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# Landscape-scale indicators of biodiversity's vulnerability to climate change

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**Abstract.** Climate change will increase the vulnerability of species across the globe to population loss and extinction. In order to develop conservation strategies to facilitate adaptation to this change, managers must understand the vulnerability of the habitats and species they are trying to manage. For most biodiversity managers, conducting vulnerability assessments for all of the species they manage would be prohibitively costly, time consuming, and potentially misleading since some data required does not yet exist. We present a rapid and cost-effective method to estimate the vulnerability of biodiversity to climate change impacts across broad areas using landscape-scale indicators. While this method does not replace species-specific vulnerability assessments, it allows biodiversity managers to focus analysis on the species likely to be most vulnerable and identify the categories of conservation strategies for implementation to reduce biodiversity's vulnerability to climate change. We applied this method to California, USA to map the portions of the state where biodiversity managers should focus on minimizing current threats to biodiversity (9%), reducing constraints to adaptation (28%), reducing exposure to climatic changes (24%), and implementing all three (9%). In 18% of the state, estimated vulnerability is low so continuing current strategies and monitoring for changes is likely sufficient, while in 12% of the state, vulnerability is so high that biodiversity managers may have to reassess current conservation goals. In combination with species-specific vulnerability assessments or alone, mapping vulnerability based on landscape-scale indicators will allow managers to take an essential step toward implementing conservation strategies to help imperiled species adapt to climate change.

**Key words:** adaptation strategies; adaptive constraints; California; climate change; climate stress; conservation; landscape exposure; landscape vulnerability.

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## Introduction

Climate change threatens global biodiversity, ecosystem function, and human systems (IPCC 2007). Already, observed impacts of climate change on species range from changes in phenology to local extirpations (Walther et al. 2002, Root et al. 2005, Parmesan 2006, Pounds et al. 2006). Even if greenhouse gas emissions are held at year 2000 levels today, the history of past greenhouse gas emissions will contribute to unavoidable warming in the future (IPCC 2007). Instead, recent emissions rates continue to rise above the highest greenhouse gas emissions scenario utilized by the Intergovernmental Panel on Climate Change (IPCC) for global assessments (Raupach et al. 2007). To prevent catastrophic loss of biodiversity, conservationists must not only find ways to curtail greenhouse gas emissions, but also help species adapt to a changing and more variable future climate through targeted implementation of conservation strategies such as protecting land, restoring habitat, encouraging compatible lands uses, and reducing fragmentation (Fischlin et al. 2007, Baron et al. 2008, Heller and Zavaleta 2009, Mawdsley et al. 2009).

To date, many researchers have focused on estimating the magnitude of the potential impacts of climate change on biodiversity (Bakkenes et al. 2002, Thomas et al. 2004, Fitzpatrick et al. 2008, Loarie et al. 2008), but few studies provide guidance for biodiversity managers to identify specific conservation actions to prevent climate change-associated biodiversity loss (Heller and Zavaleta 2009). Biodiversity managers need more detailed vulnerability assessments that combine information on the species exposure and sensitivity to climate change with the adaptive capacity (IPCC 2007, Williams et al. 2008). These assessments could help managers identify which species are likely to be the *most* vulnerable to climate change and *why* they are likely to be vulnerable, thus directly informing a strategic, prioritized conservation action plan (Glick and Stein 2010).

A variety of species-specific vulnerability assessments have been completed or are in progress (Glick and Stein 2010), but the high cost, time required, and uncertainties in the data often make them feasible for only a few biodiversity managers with large research budgets and technical capacity. One of the biggest limitations is the lack of published data on species' climatic preferences (Williams et al. 2008). Some researchers solve this by using species distribution models to generate species climate preference estimates (Glick and Stein 2010), but running these models require specialized technical expertise. In addition, there have been significant concerns raised about the methodology and performance of these models (Pearson and Dawson 2003, Hampe 2004, Beale et al. 2008). While detailed vulnerability assessments for select well-studied species are possible for some managers (Hannah et al. 2007, Hannah et al. 2008), the costs and data requirements make a comprehensive study of all of the species in an area impractical (Williams et al. 2008, Ackerly et al. 2010). Even managers with larger research budgets and sufficient technical capacity will need new tools to complement their species vulnerability assessments to generate strategies for lesser-known species.

In this paper, we present a new method to assess the vulnerability of biodiversity to climate change based on landscape-scale indicators, including historical and projected climate patterns, landscape features, and land use. We use the general concepts from a species-specific vulnerability assessment framework, and apply them to spatially-explicit and readily available data that will likely influence the vulnerability of many species. We posit that most species will be more vulnerable to climate change in areas with large changes in climate relative to historical patterns (high *climate stress*); in areas that are farther from the moderating influence of cool ocean currents, have minimal topographic diversity, lack perennial water sources and have poor connectivity along climatic gradients (high *landscape exposure*); and in areas with high levels of habitat loss and fragmentation (high *adaptive constraints*). Biodiversity managers with a limited research budget and limited capacity can combine funds with other managers to replicate this method across a large geographic scale more quickly and for less cost than a series of species-specific vulnerability assessments. For managers with a larger research budget and more capacity, this method can be a useful tool to screen for areas where species are likely to be the most vulnerable and in the greatest need of species-specific assessments and strategies. In addition, the components of this method can provide spatially-explicit information about the categories of strategies that may be needed to reduce biodiversity's vulnerability to climate change. In this paper, we detail a case study of this method for the state of California, USA, but the method can be replicated anywhere sufficient data exist.

