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Title

Back to the future: using historical climate variation to project near-term shifts in habitat suitable for coast redwood

Running head

Near term shifts in redwood habitat

Authors

M. Fernández[1, 2, 3,]*, H. H. Hamilton[4], and L. M. Kueppers [1, 5]

Institutional affiliations

[1] Sierra Nevada Research Institute, University of California, 5200 North Lake Road, Merced, CA, 95343, USA

[2] Department of Integrative Biology, University of California, Berkeley, CA, 94720, USA

[3] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig - Germany

[4] NatureServe, 4600 N. Fairfax Drive, 7th Floor, Arlington, VA, 22203, USA

[5] Earth Sciences Division, Lawrence Berkeley National Laboratory, 1 Cyclotron Rd., Berkeley, CA, 94720, USA

Corresponding author *

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Miguel Fernández
German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig - Germany Telephone number: +49 341 9733188
Email: miguel.fernandez@idiv.de

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Abstract

Studies that model the effect of climate change on terrestrial ecosystems often use climate projections from downscaled Global Climate Models (GCMs). These simulations are generally too coarse to capture patterns of fine scale climate variation, such as the sharp coastal energy and moisture gradients associated with wind-driven upwelling of cold water. Coastal upwelling may limit future increases in coastal temperatures, compromising GCMs' ability to provide realistic scenarios of future climate in these coastal ecosystems. Taking advantage of naturally occurring variability in the high-resolution historic climatic record, we developed multiple fine-scale scenarios of California climate that maintain coherent relationships between regional climate and coastal upwelling. We compared these scenarios against coarse resolution GCM projections at a regional scale to evaluate their temporal equivalency. We used these historically based scenarios to estimate potential suitable habitat for coast redwood (*Sequoia sempervirens* D. Don) under "normal" combinations of temperature and precipitation, and under anomalous combinations representative of potential future climates. We found that a scenario of warmer temperature with historically normal precipitation is equivalent to climate projected by GCMs for California by 2020-2030, and that under these conditions, climatically suitable habitat for coast redwood significantly contracts at the southern end of its current range. Our results suggest that historical climate data provide a high-resolution alternative to downscaled GCM outputs for near-term ecological forecasts. This method may be particularly useful in other regions where local climate is strongly influenced by ocean-atmosphere dynamics that are not represented by coarse-scale GCMs.

Introduction

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Although global climate models (GCMs) project changes in climatic patterns at coarse spatial scales (i.e., global and regional), the local effects of climate change are not yet well quantified (Knutti & Sedlácek, 2013), limiting our ability to incorporate them into ecological forecasts (Osmond *et al.*, 2004). Further, local climatic trends do not always follow global trends (Helmuth *et al.*, 2002; Cordero *et al.*, 2011). One example of the inability of GCMs to project complex local climate patterns occurs in California, where a cool coastal climate transitions sharply to a substantially warmer interior. While weather station data in California show a coherent statewide positive trend in minimum surface air temperature (LaDochy *et al.*, 2007), maximum temperature trends vary spatially, with cooling in coastal areas and warming in inland areas (Lebassi *et al.*, 2009).

The mechanism proposed to explain the asymmetric change in surface air temperatures involves differential heating between the ocean and continents, which has been hypothesized to result in stronger and more persistent wind-driven coastal upwelling along the coast of California in the future (Bakun, 1990; Iles *et al*., 2012; Sydeman *et al.*, 2014). Regional climate models (RCMs) indicate that increases in wind-driven coastal upwelling may limit future increases in coastal California temperatures by reducing insolation due to upwelling-induced fog and raising humidity in coastal terrestrial ecosystems (Snyder *et al.*, 2003; O'Brien *et al.*, 2012). Although long-term observations support this prediction (Seo *et al.*, 2012), it has not yet been consistently corroborated by GCM simulations (Wang *et al.*, 2010), due to simplifying assumptions and low resolution in coupled ocean-atmosphere models (Bakun *et al.*, 2010).

The limited capacity of global simulations to resolve local climates has profound implications for projecting climate change impacts (Wilby *et al.*, 2004), including shifts in species distributions (Kremen *et al.*, 2008). Range shift forecasts are most often explored using species distribution models (SDMs), which integrate geographic and climatic data associated with species occurrences (Peterson & Vieglais, 2001), yielding a spatially explicit hypothesis of current climatically suitable habitat. SDMs are also applied to estimate where future climatic conditions will be suitable for a given species, under the assumption that the species-climate relationship remains stable (Franklin, 2009; Peterson 2011). This is typically achieved by projecting fine scale hypotheses of current suitable habitat onto downscaled future global simulations (e.g.,

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Daszak *et al.*, 2012). Downscaling brings the coarse spatial resolution of the global and regional scale climate models (>50 km^2) to the resolution of current climate datasets (<1 km^2) to avoid combining data with different resolutions (Wilby *et al.*, 2004).

Multiple approaches are used to downscale GCM simulations, ranging from basic techniques such as the simple change factor approach (e.g., Tabor & Williams, 2010), to more complex ones, such as deterministic statistical approaches (e.g., Hidalgo *et al.*, 2008; Abatzoglou & Brown, 2012). Currently, downscaled datasets that have the potential to capture both the effect of wind-driven coastal upwelling on surface air temperature and humidity patterns and, at the same time, present a spatial resolution fine enough to capture the environmental heterogeneity characteristic of coastal California are limited (e.g., Abatzoglou, 2013). Yet it is this combination of properties that would enable conservation and adaptation strategies at a local scale (Flint & Flint, 2012). Researchers have used dynamically downscaled (e.g., Kueppers *et al.*, 2005) and statistically downscaled temperature and precipitation (e.g., Loarie *et al.*, 2008; Klausmeyer & Shaw, 2009) with SDMs to project potential effects of climate change on California biodiversity. However, the downscaled climate surfaces used for these studies do not include historic changes in wind-driven coastal upwelling, nor projected future upwelling regimes and coastal surface air temperature and humidity patterns, limiting confidence in range shift estimates for coastally restricted species.

