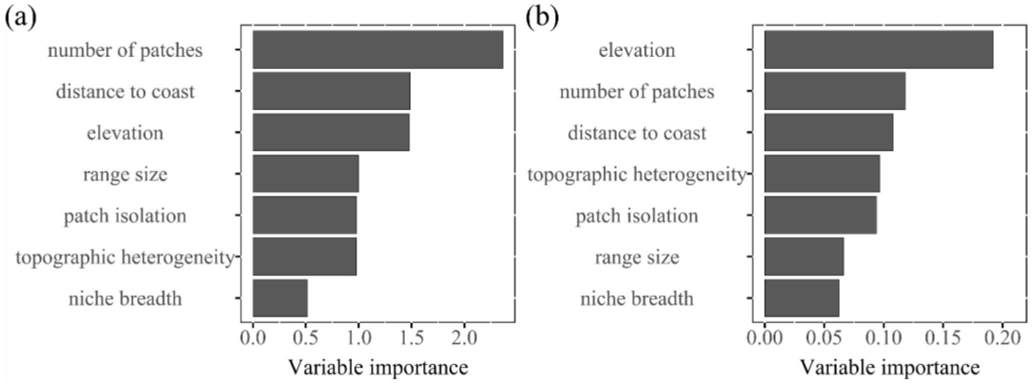

Figure S1.9 Importance of each species trait in predicting exposure to climate change (a) and land use change (b) based on the decision tree analysis under the low GHG emissions scenario (RCP 4.5).

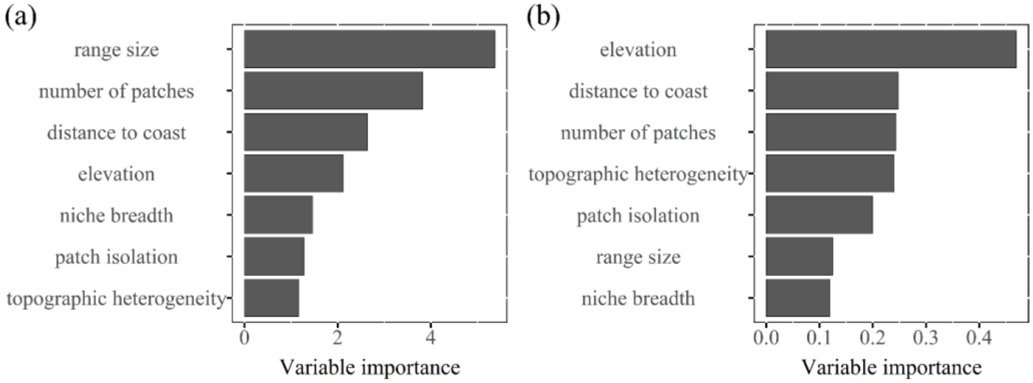

Figure S1.10 Importance of each species trait in predicting exposure to climate change (a) and land use change (b) based on the decision tree analysis under the high GHG emissions scenario (RCP 8.5).

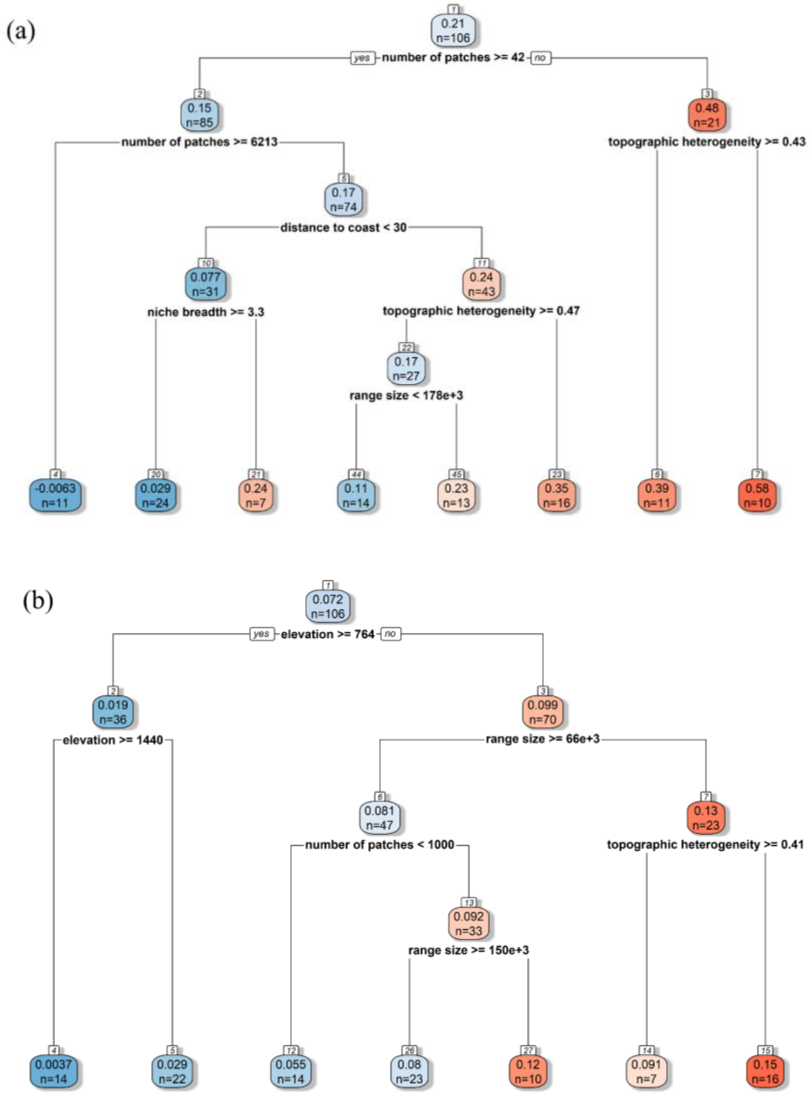

Figure S1.11 Decision tree showing exposure to (a) climate change and (b) land use change based on species' traits under the RCP 4.5 emissions scenario. In each node, the top number indicates the average exposure of the species in that group, i.e., overall species had an average climate change exposure of 0.22 for RCP 4.5) and the second number (n=#) indicates the number of species in that group. For each branch split, species to the right are more exposed than species to the left. Cool (blue) colors correspond to lower exposure values while warmer (red) colors correspond to higher exposure.