## Vulnerability Frameworks

Several authors have developed frameworks for vulnerability assessments for general systems (Füssel and Klein 2006) and for species (Williams et al. 2008, Glick and Stein 2010). Based on these

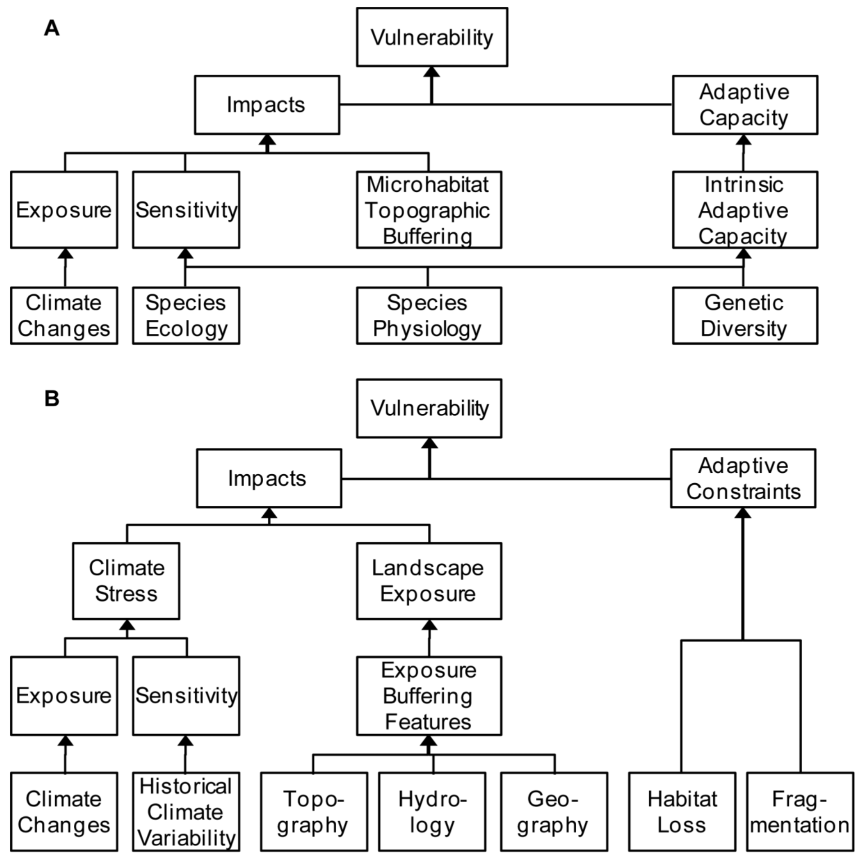


Fig. 1. Vulnerability assessment frameworks based on (A) species attributes and (B) landscape-scale indicators.

frameworks, we have produced a generalized representation of the vulnerability assessment framework for species (Fig. 1A). Species *vulnerability* is a function of climate change related impacts and the adaptive capacity of the species. *Impacts* are a combination of exposure and sensitivity to climate change, but can be mitigated by micro-habitats and topographic buffering. *Exposure* is driven by regional changes in climate, while *sensitivity* is a function of the ecology, physiology, and genetic diversity of a species, which are in turn influenced by external factors like resource management and habitat changes. Vulnerability can be mitigated by the *adaptive capacity* of the species, which is also a function of the ecology, physiology, and genetic diversity. Williams et al. (2008) provide a rich discussion of these concepts.

We used the essential elements of the species-specific vulnerability assessment framework to develop a new framework based on landscape-scale indicators (Fig. 1B). The primary components of the modified vulnerability assessment framework are climate stress, landscape exposure, and adaptive constraints. *Climate stress* combines an estimate of exposure from the projected regional climate changes and an estimate of the sensitivity of biodiversity in an area from a coping range derived from historical climate variability. *Landscape exposure* indicates how exposed biodiversity may be in a particular location based on a series of exposure-buffering features including metrics derived from topographic, hydrologic, and geographic datasets. *Adaptive constraints* measures how fragmentation and land use can reduce the adaptive capacity of the species. We chose to focus on the adaptive constraints, the inverse of adaptive capacity, since, like impacts, it positively influences vulnerability. Climate stress, landscape exposure, and adaptive constraints are combined to estimate biodiversity's vulnerability to climate change based on landscape-scale indicators.

## Methods

### *Study area and analysis method*

Unless otherwise noted, all spatial data analysis was performed using ArcGIS version 9.3 software by Environmental Systems Research Institute, Redlands, California, USA. The study area consists of all land area of the state of California, USA. For analytical purposes, we divided the state into ~640,000 800-meter by 800-meter grid cells. The size of the grid cells was based on the PRISM (Parameter-elevation Relationships on Independent Slopes Model) dataset, which is the finest scale historical dataset with annual data available for this area (Daly et al. 2008). This method can be recreated with coarser scale data, but in order to improve the granularity of the results, the finest scale data available should be used.