The aim of this study was to develop and test an alternative approach to forecasting climatically suitable habitat for a coastal species (i.e., coast redwood) that incorporates both regional and local manifestations of climate change. For this we assume that anomalous years in the historic climatic record already capture fine-scale climate dynamics and can be used as a proxy for short- to midterm future climate scenarios (Hansen *et al*,. 2012). With this approach, we not only maintain coherent relationships between regional climate and local effects of coastal upwelling, but we also preserve covariance among climatic variables in our projections (Dobrowski, 2011) as it is manifest in more extreme years.

Coast redwood (*Sequoia sempervirens*), with a distribution limited to a 50 km belt along the coast of California (Noss, 2000), is particularly well suited for our analysis. Coast redwoods

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have a well-known distribution, facilitating model evaluation. They also are the foundation species of redwood forest and share a distribution and key traits with many co-occurring species that might explain the forest species composition (Violle *et al.*, 2014). In particular coast redwoods are known to be poor regulators of water use (Burgess & Dawson, 2004; Simonin *et al.*, 2009) and eighty percent of the dominant plant species that occur in redwood forest can acquire water through their leaves (Limm *et al.*, 2009), including coast redwoods. These shared physiological traits and restricted distributions are evidence that many species in redwood forest are strongly influenced by local ocean-atmosphere interactions (Johnstone & Dawson, 2014). Finally, coast redwoods and the species that occur in redwoods forests are of conservation concern. An approach that can more reliably project zones of contraction, of expansion, and of persistence under a range of climate scenarios could be a useful tool for conservation science and practitioners.

In this paper we address three questions: (1) Do coarse spatial resolution global climate model projections of future mean regional climate have observed fine spatial resolution analogs in the historic climatic record? (2) How sensitive are SDMs to fine-scale climate analogs from the historic climatic record, using redwoods as an example, and how do these projections relate to GCM scenarios of the future? (3) Do distribution models based on fine-scale historic climatic analogs allow us to identify highly stable and unstable zones that could support climate adaptation planning for redwood forests? To address these questions, we used naturally occurring variability in the historic climatic record to develop multiple atemporal scenarios of California climate. To provide a temporal context, we compared these scenarios to GCM projections from the archive of the Coupled Model Intercomparison Project Phase 5 (CMIP5). We developed estimates of climatically suitable habitat for redwoods under historically "normal" temperature and precipitation patterns, and for multiple historically based climate scenarios. We combined the resulting habitat scenarios, based on historic climate, into an ensemble that identifies coherent sub-regions robust to near-term climate change, as well as sub-regions projected to experience almost certain departures from 20th century climate. This approach suggests refugial portions of the current redwood forest distribution that are forecast to remain climatically suitable in the near-term, which can inform redwood management, restoration, monitoring and conservation initiatives.

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Materials and methods

Climate change scenarios for California

We used the tails of the distribution of observed temperature and precipitation (Hansen *et al.*, 2012) as analogs of future scenarios of California coastal climate at a spatial scale finer than those produced by GCMs. This approach, similar to the climatic-analogs method developed by Lorenz (1969), takes advantage of spatially gridded climatic time series data, circumvents the need to run RCMs at finer resolutions in a regional sub-domain (e.g., dynamical downscaling; Ahmed *et al.*, 2013) and avoids the need to establish complex relationships between current observations and large scale variables (i.e., statistical downscaling; Wilby & Dawson, 2013). However, instead of searching for equivalent gridded surfaces for the climatic variables at the resolution of the GCMs (Zorita & Von Storch, 1999), we selected climatically anomalous years at the statewide scale from the historic record.

To identify historic anomalous years, we used data from a network of 195 Cooperative Observer Network climate stations for the State of California, hosted at the California Climate Data Archive (CCDA). These long-term measurements, which are also part of the Global Historical Climatology Network (GHCN), are the most comprehensive and harmonized climate record available for temperature and precipitation in California (Abatzoglou *et al.*, 2009); and they are often used for validating GCMs. We examined four annual climatic variables, but here we focus on mean annual temperature and annual total precipitation; results for maximum and minimum temperature yielded similar results (*Appendix A*, Figs. S1-S4). We computed annual departures from statewide means for the full historic record (1895 to 2010; Fig. 1), and assigned departures for each year (x) to one of three possible categories: (1) $x > \mu + s$; (2) $x < \mu - s$; and (3) $\mu - s < x < \mu + s$, where s is one standard deviation from the mean (μ). We classified years according to both annual mean temperature and total annual precipitation (Fig. 2), with "normal" years within one standard deviation of the mean for both variables, and other years grouped to represent eight scenarios of less probable (i.e., anomalous) combinations of temperature and precipitation.

Comparison of historically based scenarios and GCM projections

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To provide a temporal context to these historically based climate scenarios, we directly compared them to outputs from the Coupled Model Intercomparison Project Phase 5 (CMIP5) GCMs run under Representative Concentration Pathway (RCP) 4.5 (Thomson *et al.*, 2011) using the averaged standardized Euclidean distance (Diffenbaugh & Giorgi, 2012) to evaluate similarity. The RCP4.5 greenhouse gas concentration trajectory provides a conservative estimate of future global temperature compared with alternative trajectories (Peters *et al.*, 2012), although trajectories of temperature change do not diverge substantially among RCPs until after the 2040's (Knutti & Sedlacek, 2013). From 19 GCMs in the CMIP5 archive, we obtained mean monthly temperature and total monthly precipitation for California for the period 1895 to 2099 at their native spatial resolution. We calculated mean annual temperature, annual total precipitation and anomalies for each year from 2020 to 2099, using the same baseline period deployed in the selection of historically anomalous years (i.e., 1895 to 2010) for each GCM. We then calculated mean anomalies (i.e., averaged over 19 GCMs) for four future 10-year periods: 2020 to 2029, 2030 to 2039, 2040 to 2049 and 2050 to 2059 and compared the means to the climate anomalies obtained from the observed historical period to identify historical years analogous to future climates as projected by the GCMs (Fig. 3).

Species distribution modeling

Climate variables

We obtained historically based climate scenarios in gridded form at 800m resolution from the monthly time-series (1895 to 2010) Parameter-elevation Relationships on Independent Slopes Model dataset (PRISM; Daly *et al.*, 2000), and grouped years based on the analysis of CCDA weather stations. Over the spatial domain of the conterminous U.S., PRISM incorporates the effects of temperature inversions, cold-air pooling and coastal effects, providing one of the finest spatial resolutions of climate patterns relative to other similar products (but see Flint & Flint, 2012). PRISM values are estimated using a local regression where surrounding weather stations used to populate the regression are weighted by their physiographic similarity to the grid cell being modeled. PRISM constitutes a well-vetted and critical climate data resource for a diversity of studies in fields including ecology, biogeography, conservation and natural resource management (e.g., Fitzgerald & Gordon *et al.*, 2012; Franklin *et al.*, 2013; Torregrosa *et al.*, 2013).