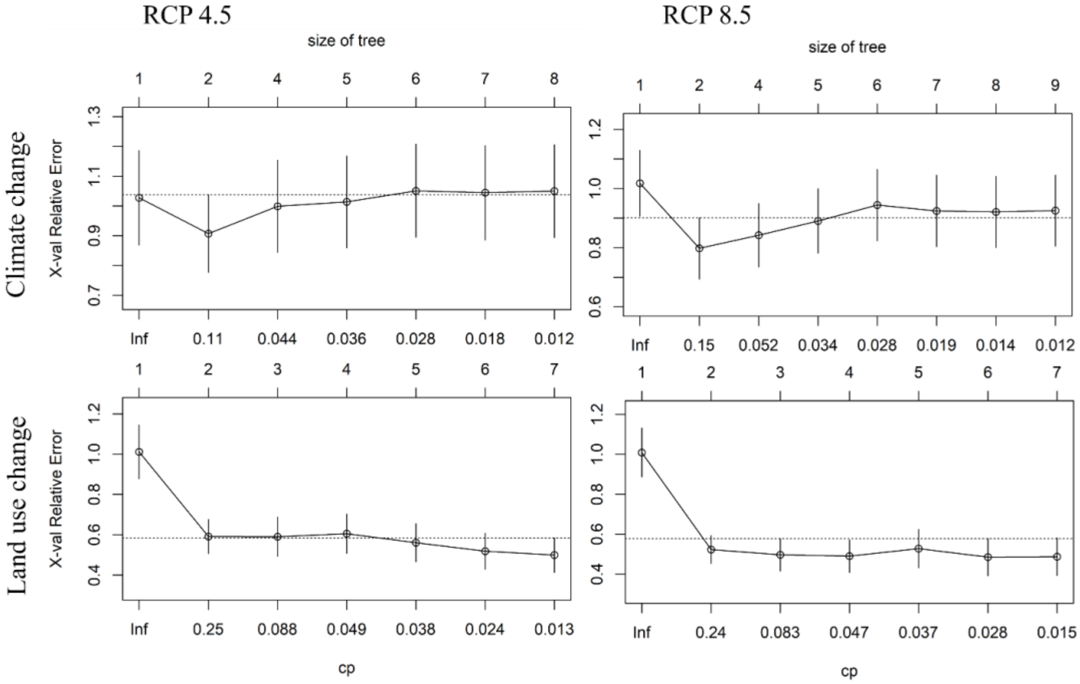

Figure S1.12 Decision tree misclassification error rate as a function of the complexity parameter and tree size based on 10-fold cross-validation for exposure to climate and land use change under the two RCP emissions scenarios.

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Chapter 2 Supporting Information

Table S2.1 Details about SDM overview, data, modeling, and predictions (Zurell et al. 2020)

ODMAP element	**Contents**
Overview	
Authorship	**Authors:** M. Brooke Rose, Santiago J.E. Velazco, Helen Regan, Alan L. Flint, Lorraine E. Flint, James Thorne, and Janet Franklin **Contact email:** mrose048@ucr.edu **Title:** Uncertainty in consensus predictions of plant species' vulnerability to climate change in the California Floristic Province
Model objective	**SDM objective:** mapping species occupied suitable area and predicting future suitability under climate change to compare the variability introduced by consensus method, global circulation model (GCM), and representative concentration pathway (RCP) scenario **Main target output:** continuous habitat suitability index (probability of species presence)
Taxon	82 terrestrial plant species native to California/ the California Floristic Province
Location	California Floristic Province
Scale of analysis	Spatial extent (Lon/Lat): California Floristic Province: Longitude 124.41° W-116.05° W, Latitude 32.53° N – 42.01° N Spatial resolution: 270m Temporal extent: period of climate normals (30-year average for 1980-2010) - used for model-building and delineating currently occupied habitat Temporal projection: 30-year average for 2040-2069 & 2070-2099 - used for model projections and estimating suitability loss

Biodiversity data overview	Observation type: field surveys compiled from multiple agencies and Calflora data – 68,568 records Response type: presence/absence
Type of predictors	Climatic, edaphic, and topographic
Conceptual model/hypotheses	Hypothesis: Climate, soils, and landform are correlated with plant distributions.
Assumptions	We assumed that the species-environment relationship was in equilibrium and that all relevant predictor variables were included in our models.
SDM algorithms	**Model algorithms:** GLM (for species with more than 100 occurrences), GAM, BRT, SVM, RF, ANN **Model complexity:** The data determined model complexity in each case. BRT, SVM, RF, and ANN were tuned using a range of hyperparameters for each model. **Model averaging: Five consensus methods were used to combine suitability predictions made by** Average of cells above each model's threshold value for models with an AUC greater than or equal to .7.
Model workflow	*flexsdm* package (https://github.com/sjevelazco/flexsdm)
Software	Software: R
Data	
Biodiversity data	**Taxon**: 82 terrestrial plant species (see Appendix S1 of paper for table) **Taxonomic reference system**: Jepson Flora of California **Ecological level**: species and some subspecies **Data sources**: **Clipping:** presence and absence data were restricted to the California Floristic Province **Potential errors and biases:** A few species included (example: *Pinus quadrifolia*) have geographic distributions that extend into Baja California. Because of data availability

	limitations, we only included occurrences within the state of California.
Data cleaning	To filter observations outside of species' natural habitat, we excluded occurrence records that included any of the following words in the "location description": "botanic", "botanical", "zoo", "square", "campus", "cultivated". We also removed data with missing or duplicate geographic coordinates, retaining only one presence or absence per raster cell in our final model data for each species. Our final dataset consisted of 68,568 plot records
Data Partitioning	We used spatial block and band cross-validation frameworks to partition occurrence data. For species with more than 30 occurrence records, we tested 30 different block grid-sizes, ranging from a resolution of 13.5 km^2 and 81 km^2, dividing species presence and absence records into three to four spatially structured partitions that reduce spatial autocorrelation. Similarly, for species with fewer than 30 occurrences, we tested between 3-30 latitudinal bands and partitioned species' records into two partitions for testing and training. For both partition approaches, the selection of the best partition was the one that split presences (and absence) data that equilibrate the spatial autocorrelation (measured by Moran's I), environmental similarity (Euclidean distance), and differences in the amount of data among partition groups (Standard Deviation - SD; Velazco et al., 2019, Velazco et al., 2022)
Predictor variables	**Predictor variables:** climatic water deficit (cwd), actual evapotranspiration (aet), minimum monthly temperature (tmin), and wet- and dry-season precipitation (ppt djf and ppt jja), soil pH, available water holding capacity (awc), soil depth, percent clay, categorical landform data