### *Future climate data*

We calculated exposure to climate change by downscaling projections of future climate from an ensemble of General Circulation Models (GCMs) run to support the IPCC's Fourth Assessment Report archived in the World Climate Research Programme's (WCRP) Coupled Model Intercomparison Project (CMIP) phase 3 multi-model dataset. We compiled monthly and annual climate data from the daily climate projections from the 11 GCMs that provided projections for maximum and minimum temperatures for one 20-year time period (2046–2065 or mid 21st century) (see Table 1). We focused on the A2 emissions scenario (Nakicenovic and Swart 2000) because of the three emissions scenarios analyzed by most modeling groups, the A2 scenario is the closest to the observed trends since 2000 (Raupach et al. 2007). For the GCMs that provided multiple realizations, we averaged the results. We then downscaled the future climate projections to the 800-meter grid cell size using the change factor approach as described by Klausmeyer and Shaw (2009).

### *Historical climate data*

We calculated the range of historical variability in climate variables with the historical climatology developed using the PRISM interpolation method (Daly et al. 2008). These data provide estimates of minimum temperature, maximum temperature, and precipitation for each 800-meter grid cell in the conterminous United States for each month from 1895 to 2007. For each climate variable, we generated 20-year moving averages to better reflect long term trends in

Table 1. General circulation models (GCMs) downscaled and analyzed. Table 8.1 in Chapter 8 of the Intergovernmental Panel on Climate Change's (IPCC) Working Group 1 Fourth Assessment Report contains more information about these models and the references for the ocean, atmosphere and coupling components.

| IPCC GCM Name | Country | Center Name |
|---|---|---|
| BCCR-BCM2.0 | Norway | Bjerknes Centre for Climate Research |
| CGCM3.1(T47) | Canada | Canadian Centre for Climate Modeling and Analysis |
| CNRM-CM3 | France | Météo-France/Centre National de Recherches Météorologiques |
| CSIRO-Mk3.0 | Australia | Commonwealth Scientific and Industrial Research Organisation (CSIRO) Atmospheric Research |
| CSIRO-Mk3.5 | Australia | Commonwealth Scientific and Industrial Research Organisation (CSIRO) Atmospheric Research |
| ECHAM5/MPI-OM | Germany | Max Planck Institute for Meteorology |
| ECHO-G | Germany and Korea | Meteorological Institute of the University of Bonn (MIUB), Meteorological Research Institute of KMA (METRI), and Model and Data group (M&D) |
| GFDL-CM2.0 | USA | U.S. Dept. of Commerce/National Oceanic and Atmospheric Administration (NOAA)/Geophysical Fluid Dynamics Laboratory (GFDL) |
| GFDL-CM2.1 | USA | U.S. Dept. of Commerce/National Oceanic and Atmospheric Administration (NOAA)/Geophysical Fluid Dynamics Laboratory (GFDL) |
| GISS-ER | USA | National Aeronautics and Space Administration (NASA) / Goddard Institute for Space Studies (GISS) |
| IPSL-CM4 | France | Institut Pierre Simon Laplace |
| MIROC3.2(medres) | Japan | Center for Climate System Research (The University of Tokyo), National Institute for Environmental Studies, and Frontier Research Center for Global Change (JAMSTEC) |
| MRI-CGCM2.3.2 | Japan | Meteorological Research Institute |

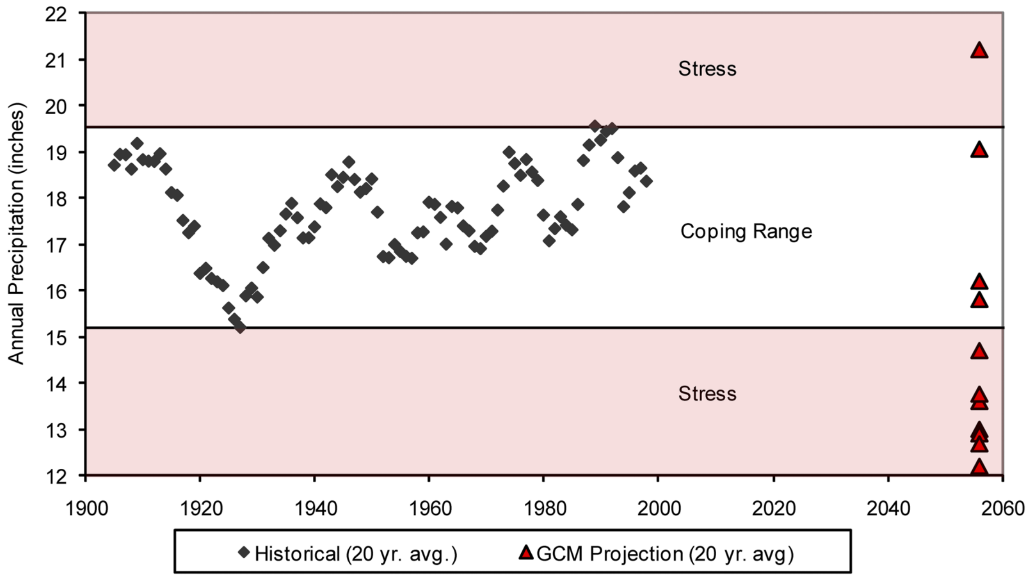


Fig. 2. Combination of the sensitivity derived from the coping range as defined by the historical climate variability with exposure derived from projections from multiple General Circulation Models (GCMs) for a hypothetical location. The percent of the GCMs that fall outside of the coping range is used to calculate the climate stress index for an area.