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To generate the SDMs we used monthly maximum and minimum temperature, total precipitation and vapor pressure from the PRISM gridded time series dataset (*Appendix A*, Figs. S1-S4). We also included a derived variable to capture monthly climatic water deficit (*WD*; Stephenson, 1990; Stephenson, 1998). We calculated the *WD* (*Appendix A*, Fig. S9), as the difference between precipitation and potential evapotranspiration (Paltineanu *et al.*, 2009; Ellis *et al.*, 2010) for each month of every year from 1895 to 2010 following Hamon (1963; see *Appendix B* for details on *WD* derivation), which is a refinement of the Thornthwaite method (Thornthwaite & Matter, 1955). This method has been proven to be robust under a wide range of conditions (Vörösmarty *et al.*, 1998) and, when compared to alternative approaches, it provided the most accurate approximation when the inputs are limited to temperature and precipitation (Lu *et al.*, 2005). While calculation of *WD* as the difference between potential evapotranspiration and actual evapotranspiration would have been desirable (e.g., Flint *et al.*, 2013; Chardon *et al.*, 2014; McIntyre *et al.*, 2015), lack of complete soil depth and texture datasets across the full study domain limited a reliable estimate of actual evapotranspiration. Further, SDMs that included a more accurate approximation of *WD* (*Appendix A*, Fig. S13A) differed only by 15.51% (SD=5.46) with no discernible spatial pattern (*Appendix A*, Fig. S13B).

Species occurrence data

To build the species distribution models, we compiled all coast redwood occurrence data from museum specimens including, (1) georeferenced specimens from the Consortium of California Herbaria, a centralized repository for 16 regional herbaria (accessed June 2012), and (2) the Global Biodiversity Information Facility, a global consortium of biodiversity data-holding institutions (accessed June 2012). For evaluating the models, we obtained independent occurrence data from redwood specimens held at the California Academy of Sciences, which we retrospectively georeferenced following the protocols of Chapman & Wieczorek, (2006). We define a species occurrence as a unique locality expressed as latitude and longitude with positional uncertainty represented by a maximum error estimate of less than 800 m, supported by a vouchered specimen collected between 1895 and 2010.

Species distribution models

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We generated species distribution models using MaxEnt v3.3.3k (Phillips *et al.*, 2006), a method particularly effective under conditions of presence-only observation data (Elith & Leathwick, 2009). MaxEnt uses the principle of maximum entropy to estimate a set of rules correlating environmental variables and species occurrences to approximate the potential bioclimatic habitat of the target species (Phillips & Dudik, 2008). The MaxEnt algorithm is related to Bayesian theory and considers redundant information without overfitting; eliminating the need to apply a variable reduction technique before running the models (but see Parolo *et al.*, 2008). We calibrated the models using an approach that addresses spatial autocorrelation by using a spatially structured partitioning procedure adapted from Fernandez *et al.*, (2013). This process randomly resamples species' observations into different subsets where 80% of the localities are used for training and 20% are used for testing the model. We created 100 subsets of the species observations that were used to produce 100 MaxEnt models representing "normal" conditions, defined here as the average values of variables across 1895-2010 that fall within the central quadrant (Fig. 2; *Appendix A*, Figs. S3 and S4). We used the default values in the MaxEnt algorithms for the maximum number of iterations and convergence threshold (i.e., 500, 10^{-5}).

We averaged the 100 bootstrapped niche model results into a final model that provided a continuous index of relative suitability under "normal" conditions. We converted the probabilistic output into a presence/absence map based on a widely accepted thresholding approach using the value of the points on the receiver operating characteristic curve where the sum of sensitivity and specificity is maximized (Loarie *et al.*, 2008).

We evaluated the final model produced for "normal" conditions using three complementary approaches. First, we took advantage of our independent evaluation data by measuring how often the model successfully predicts the withheld independent localities (i.e., prediction success) from georeferenced specimens (Zweig & Campbell, 1993). Since prediction success is a function of the threshold for assigning presence, we also evaluated the models using the area under the receiver operating characteristic curve (AUC). AUC is a threshold-independent metric that summarizes a model's overall performance over every possible threshold (Lobo *et al.*, 2008). Although this approach has been criticized for being sensitive to the total geographic extent over which models are produced (VanDerWal *et al.*, 2009), this should not affect our results because

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we kept extent constant. While these metrics are statistically defensible, they are still hampered by the lack of true absence data (Lobo *et al.*, 2010). Since the current distribution of redwoods is relatively well known and mapped, we compared the models for "normal" conditions to the known distribution of redwoods using the True Skill Statistic (TSS) criterion (Allouche *et al.*, 2006). We used the Classification and Assessment with Landsat of Visible Ecological Groupings (CALVEG), a fine scale dataset that was primarily derived from remote sensing and produced by the U.S. Department of Agriculture, as the known current redwood distribution (*Appendix A*, Fig. S12).

We projected the bootstrap simulations that contributed to the final model under the "normal" conditions into each of the anomalous years, and aggregated projections by each of the eight scenarios. Since each scenario has a different number of years, we combined the probabilistic outputs from MaxEnt for each group of years before selecting the threshold following Marmion *et al.*, (2009). We converted the results into presence/absence maps (*Appendix A*, Fig. S10) based on the same threshold rule applied under "normal" conditions.

Analysis of redwood distributions

To quantify changes in the distribution of suitable habitat, we compared the spatial patterns, as well as metrics of distribution area, distance and direction change. First, we evaluated the differences in spatial patterns by subtracting gridded model outputs under each scenario from the distribution under "normal" conditions and mapped the differences. Second, we calculated the change in total area between the current distribution and the distributions under each scenario. To calculate areas, we converted all gridded model outputs into polygons and projected them into an equal area projection (Albers Equal Area Conic); we measured areas using the Spatial Statistics toolset in ArcGIS v.10.1. Third, we calculated the shifts in distance and direction under each scenario using centroids. Using the Geographic Distributions toolset in ArcGIS v.10.1, we calculated centroids by projecting the data into Azimuthal Equidistant projection and measuring the centers of mass of the distributions.