	Data sources: Bioclimatic variables - Basin Characterization Model (Flint et al. 2013); Soil variables - Gridded National Soil Survey Geographic Database (gNATSGO); Categorical landforms -Ecologically-relevant landforms (Theobald et al. 2015) **Data processing:** Masking and cropping the raster data to the extent of the study area (CFP) and resampling soil and terrain variables to match the spatial resolution of the bioclimatic variables (270m) **Spatial resolution of raw data:** 270m, 10m, 30m **Projection:** NAD83 / California Albers
Transfer data for projection	**Climate models and scenarios and data sources:** Two climate models: CNRM-CM5 (Centre National de Recherches Meteorologiques climate model version 5) and HadGEM2-ES (Hadley Centre Global Environmental Model version 2- Earth system configuration); two Representative Concentration Pathways (4.5; 8.5) from the 5th Climate Model Intercomparison Project, used to drive the Basin Characterization Model (BCM) (Flint et al., 2013) Climate normals for two time periods (2040-2069 and 2070-2099), and for the same bioclimatic variables used as predictors, were acquired from the BCM and used (at the same 270-m resolution, projection, and extent) to project the SDM to future climate scenarios.
Model	
Variable pre-selection	Ecological relevance for plant species distributions
Multicollinearity	Several of our predictor variables were highly correlated; however, they are biologically meaningful to plant species in the CFP.
Model settings	See Table S2 for tuning parameters.
Threshold selection	The best hyperparameter values were based on the TSS and Sorensen metrics and the

	threshold that maximizes them for presence-absence and presence-only data, respectively
Assessment	
Performance statistic	In our ensembles, we excluded individual model predictions with an AUC < .7 for presence-absence models. (see Figure S2.1 for model performance summary)
Plausibility check	Habitat suitability maps were reviewed by Janet Franklin/expert botanist to assess the plausibility of the spatial projections.
Prediction	
Prediction output	**Prediction unit:** probability of species presence/habitat suitability **Post-processing:** Current species distributions were restricted to suitable habitat patches that contain at least one species occurrence (occurrence-based restriction) (Mendes et al. 2020)

Table S2.1 Number of species in each category of extreme habitat suitability change made by each consensus method under each climate change scenario for the end-of-century time period (2070-2099).

Consensus method	**Number of predictions**														
	CNRM-CM5								**HadGEM2-ES**						
	RCP 4.5				**RCP 8.5**				**RCP 4.5**				**RCP 8.5**		
	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c
MEAN	5	20	17	53	12	19	18	53	6	20	16	46	14	16	27
MEANW	3	15	18	55	10	14	19	53	4	16	15	50	14	13	29
MEANSUP	4	13	14	57	12	13	11	54	4	16	10	54	15	14	16
MEANTHR	7	24	16	50	23	21	12	49	9	25	12	45	18	27	19
MEDIAN	7	30	18	41	20	27	19	42	10	34	19	37	20	28	23
Total #	**26**	**102**	**83**	**256**	**77**	**94**	**79**	**251**	**33**	**111**	**72**	**232**	**81**	**98**	**114**
Expected per # method	**5.2**	**20.4**	**16.6**	**51.2**	**15.4**	**18.8**	**15.8**	**50.2**	**6.6**	**22.2**	**14.4**	**46.5**	**16.2**	**19.6**	**22.8**

Extreme change categories are a) low stability; b) low gain; c) high stability; d) high gain.

Table S2.2 Results of 42 simple univariate regression models of HSC uncertainty (standard deviation) as a function of species' rarity and geographic traits; R^2 for each model is in parentheses.

	Uncertainty sources					
	Full dispersal			No dispersal		
	SDM Consensus Method	GCM	RCP	SDM Consensus Method	GCM	RCP
Prevalence	$-^{+++}$**(0.13)**	n.s.	n.s.	**-**$^{++}$**(0.09)**	n.s.	n.s.
Range size	$-^{+++}$**(0.25)**	**-**$^{+++}$**(0.27)**	**-**$^{+++}$**(0.31)**	n.s.	**-**$^{+++}$**(0.18)**	**-**$^{+++}$**(0.15)**
Niche breadth	n.s.	n.s.	n.s.	n.s.	**-**$^{++}$**(0.11)**	**-**$^{++}$**(0.08)**
Elevation	n.s.	n.s.	n.s.	**+**$^{+}$**(0.04)**	n.s.	n.s.
Elevation range	n.s.	**-**$^{++}$**(0.08)**	**-**$^{+}$**(0.06)**	n.s.	**-**$^{++}$**(0.11)**	**-**$^{+++}$**(0.20)**
Topographic heterogeneity	n.s.	n.s.	n.s.	**+**$^{+}$**(0.04)**$^{+}$	n.s.	n.s.
Topographic heterogeneity range	n.s.	**-**$^{+}$**(0.04)**	**-**$^{+}$**(0.05)**	**-**$^{+}$**(0.07)**	**-**$^{++}$**(0.08)**	**-**$^{++}$**(0.10)**

SDM: species distribution model; GCM: global circulation model; RCP: emissions Representative Concentration Pathways. +: positive relationship; -: negative relationship. Standard deviation of habitat suitability change (HSC) was log-transformed in all models. (+) denote the significance of the F-statistic: $^{+++}P < 0.001$, $^{++}P < 0.01$, $^{+}P < 0.05$. (n.s.) non-significant.