climate, rather than inter-annual extreme values, and to better compare with our 20-year average projections of future climate. The range of historical variability was calculated by determining the maximum and minimum values from the set of 20-year average historical climate data for each grid cell in the study area.

### Climate stress

*Climate stress* is a combination of the projected exposure and the estimated sensitivity of an area. We estimate exposure by calculating the changes in relevant climate variables projected by an ensemble of GCMs. Estimating species sensitivity from landscape-scale indicators is not as straightforward, and requires some simplifying assumptions. We assume that a suite of species at any given place functions best within some range of climate, or a coping range. This concept of a climatic coping range is defined as the capacity of systems to accommodate variations in climatic conditions (Hewitt and Burton 1971, Smith et al. 2001, Carter et al. 2007). Many communities of species have a climatically defined coping range, and changes in climate that exceeds the boundaries of this coping range will stress the community. In order to estimate the extent of the coping range, we look at the range of climates for a place based on local historical climatic variability. If future climatic conditions are projected to exceed the local historical range of variability, the stress to the community is considered greater than if the projected future conditions are within the range of variability (Fig. 2). To estimate the historical range of variability, we used the historical PRISM data. The benefit of this method is that it can be implemented with climatic data that is increasingly available across large geographic areas, and it does not require specific knowledge of the idiosyncratic climatic limits of individual species and communities.

We performed a sensitivity test of our results to the time period that defines the coping range. Researchers recently reconstructed long-term aridity changes in the western United States using tree ring records (Cook et al. 2004). While the spatial resolution of their data is too coarse for this analysis, we were able to test the range of variability in the 20-year running average of the Palmer Drought Severity Index (PDSI) for the 12 grid points that fall in California for two time periods: 1300–2003 and 1895–2003 (Cook and Krusic 2004). While the reconstruction was completed back to the year 800, the lack of tree ring data makes these earlier records much more uncertain (Stahle et al. 2007). Using these data, there were 1–3 drier periods in the southern part of the state in the longer time period, but these all occurred prior to 1600. In the northeastern most grid point, there were two wetter periods in the longer time period, but for the rest of the state, the variability in 20th century is equal to or greater that of the last 700 years. Thus, the range of climates observed in the 20th century is a reasonable approximation of the longer term variability in the climate to which the local communities are adapted in California.

We focused on three climate variables that influence the distribution of plants in California and elsewhere: annual precipitation, January minimum temperatures, and July maximum temperatures (Pavlik et al. 1991, Dallman 1998, Inouye 2000, Williams et al. 2007, Dobrowski 2011). Similar studies have focused on other climate variables such as climatic water balance, cloud cover, and vapor pressure (Iwamura et al. 2010, Dobrowski 2011), but historical and/or multiple future projections of these data are not yet available at the fine spatial scale (800 meter) of this analysis. We considered several other temperature variables available in the downscaled GCM and PRISM datasets such as January maximum temperatures and average annual maximum temperature, but there was minimal spatial variation in climate stress calculated from these other variables in California (Fig. 3) indicating that their inclusion would not provide additional insight.

A stress metric is calculated separately for each climate variable as the count of the 11 GCMs analyzed that project future conditions outside the historical coping range. If all GCMs project future conditions that are within the range of historical variability for a climate variable, the stress metric would be 0 (low stress). Alternatively, if all GCMs project future conditions that are outside the range of historical variability, the stress metric would be 11 (high stress). In order to weight the impact of the stress metric for the two temperature variables the same as that of the one precipitation variable, we averaged the stress metrics for the two temperature variables and added the result to the stress metric for precipitation. We then normalized the combined metric of *climate stress* to range from 0 (low stress) to 100 (high stress), using Eq. 1 where $S_{tmin}$ is the stress metric for January minimum temperatures, $S_{tmax}$ is the stress metric for July maximum temperature, and $S_{prec}$ is the stress metric for precipitation.

$$\left(\frac{\left(\frac{S_{tmin}+S_{tmax}}{2}+S_{prec}\right)}{22}\right)\times 100. \qquad (1)$$

### *Landscape exposure*

*Landscape exposure* includes a combination of landscape features (topographic, hydrologic, and geographic) that generally reduce or enhance exposure to climate change for a wide range of species. These features can be categorized by the general timeframe for which they could reduce or enhance species' exposure:

- Days to weeks: Topographic diversity
- Months to years: Distance to the ocean, distance to stable water sources such as large lakes or springs
- Decades to centuries: River corridors, elevation gradients

While exposure to climate change could be mediated by a variety of things, including tree canopies and man-made stock ponds, we focus here on the more permanent landscape features that are not likely to change over the next 100 years. In addition, individual species may reduce exposure to climate change by utilizing certain landscape features, such as caves or tree hollows, but we focus on the features that could mediate exposure for a wide range of species. For each factor we generated a continuous grid representing raw values from lower exposure to higher exposure (e.g., range in elevation in meters, distance to stable water sources in kilometers). To combine these raw grids equally, we reclassified them to a 0–10 scale based on spatial deciles. In other words, we reclassified the raw values into ten bins so that each of the ten values cover roughly one tenth of the state. We then multiplied these grids by 10 and averaged them with equal weighting to get a composite landscape exposure index with values ranging from 0 (low exposure) to 100 (high exposure). The five factors are described below.