Results

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Observed analogs for GCM projections in the historic climatic record

We used natural variability in the historic record to develop multiple atemporal scenarios of California climate; to provide a temporal context we directly compared these scenarios to GCM projections from the CMIP5 archive. The historically based climate scenario that most closely matches GCM projections for 21st century California climate change has higher temperature but relatively unchanged precipitation (Fig. 3). Moreover, most of the years used to develop the historically based warmer (normal precipitation) scenario are within one standard deviation of mean projections for the 2020s; GCM temperature projections continue to increase but with little change in statewide annual precipitation in subsequent decades (Fig. 3). Although mean GCM projections are located within our warmer (normal precipitation) scenario, one standard deviation across models for annual total precipitation extends into the drier-warmer and wetter-warmer scenarios as well, highlighting continued uncertainty regarding future precipitation in California.

SDM sensitivity to fine-scale changes in climate using redwood as an example

We developed estimates of climatically suitable habitat for redwood under historical "normal" temperature and precipitation, and for multiple historical anomalous climate scenarios (*Appendix A*, Fig. S10). The potential distribution for coast redwood was synthesized across the years falling in each group of anomalous climate conditions to produce ensemble estimates for each historically based scenario (Fig. 4; *Appendix A*, Fig. S11). The redwood distribution projected into the warm (normal precipitation) scenario, which most closely resembles the CMIP5 projections for California, showed a range contraction in the south, with a 50% reduction of the climatically suitable area under "normal" conditions (8,809 km^2; Fig. 5), and with no suitable bioclimate remaining south of San Francisco Bay. This contraction is balanced by an expansion in the north, with a 34% gain in area (5,895 km^2; Fig. 5). The stable area for this scenario is restricted to the coastal region in the central part of the current redwood distribution (Fig. 4B).

The combination of drier and warmer conditions (Fig. 4A) produced the most extreme degree of contraction in the projected bioclimatic habitat for redwood, with a 79% reduction in area from "normal" conditions (Fig. 5). The drier scenario (normal temperatures; Fig. 4D) presented the next highest degree of contraction with a loss in suitable habitat of 63% (Fig. 5). Conversely, the highest degree of expansion was found in the wetter and cooler scenario (Fig. 4H) with a gain of

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44% of the climatically suitable area under "normal conditions" (Fig. 5). The second largest degree of expansion was hypothesized by the wetter and warmer scenario (Fig. 4C) with a projected increase in area equal to 37% (Fig. 5).

When the centroids of each projected distribution were compared to the centroid of the historical mean redwood distribution, the scenarios with the largest relative shifts were the warmer scenario (normal precipitation; Fig. 4B) and the drier and warmer scenario (Fig. 4A), with shifts of 201 and 192 km, respectively (Fig.6). The wetter and cooler scenario (Fig. 4H) showed the lowest degree of geographic shift of 10 km (Fig. 6). All of the scenarios, except the wetter and cooler scenario, presented an average north-northwest (337^{o} +/-5^{o}) direction of displacement (Fig. 6).

Identification of stable and unstable regions for redwoods

We combined our historically-based climatically suitable habitat scenarios into an ensemble to identify sub-regions that were (1) consistently robust to modest climate change (refugia), and (2) highly sensitive to modest climate change (unstable). When we overlaid the stable areas from all historically based scenarios, the most stable region is located in the north-central portion of the redwood range (Fig. 7) restricted to an area of 3,010 km^2. When we restricted the ensemble to include only the realistic, warmer scenarios, the stable area expanded somewhat to 3,642 km^2. When we overlaid the contraction areas from all historically based scenarios, we found that the most climatically unstable regions are located in the southern and parts of the central range of coast redwoods, particularly along the eastern edge of its distribution (Fig. 7).

Discussion

In this study, we developed an approach that uses historical climate variability in the context of GCM projections to project near-term consequences of climate change in coastal ecosystems sensitive to fine-scale ocean-atmosphere dynamics. Among the eight high-resolution scenarios we developed for California coastal climate, three (Fig. 4A, 4B and 4C) reflect warming but uncertain precipitation change (Pierce *et al.*, 2013). Consistent with Hansen *et al.*, (2012), the warmer (normal precipitation) scenario is equivalent to mean climate changes projected for

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California for the 2020s-2030s by CMIP5 GCMs using RCP4.5 scenarios (Fig. 3), suggesting this historically based "equivalent" can be an alternative to downscaled GCM projections that incorporates the effect of wind-driven costal upwelling. Such an equivalent is well suited for projecting future shifts in climatically suitable habitat for redwoods because it captures fine scale climate variation, such as the sharp coastal energy/moisture gradients associated with the upwelling zone in California. It is also useful because it circumvents problems associated with downscaling variables separately, and maintains temporal consistency and regional climate coherence, which are needed for hydrological and ecological studies (Flint & Flint, 2012). However, while this approach may produce more biophysically accurate estimates of bioclimate shifts, it is also restricted to the next two decades for California due to the rapid rate of climate change and to the limited availability of anomalously warm years in the last century. Efforts to develop climate records further back in time, for example, using climate proxies such as tree rings or lake sediment cores, could facilitate development of additional scenarios. Higher frequency historic climatic records (i.e., daily data) could also be used to construct alternative scenarios.

Resource managers seeking greater spatial precision in their future projections confront a challenge (McPherson *et al.*, 2006; Kremen *et al.*, 2008): the spatial resolution of global climate simulations is still insufficient to identify how global stressors are modified by small-scale heterogeneity and manifest locally (Kirincich *et al.*, 2005). Our approach offers a method for ecological forecasting that addresses the issue of how climate variability manifests at local scales. Our historically based ensembles, analogous to GCM projections, suggest near-term (2020's - 2030's) bioclimatic shifts northward with contractions in coast redwood suitable habitat at the southern and parts of the central portion of their current range — a spatially-explicit hypothesis relevant to climate change adaptation planning (Flint & Flint, 2012). In addition to the GCM-referenced scenarios, the historical record contained sufficient variability to produce five additional boundary free scenarios (Tebaldi & Knutti, 2007) and their corresponding projected SDMs. These spatially-explicit divergent hypotheses also reveal substantial changes in the distribution of redwood bioclimate, providing hypotheses about redwood sensitivity to conditions not projected by global climate models (e.g., cooler temperatures) that could be tested with paleoecological data. Unique to long-lived trees, an

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independent bioclimatic dataset exists in the form of tree rings, which provide measures of physiological response to environmental change. Analyses of the dendrochronological record can confirm or counter hypothesized sensitivity of redwoods to natural climatic variability. Rapidly expanding citizen science observations offer another possibility for obtaining time-series data that connect biodiversity, climate, and environment to test these hypotheses.