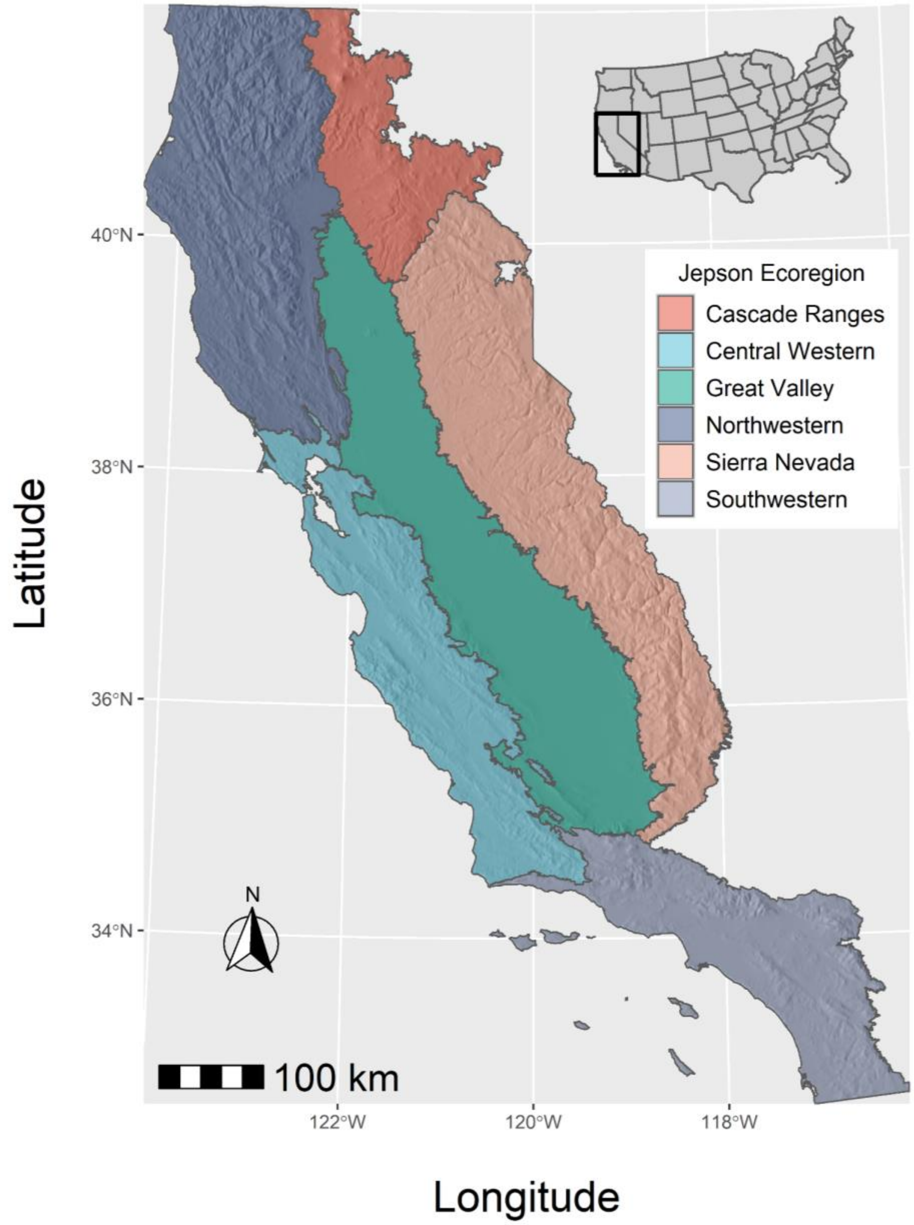

Figure S2.1. California Floristic Province Jepson Ecoregions, study area for the 82 plant species modeled in the current study.

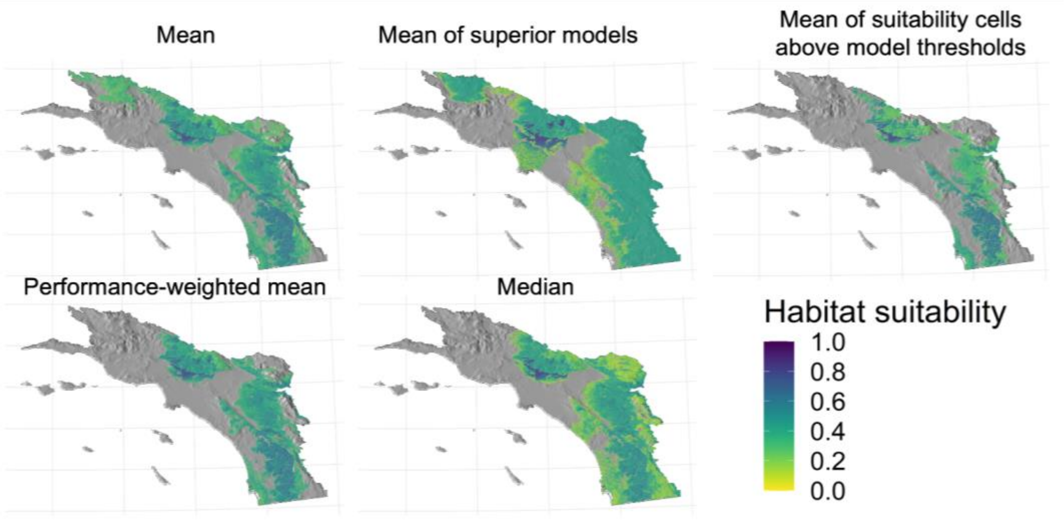

Figure S2.2. Consensus suitability maps for Engelmann oak (*Quercus engelmannii*), a rare tree species found only in southern California.