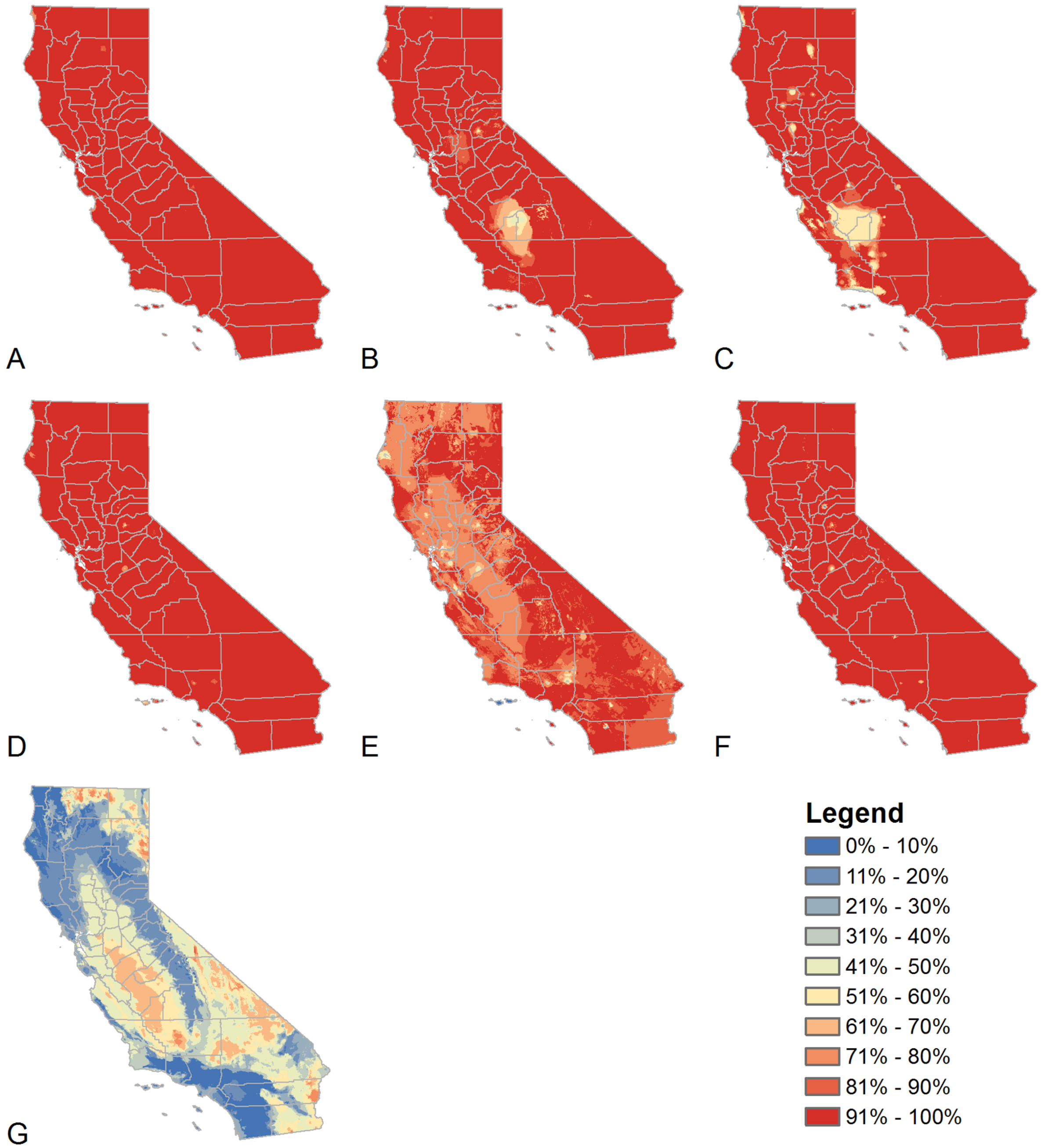


Fig. 3. Stress metrics for (A) annual maximum temperature, (B) January maximum temperature, (C) July maximum temperature, (D) annual minimum temperature, (E) January minimum temperature, (F) July minimum temperature, (G) annual precipitation. Percentages indicate the number of GCMs (n = 11) that project climates outside of this historical coping range by 2046–2065 under the a2 emission scenario.