Increasingly, dynamic, synthetic conservation planning frameworks require improved understanding of the spatio-temporal relationships between biodiversity and climate. The ecological forecasts presented here suggest regions of near-future climate stability and climate stress across the range of coast redwood. The identification of coherent sub-regions: (1) robust to modest climate change (refugia), and (2) highly sensitive to modest climate change (instability) can inform the spatial prioritization of areas with higher degrees of natural resistance to climate change, that act as natural climate refugia (Fig. 7). While we built these forecasts using coast redwood as the target species, we expect the projections also to be valuable for shorter-lived species with similar bioclimatic constraints (Limm *et al.*, 2009). Their long life-span suggests redwood trees can tolerate a significant amount of climate variability whereas shorter-lived species may respond quickly to near-term climate change. Experimental heating is increasingly used to understand biodiversity response to climate warming (Aronson & McNulty, 2009). Such experiments, in combination with other climate manipulations (e.g., soil water reductions), could be deployed in areas projected to be stable and those expected to be unstable to test whether young redwoods are indeed more sensitive to climate change in unstable sites. Further, such experiments could also help test whether the redwood bioclimatic envelope is a good proxy for bioclimatic envelopes of co-occurring species. Areas outside of the current coast redwood range but that are predicted as climatically suitable and stable under our projected scenarios of climate change could be investigated as sites for assisted migration and forest restoration efforts (Lunt *et al.*, 2013).

Although there is evidence that coastal upwelling might limit future increases in costal California temperatures (Snyder *et al.*, 2003; O'Brien *et al.*, 2012), there are also measurements that show a slight decline in fog during the driest months in the same area (Johnstone *et al.*, 2010). Given the strong reliance of redwoods and other co-occurring species on fog, future research should

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explore the relationship between fog and regional climate over the 20th century to understand whether the regionally warm years we selected are low or high fog years and whether fog can be used more explicitly to develop future climate scenarios.

In summary, historical climate variability offers an untapped resource for developing robust climate scenarios in regions with fine-scale, dynamic responses to global climate change. The tails of observed climate distributions can be an alternative to GCM projections, at least for near term forecasting. While we expect this approach to be particularly valuable in western continental margins where changes in wind-driven upwelling affect coastal climate and for short-lived organisms, we recognize that long-lived organisms such as redwoods will likely have lagged biogeographic responses to climate change. However, demographic, ecophysiological and ecohydrological changes may manifest more quickly, and these spatially explicit scenarios provide guidance on where to expect change first.

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Figure legends

Figure 1. Mean annual temperature (top) and annual precipitation (bottom) departures from the 1895 to 2010 mean (solid line) for California based on the CCDA dataset (Abatzoglou *et al.*, 2009). Dashed lines represent +/- one standard deviation for each variable.

Figure 2. Assignment of individual years to climate scenarios. White or gray circles indicate mean annual temperature and total precipitation departures for individual years between 1895 and 2010 relative to the 1895-2010 means (solid lines). Dashed lines represent +/- one standard deviation from the means. Years falling into the eight peripheral boxes (gray circles) define climatic scenarios for our analysis.

Figure 3. Multi-model mean annual temperature and precipitation anomalies for California projected for three decades in the 21st century (colored circles) compared to historical annual temperature and precipitation anomalies (circles as in Figure 2).

Figure 4. Composite maps of the projected expansion, contraction and stability for the eight scenarios we developed.

Figure 5. Ensemble average changes in area of climatically suitable habitat for coast redwood among scenarios identified in Figure 2.

Figure 6. The shift in the center of mass of modeled climatically suitable habitat for coast redwood for each of the eight scenarios relative to center of mass under “normal” conditions.

Figure 7. Ensemble scenarios for climatically stable sub-regions. Left, map of stability. Right, map of contraction.