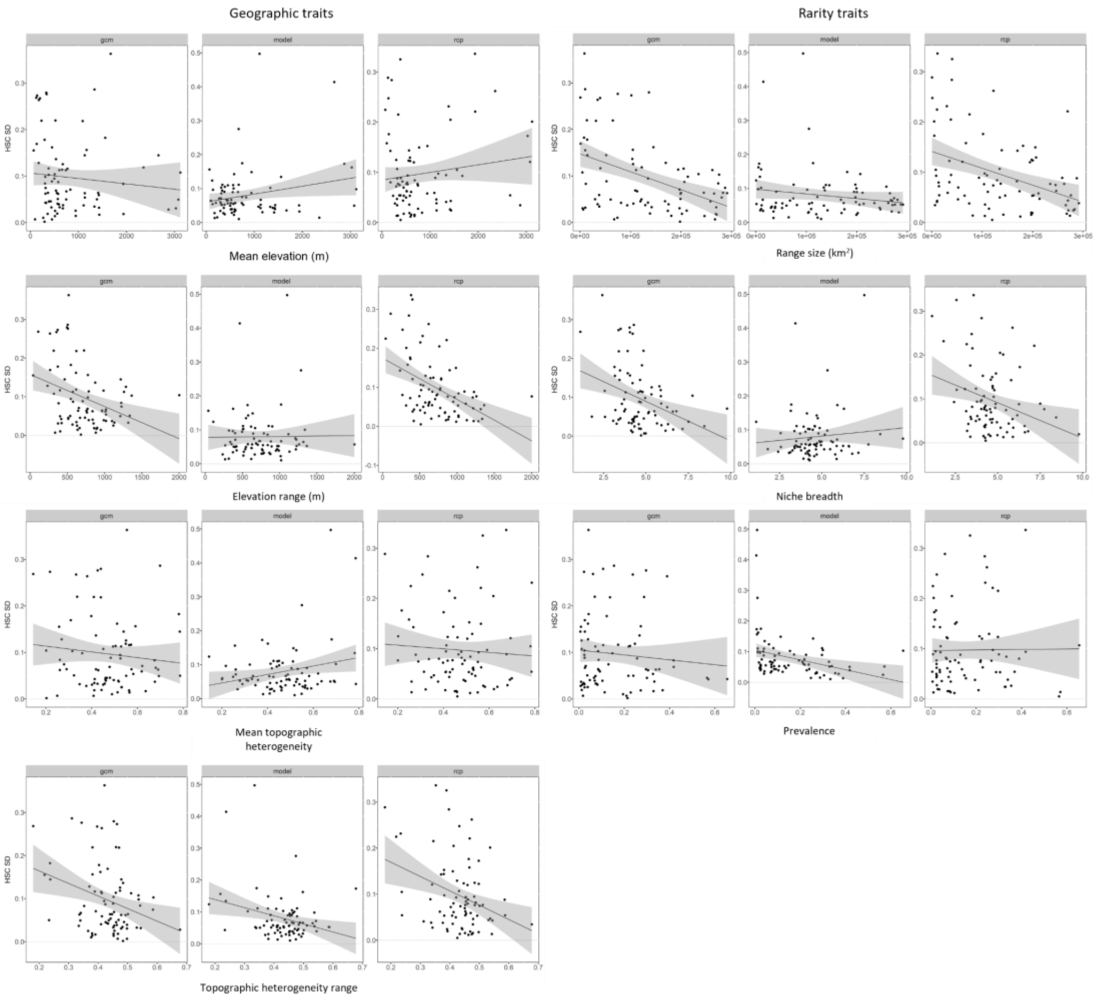

Figure S2.3. Scatterplots of species characteristics and uncertainty in future HSC (standard deviation in HSC) due to each factor (gcm = global circulation model, model = consensus method, and rcp = representative concentration pathway) under null dispersal scenarios.