*Topographic diversity*

South facing slopes receive more solar radiation during the day than their north facing counterparts, influencing surface temperature, air temperature, soil moisture and vegetation patterns (McCutchan and Fox 1986, Warren 2008, Scherrer and Korner 2009, Dobrowski 2011). Areas with a diversity of slopes and aspects will provide a diversity of micro-climates for species to reduce exposure to a changing climate. We calculated the incoming solar radiation using the ~30-meter National Elevation Dataset (U.S. Geological Survey 2008) and the Solar Tools in ArcGIS. We then calculated the range in solar radiation values in each 800-meter grid cell in the study area, giving the grid cells with the highest range a value of 0 (lower exposure) and the grid cells with the lowest range a value of 10 (higher exposure).

### *Distance to the ocean*

Large water bodies tend to heat and cool more slowly than the land, so as air flows from the water body over land it tends to moderate the proximate climate. This effect in especially pronounced in California due to the relatively cold coastal California Current (Daly et al. 2002). Summer fog also plays a role in reducing summer temperatures in California and increasing moisture availability, so inland areas tend to be more exposed to climatic variability and extremes. The distance to the ocean was calculated as described in Daly et al. using an advection model that calculates the optimal path length to the ocean incorporating the prevailing wind patterns and minimizing the number of mountains and the distance air must traverse as it flows from the ocean to the land (Daly et al. 2008). Grid cells on the coast were given a value of 0 (lower exposure) and grid cells with an optimal path length greater than 700 kilometers (the maximum path distance calculated by Daly et al.) to the ocean were given a value of 10 (higher exposure).

### *Distance to stable water sources*

Droughts may become more frequent and severe as the climate changes, so reliable sources of fresh water will become even more important than they are today. We assume that exposure to climate change will be greater the greater the distance to stable water sources. We identified all of the seeps and springs and large perennial water bodies (>100 hectares) as the stable water sources that are most likely to persist even in a drought. We calculated the straight-line distance to these water sources as mapped in the National Hydrology Dataset (U.S. Geological Survey 2009) using ArcGIS. Grid cells that contain a stable water source were given a value of 0 (lower exposure) and grid cells that are greater than 15 km were given a value of 10 (higher exposure).

### *Elevation gradients*

A wealth of studies has identified elevation gradients as important landscape features that can reduce exposure to climate change over a long time frame (Cowling and Pressey 2001, Noss 2001, Cowling et al. 2003, Rouget et al. 2003). Elevation has a direct effect on temperatures and often influences precipitation patterns (Daly et al. 2008). A lack of diversity of elevations across a landscape will often reduce the number of different climatic zones a species has access to, thus increasing exposure to climate change. We calculated the elevation range in a 10-kilometer moving window using the ~30-meter National Elevation Dataset (U.S. Geological Survey 2008). Grid cells with the highest range in elevations (greater than 1,600 meters) were given a value of 0 (lower exposure) and grid cells with the lowest range in elevations (less than 200 meters) were given a value of 10 (higher exposure).

### *Riparian corridors*

Forested riparian corridors can reduce exposure to climate change by providing local air and water temperature refugia and by increasing connectivity across environmental gradients (Naiman et al. 1993, Naiman and Décamps 1997, Hilty and Merenlender 2004, Caissie 2006, Seavy et al. 2009). In fact, current biodiversity patterns can in part be explained by the maximum elevation reached in a watershed. One study found that watersheds in Madagascar with river sources at relatively low elevations were zones of isolation during periods of climate change, and watersheds with river sources at high elevation were zones of retreat and dispersion for native species (Wilme et al. 2006). We mapped all the second order and higher streams from the National Hydrology Dataset (U.S. Geological Survey 2009) and then ranked them based on the maximum elevation reached by all contributing streams. For streams that do not reach the ocean (endorheic basins), we subtracted the minimum elevation in the basin from the maximum elevation to get the range of elevations linked by the stream. Grid cells that contain a second order stream that connects the ocean to the highest elevations in the state (greater than 2,500 meters) were given a value of 0 (lower exposure) and grid cells that do not contain a second order stream were given a value of 10 (higher exposure).

### *Adaptive constraints*

*Adaptive constraints* are derived from habitat loss and fragmentation. Habitat loss is based on the percentage of each 800-meter grid cell in the state that is mapped as cultivated crops or developed in the National Land Cover 2001 Dataset (Homer et al. 2004). The resulting metric ranges from 0 (no habitat loss) to 100 (total habitat loss).

Researchers have proposed a variety of landscape scale fragmentation metrics for use in conservation planning, but most fail to correlate with ecological processes (Tischendorf 2001, Girvetz et al. 2007). Effective mesh size is an ecologically relevant metric that is based on the probability that any two locations in the landscape are connected (Jaeger 2000). This metric was recently calculated for a variety of planning units and fragmentation geographies for California, and a GIS-based tool was created so the same metric can be generated for other geographies (Girvetz et al. 2008). We selected the finest scale planning units (planning watersheds) and the fragmentation geography that includes highways, major roads, minor roads, urban and agricultural areas. We converted the watershed based data on effective mesh size to our 800-meter grid cells. The effective mesh size measure was highly skewed so we did a log base 10 transformation to generate a more normal distribution of values, and then rescaled the result to range from 0 (low fragmentation) to 100 (high fragmentation). The effective mesh size metric was not calculated for the Channel Islands, so we only considered habitat loss to calculate adaptive constraints for this area. For the rest of the state, we averaged the habitat loss and fragmentation metrics to generate the adaptive constraints measure ranging from 0 (low adaptive constraints) to 100 (high adaptive constraints).