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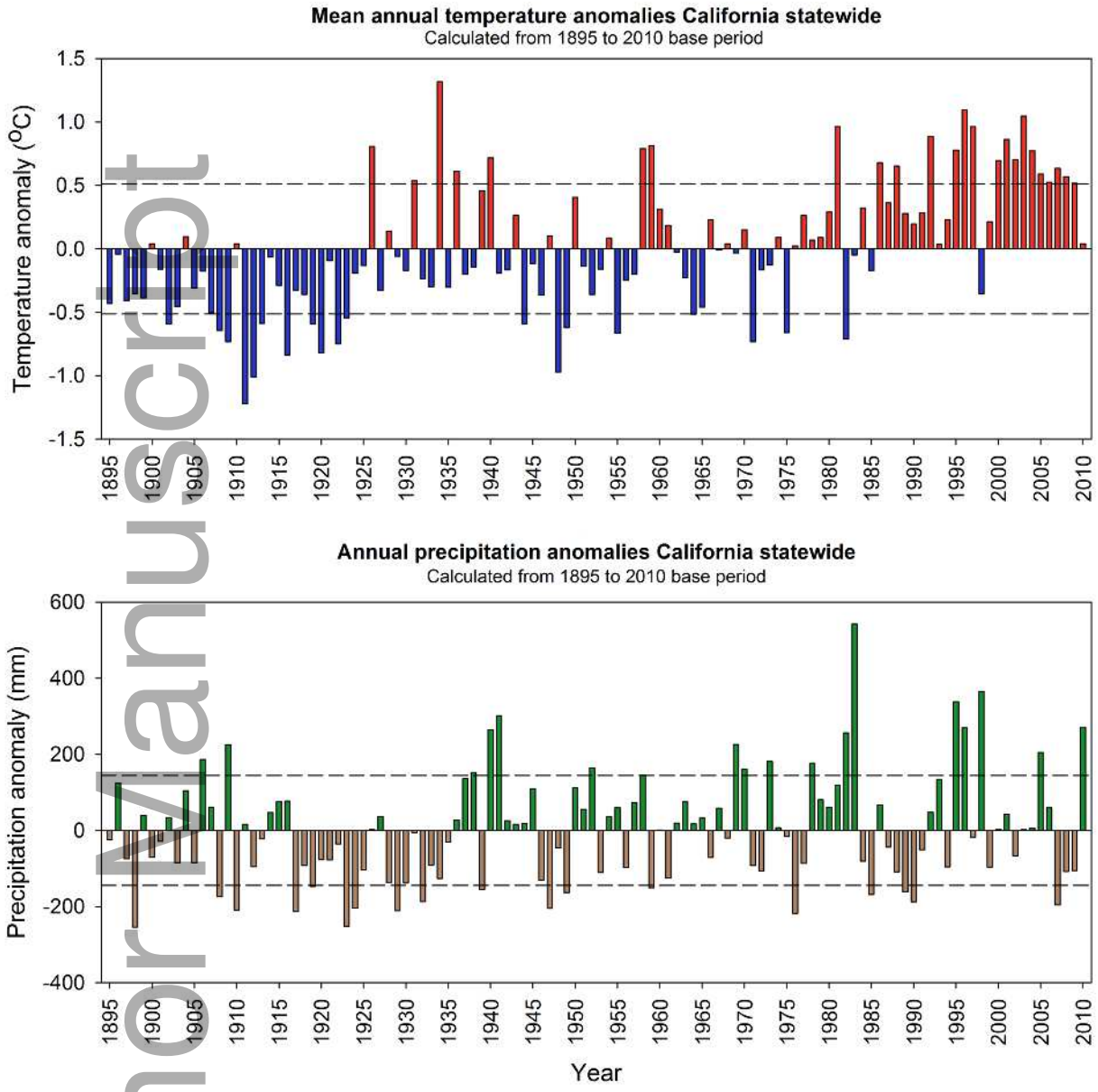

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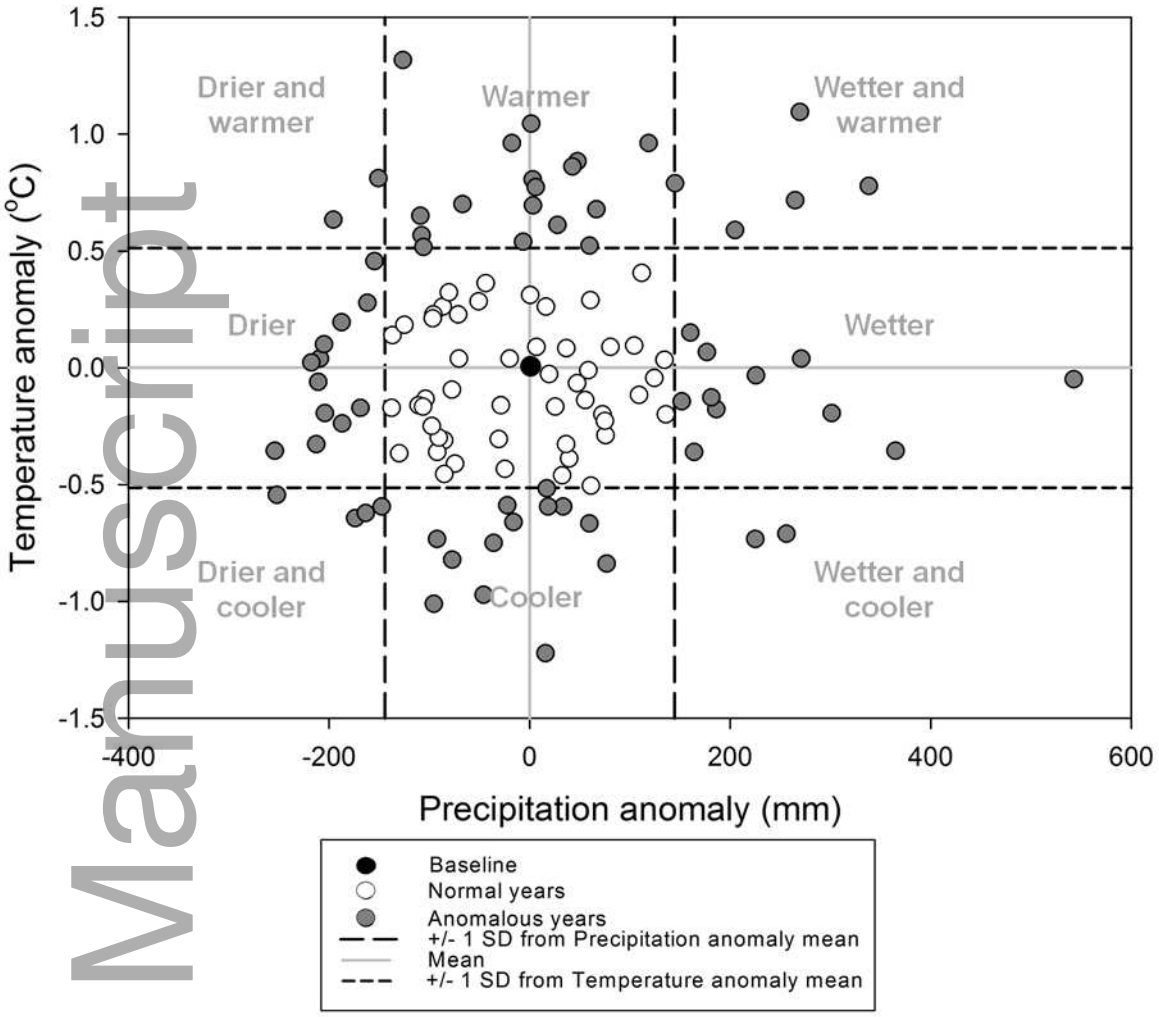