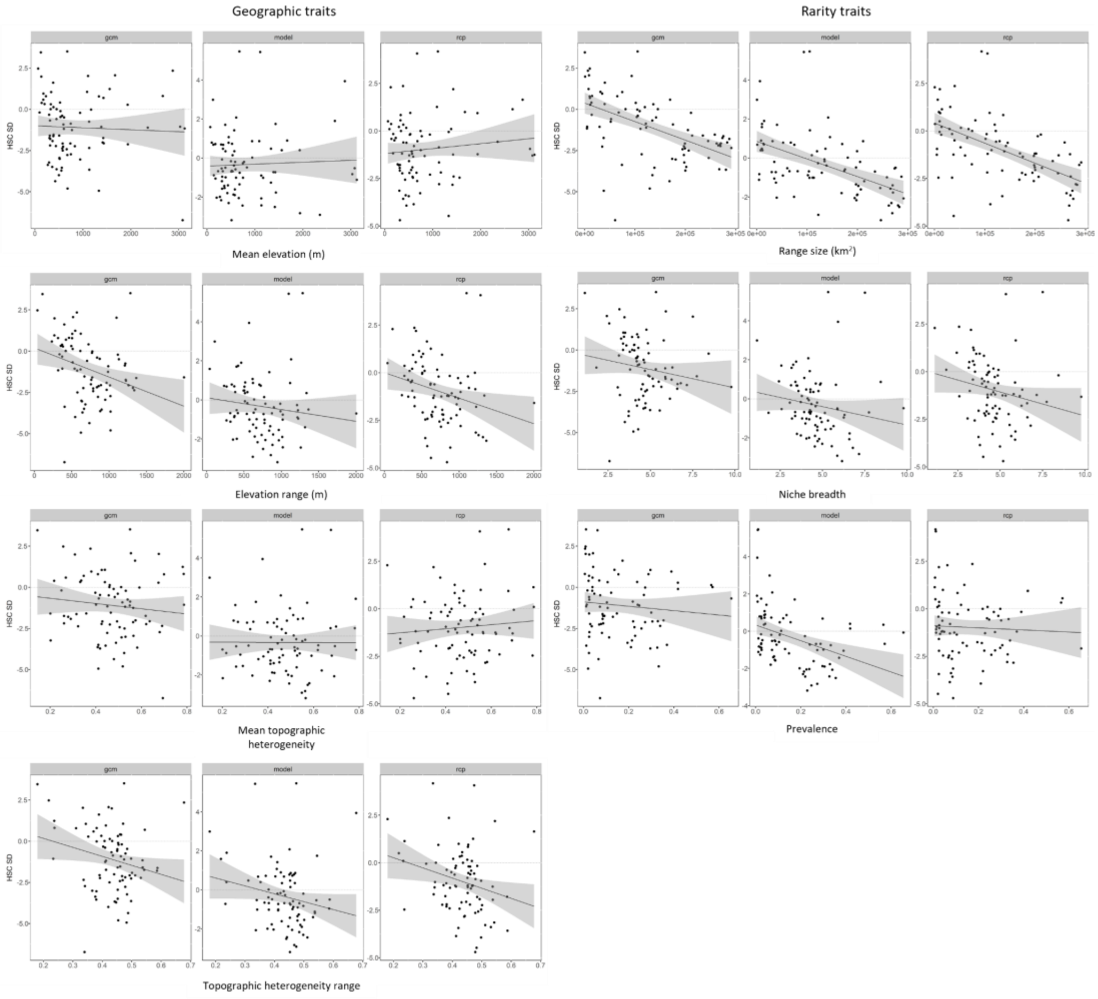

Figure S2.4. Scatterplots of species characteristics and uncertainty in future HSC (standard deviation in HSC) due to each factor (gcm = global circulation model, model = consensus method, and rcp = representative concentration pathway) under full dispersal scenarios. The standard deviation of HSC has been log transformed for easier visualization.

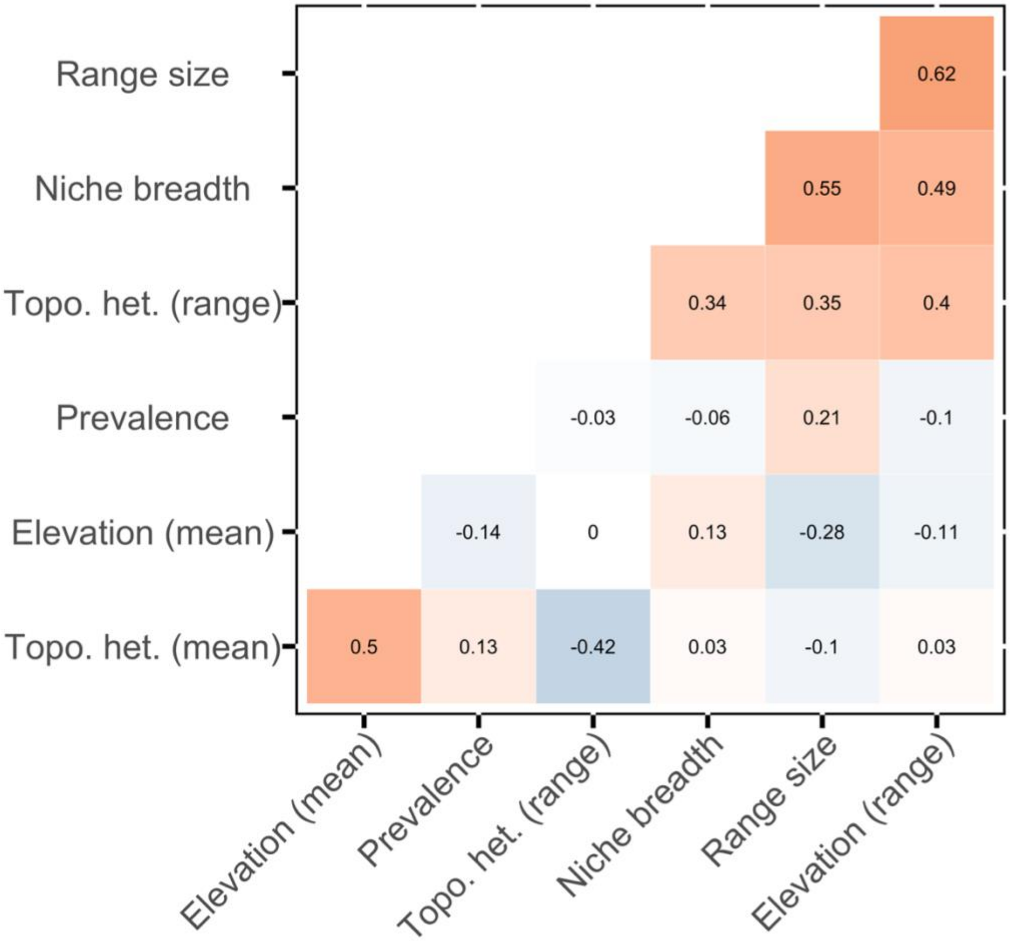

Figure S2.5. Correlation matrix of species-level rarity and geographic traits used as predictors of habitat suitability change (HSC) uncertainty.