### *Landscape vulnerability*

To map our estimate of the vulnerability of biodiversity to climate change, we added climate stress, landscape exposure and adaptive constraints to generate one measure ranging from 0 (low vulnerability) to 300 (high vulnerability). We also wanted to capture the various interacting components of vulnerability, so developed a method to combine the three primary components categorically. This involved masking out areas with little remaining natural habitat (areas that are $>50\%$ cultivated crops or developed) then selecting the median value from the resulting grid. We then split each grid into "low" and "high" categories based on the median value and combined the three to generate eight unique categories of climate stress, landscape exposure, and adaptive constraints. The division between low and high is meant for a relative comparison within the state, and not an absolute comparison. For example, the projected climate stress is high for most of the state based on historical variability. We then summarized how much of each of the nine largest terrestrial ecoregions in the state are covered by the eight vulnerability categories.

For each of the eight vulnerability categories, we defined a summary strategy to facilitate the adaptation of biodiversity to climate change. These summary strategies are based on the degree and nature of the vulnerability. For areas with low climate stress, low landscape exposure, and low adaptive constraints, the vulnerability to climate change is low so the summary strategy is to continue "current strategies". In other words, climate change is likely to pose minimal additional threats to the area, so current conservation strategies are likely to be sufficient. However, all land managers should monitor lands more closely for any unforeseen impacts of climate change. If exposure and constraints are low, but projected climate stress is high, the summary strategy is to "minimize existing threats" to biodiversity to try to offset the impacts of high climate stress. These strategies will depend on the local species, but they have likely already been identified in existing conservation plans (e.g., forest thinning, invasive species removal). The pace and scale of implementation of these strategies will likely need to be increased in order to offset the projected stresses from climate change.

In areas with high landscape exposure, the summary strategy is to "reduce exposure". One way to reduce exposure is to reduce greenhouse gas emissions to slow the pace and magnitude of climate change. Land managers can inventory their emissions and strive to sequester more greenhouse gasses then they produce through practices like afforestation, minimizing deforestation, and optimizing grazing (McCarl and Schneider 2001, Liebig et al. 2005). These strategies will only be effective if replicated at a global scale, so land managers will need to consider local actions to reduce exposure. They are unlikely to be able to change some of the more permanent landscape features identified above like distance to coast and topographic diversity, but they may be able to reduce exposure through other management strategies. These could include the restoration of riparian forest to increase shade and enhance connectivity, or managing dams to increase the duration and extent of perennial stream flows. We used the climate stress factor to determine the ranking of importance of acting in these areas, with areas of high stress being the highest priority or "tier 1" and the areas with low stress being a lower priority or "tier 2". In tier 1 areas of high stress, managers may consider more proactive management measures, such as pumping ground water to restore flows to springs that have gone dry. The long-term environmental and economic costs and benefits of these strategies will need to be thoroughly examined.

In areas with high adaptive constraints, the summary strategy is to "reduce constraints". Examples of these strategies include habitat restoration of degraded or converted lands, and enhancing connectivity through building wildlife friendly road crossings or restoring riparian corridors through degraded lands. As with "reduce exposure" areas, we used the climate stress factor to differentiate highest priority or tier 1 areas and lower priority or tier 2 areas. In areas with low climate stress but high exposure and constraints, the summary strategy is to "reduce exposure and constraints", by using a combination of the strategies listed above.

Finally, in the most vulnerable areas with high stress, exposure, and constraints, the conservation of current biodiversity may not be possible, and a biodiversity manager may have to "reassess goals" of protecting that suite of species in that location. Instead, the manager may look for ways to facilitate a transition to a new suite of species.

## Results

*Climate stress* is high (100% of the GCMs project that the mid-century conditions will be outside the observed range in the 20th century) for over a third (35%) of the state for January minimum temperatures (Fig. 3E), and for most (86%) of the state for July maximum temperatures (Fig. 3C). Projected stresses associated with precipitation are less extreme. For over a third of the state, notably the North and South Coast and the Sierra Nevada, 80% or more of the GCMs project that future annual precipitation totals will be within the range of historical variability (Fig. 3G). After combining the stress metrics for precipitation and temperature to estimate climate stress (Fig. 4A), areas with the highest stress include the Klamath Basin, the Modoc, the Sacramento Valley, and various locations in the Mojave and Sonoran Deserts. The areas with lower stress include the Santa Barbara coast and the South Coast mountains.

A map of *landscape exposure* is presented in Fig. 4B. Areas with the highest exposure include the flatter inland portions of the state, including the Modoc Plateau, the Central Valley, portions of the Mojave and Sonoran Deserts, and the Imperial Valley, while the coastal mountain ranges have the lowest exposure.