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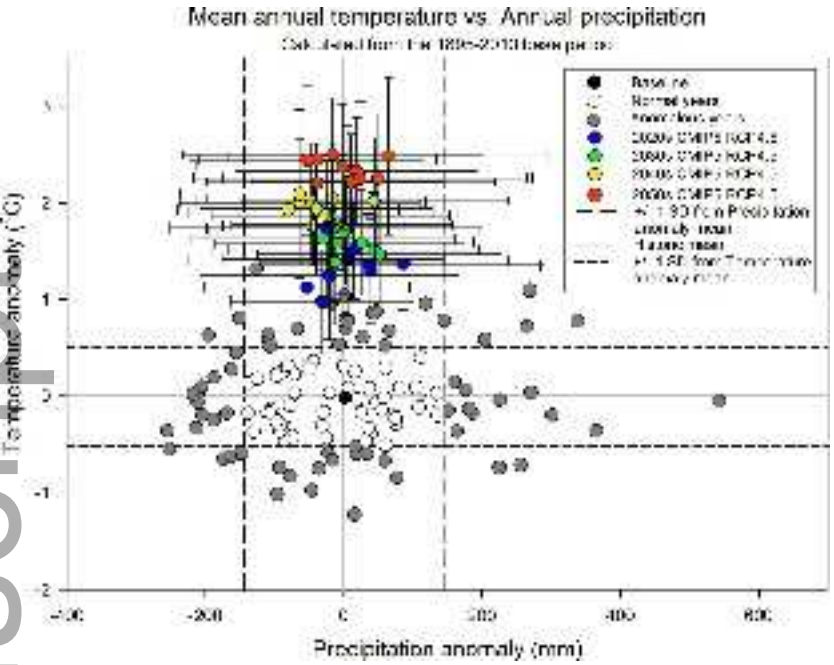

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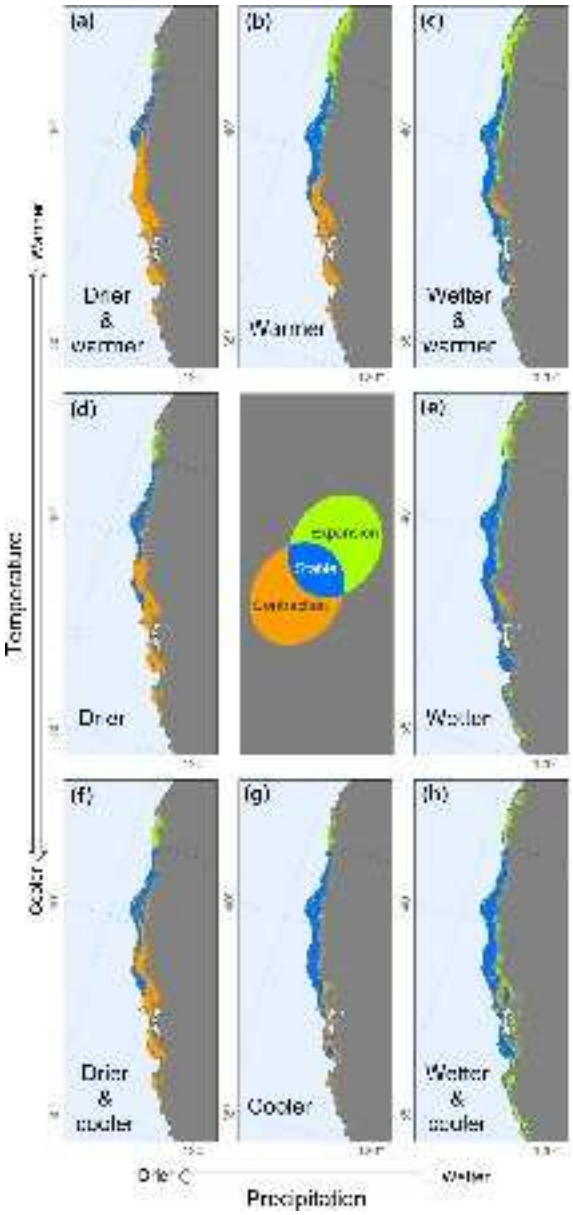

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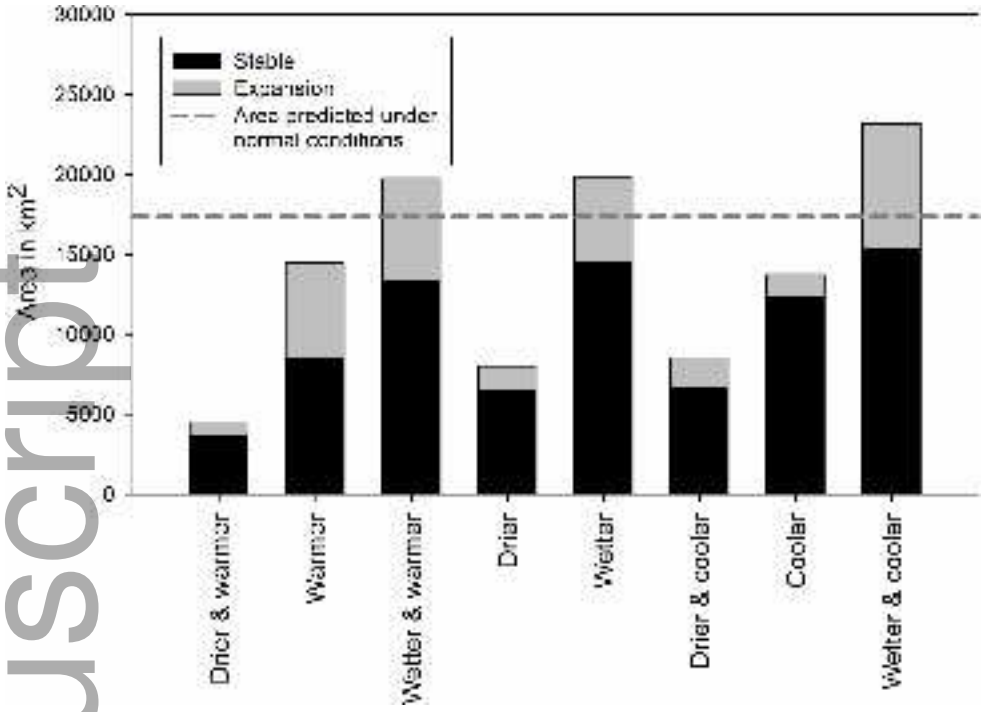