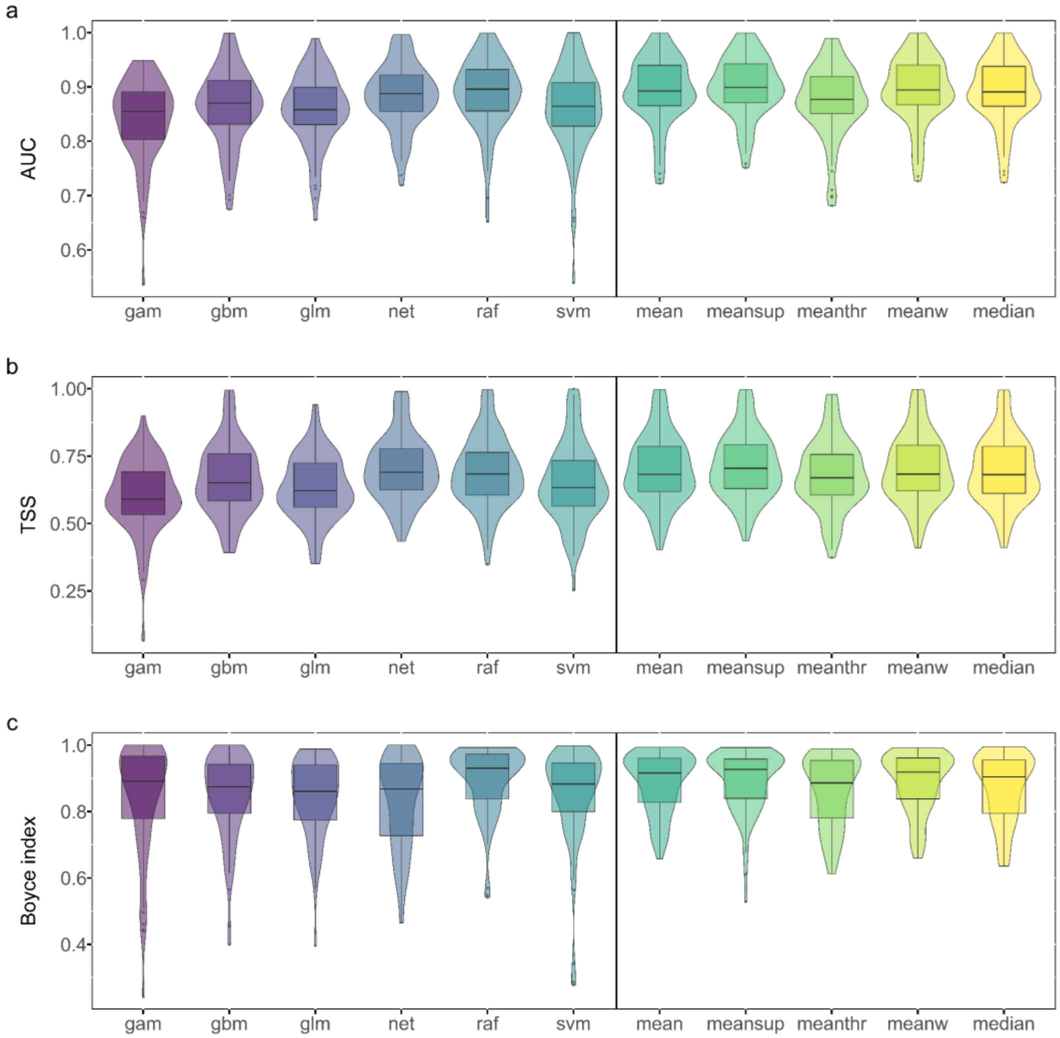

Figure S2.6. Boxplot showing model performance according to area under the receiver operating characteristic (AUC) (a), true skill statistic (TSS) (b), and Boyce index (c). Of the original models, 14 models were excluded from the ensembles because of low performance (AUC <.7) and included five GAMs, two GBMs, two GLMs, two RAFs, and three SVMs.

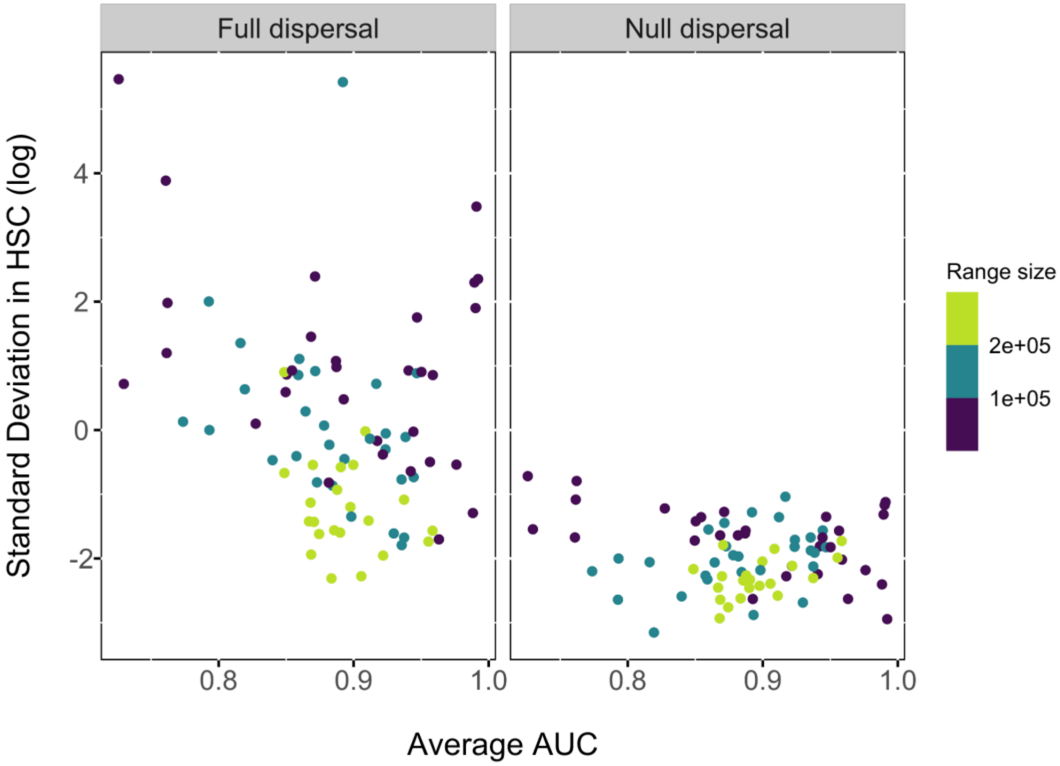

Figure S2.7. Relationship between standard deviation in species-level HSC (log) (uncertainty) and average SDM consensus AUC (model performance) under full and null dispersal scenarios. Point color represents species' range size (dark purple = small range, blue/teal = intermediate range, and bright green = large range).

Additional methodological details for the Basin Characterization Model bioclimatic variables

To project future habitat suitability for the study plant species, we used bioclimatic variables and scenarios produced by the Basin Characterization Model (BCM), which is used to simulate hydrologic responses to climatic factors at a relatively fine spatial scale (270 m) (Flint et al., 2013). The BCM uses historical PRISM precipitation and temperature data (Daly et al., 2008) at 800-m that have been spatially downscaled to 270 m using Gradient-Inverse-Distance Squared (GIDS) downscaling (Nalder and Weins 1998). Variables produced by the BCM characterized for a 30-year time period (1980-2010) and used as predictor variables in the SDMs produced in this manuscript include actual evapotranspiration, climatic water deficit, minimum temperature of the coldest month, winter precipitation, and summer precipitation. For the current research, we used projections of bioclimatic variables produced by the BCM for two global climate models (CNRM-CM5 and HadGEM2-ES) and two emissions scenarios (RCP 4.5 and 8.5). These scenarios capture the wide variability predicted by various climate models across California.

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Supporting Information Chapter 3

Table S3.1 Species list, vegetation communities, and biogeographic characteristics

Species	Vegetation association	Range extent (km^2)	Average distance to coast (km)	Average elevation (m)
Abies magnifica	montane forest	122318.9	217.54	2354.65
Adenostoma sparsifolium	chaparral	31451.73	56.27	1092.43
Aesculus californica	valley and foothill woodland	206753.5	87.76	590.57
Arctostaphylos glandulosa	chaparral	205228.7	28.81	778.01
Arctostaphylos glauca	chaparral	180863.1	68.16	949.64
Arctostaphylos pringlei	chaparral	8770.04	82.82	1671.28
Arctostaphylos rudis	chaparral	553.67	12.85	126.16
Artemisia californica	coastal sage scrub	134537.7	21.96	317.18
Artemisia rothrockii	montane forest	6505.64	243.74	2894.22
Asclepias eriocarpa	valley grassland	199277.2	64.3	573.74
Asclepias fascicularis	valley and foothill woodland	245339.9	64.38	360.13
Calocedrus decurrens	montane forest	283224.9	150.08	1425.12
Calochortus albus	valley and foothill woodland	168563.2	74.74	432.11
Ceanothus greggii	chaparral	38159.46	74.99	1336.27
Ceanothus megacarpus	chaparral	40241.27	9.44	387.37
Ceanothus oliganthus	chaparral	111065.9	28.89	605.37

Ceanothus tomentosus	chaparral	52500.31	47.68	455.92
Ceanothus verrucosus	chaparral	1162.55	9.02	134.95
Chamaebatia foliolosa	montane forest	37821.62	201.01	1437.8
Croton setiger	valley and foothill woodland	265630.4	70.76	321.14
Delphinium hesperium	valley and foothill woodland	138614.2	55.97	566.06
Dichelostemma capitatum	valley and foothill woodland	267530.1	77.36	455.06
Encelia californica	coastal sage scrub	64991.31	11.92	231.76
Ericameria ericoides	coastal strand	101614.9	12.48	141.85
Erigeron petrophilus	valley and foothill woodland	93556.21	92.75	1157.5
Eriodictyon trichocalyx	chaparral	51919.15	72.61	1143.47
Eriogonum fasciculatum	coastal sage scrub	199215.7	41.4	586.34
Frangula californica	coastal sage scrub	269936	47.74	440.28
Galium angustifolium	chaparral	121748.6	39.59	762.58
Hazardia squarrosa	coastal sage scrub	78261.07	16.16	377.04
Hesperoyucca whipplei	chaparral	129329.8	45.11	684.53
Heteromeles arbutifolia	chaparral	258529.1	41.57	397.13
Juglans californica	valley and foothill woodland	136537.6	27.54	337.56
Juncus balticus	wetland-riparian	234796.5	99.06	509.5

Keckiella antirrhinoides	chaparral	34934.52	47.54	585.34
Lepechinia calycina	chaparral	134704.5	74.63	501.89
Lonicera subspicata	chaparral	141916.2	39.86	638.3
Lupinus arboreus	coastal strand	67698.95	7.16	95.28
Malosma laurina	chaparral	81277.53	15.85	333.13
Opuntia littoralis	coastal sage scrub	39764.52	17.83	203.57
Picea breweriana	montane forest	7928.68	61.25	1559.86
Pickeringia montana	chaparral	173935.8	29.39	517.05
Pinus attenuata	closed-cone pine forest	197300	64.91	835.16
Pinus balfouriana	montane forest	60678.9	240.77	3082.51
Pinus coulteri	montane forest	104766.8	55.09	1173.71
Pinus jeffreyi	montane forest	269241.4	172.04	1940.78
Pinus lambertiana	montane forest	270603.7	132.94	1442.67
Pinus muricata	closed-cone pine forest	169793.7	5.9	174.14
Pinus quadrifolia	pinon-juniper woodland	10581.66	80.85	1429.05
Pinus sabiniana	valley and foothill woodland	194532.1	116.98	676.48
Pinus torreyana	chaparral	10342.83	1.72	68.45
Platanus racemosa	wetland-riparian	213534.6	62.54	313.04
Poa stebbinsii	alpine	4705.31	243.54	3121.36
Prunus ilicifolia	chaparral	175447.1	33.1	606
Pseudotsuga macrocarpa	chaparral	29817.65	41.59	1394.72
Ptilagrostis kingii	montane forest	5054.78	247.02	3044.04

Quercus agrifolia	valley and foothill woodland	201902.9	22.91	364.54
Quercus chrysolepis	montane forest	291381.5	109.3	1148.79
Quercus douglasii	valley and foothill woodland	200064.3	105.17	556.01
Quercus engelmannii	valley and foothill woodland	13564.01	37.09	538.85
Quercus kelloggii	montane forest	280708.2	145.78	1140.84
Quercus lobata	valley and foothill woodland	198017.4	80.59	290.49
Quercus sadleriana	montane forest	10247.76	43.63	1338.96
Quercus wislizeni	valley and foothill woodland	262294.5	127.64	760.26
Rhododendron occidentale	wetland-riparian	211292.8	88.06	976.54
Rhus ovata	chaparral	109490.4	29.06	542.58
Ribes lasianthum	montane forest	14764.72	237.12	2645.99
Ribes malvaceum	chaparral	145461.5	21.51	457
Rosa californica	chaparral	273878.6	61.87	305.89
Salix lasiolepis	wetland-riparian	287459.8	72.49	321.35
Salvia apiana	coastal sage scrub	103617.2	36.85	538.77
Salvia columbariae	chaparral	197193	58.04	684.17
Salvia leucophylla	coastal sage scrub	74798.36	17.36	340.72
Salvia mellifera	coastal sage scrub	119704.1	24.62	391.2
Sambucus nigra	valley and foothill woodland	275663.9	69.07	394.81
Scutellaria californica	valley and foothill woodland	105211.7	124.73	675.97
Sequoia sempervirens	redwood forest	74176.84	11.77	274.43

Sequoiadendron giganteum	montane forest	11397.83	219.38	1935.21
Torreya californica	montane forest	113349	107.7	764.78
Trichostema lanatum	coastal sage scrub	105632.1	23.46	572.2
Umbellularia californica	redwood forest	246600.3	60.17	519.41
Xylococcus bicolor	chaparral	14176.86	22.61	300.91