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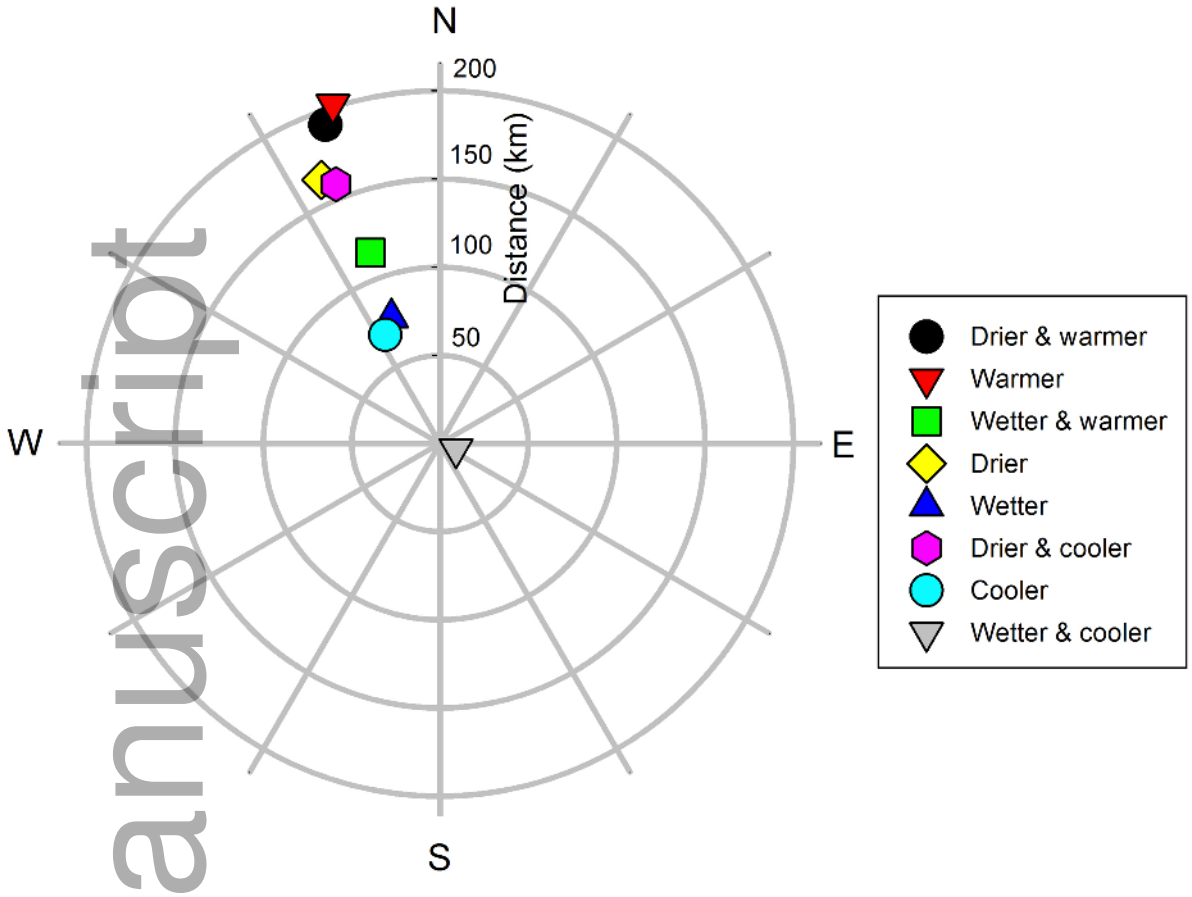

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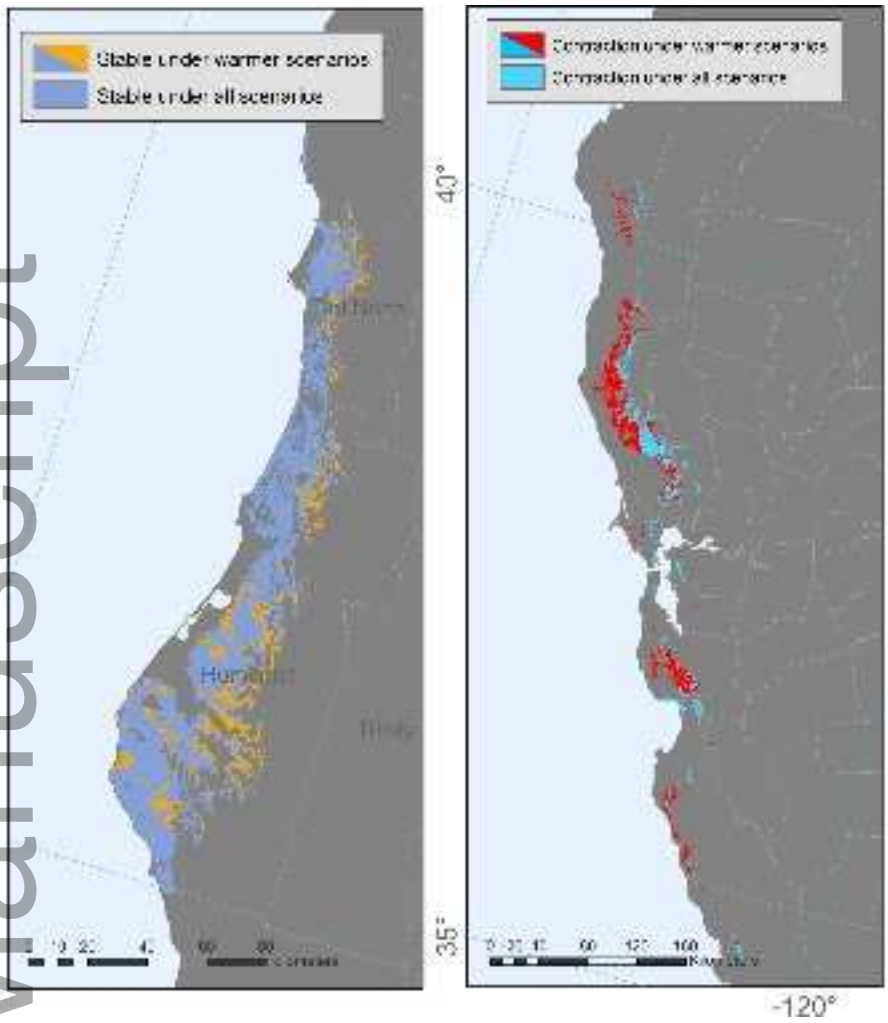

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