A map of *adaptive constraints* is presented in Fig. 4C. Native habitat has been lost to residential and urban development and cultivated crops in 15% of California. These converted areas, when combined with the state's extensive road network, fragment the remaining habitat blocks, adding additional constraints to adaptation. When combining habitat loss and fragmentation, constraints on potential species adaptation are greatest in the Modoc, Sierra foothills, San Francisco Bay Area, western Mojave, and the areas around San Diego and San Luis Obispo.

To estimate the vulnerability of biodiversity to climate change, we added climate stress, landscape exposure, and adaptive constraints (Fig. 4D). After masking out areas that are mostly converted to cultivated crops and development, the vulnerability score varies from 60 to 247, a 4-fold variation. We also summarized the average

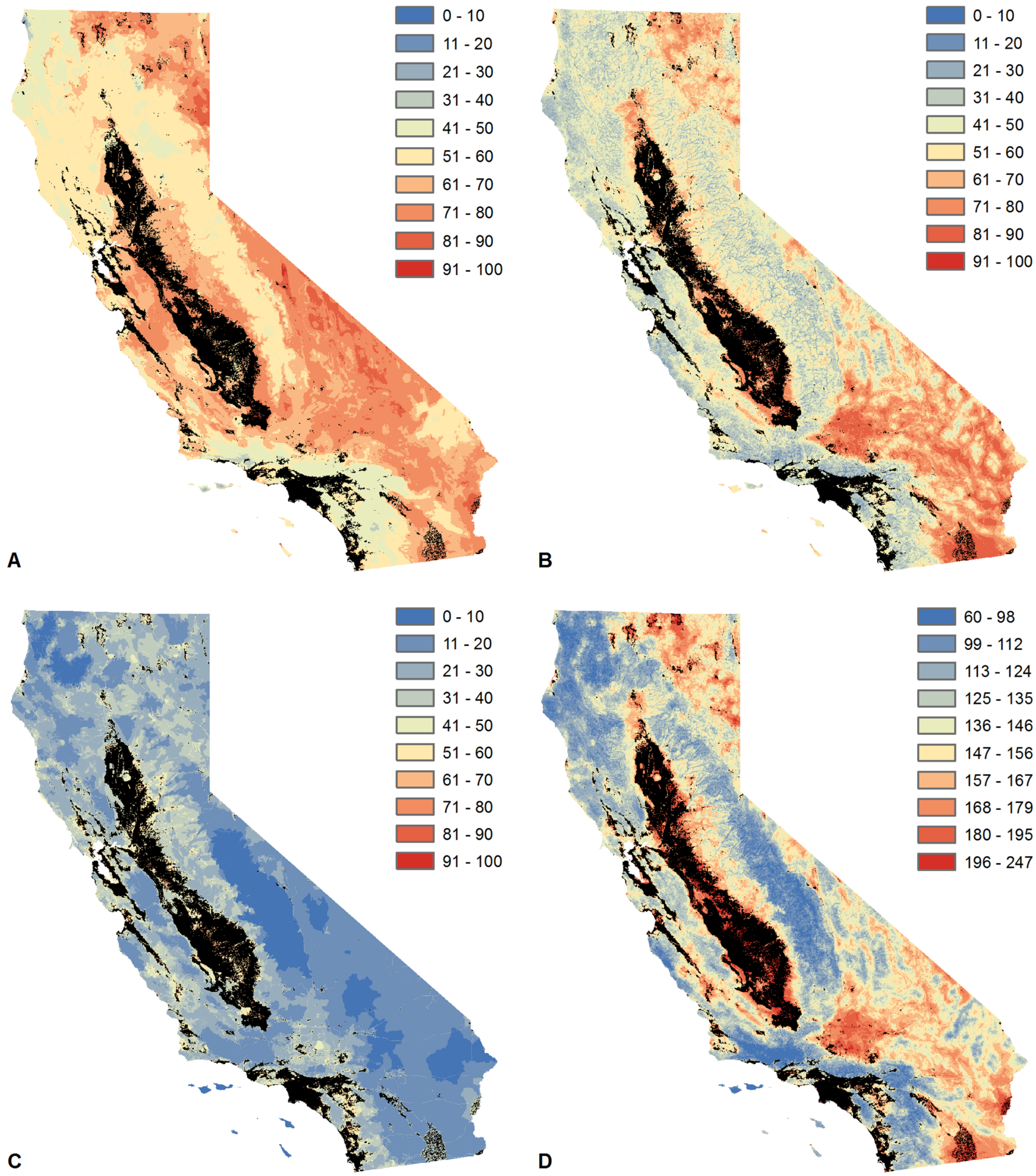


Fig. 4. Maps of (A) climate stress, (B) landscape exposure, (C) adaptive constraints, and (D) estimated vulnerability of biodiversity. Black areas on the maps represent areas that are >50% cultivated crops or developed.

vulnerability score for undeveloped areas by ecoregion and found that the California portion of the Sonoran Desert ecoregion is the most vulnerable while the Sierra Nevada is the least vulnerable (Fig. 5).

Fig. 6C shows how each of the eight strategy categories to reduce vulnerability are distributed statewide, ranging from 7% (reduce exposure—

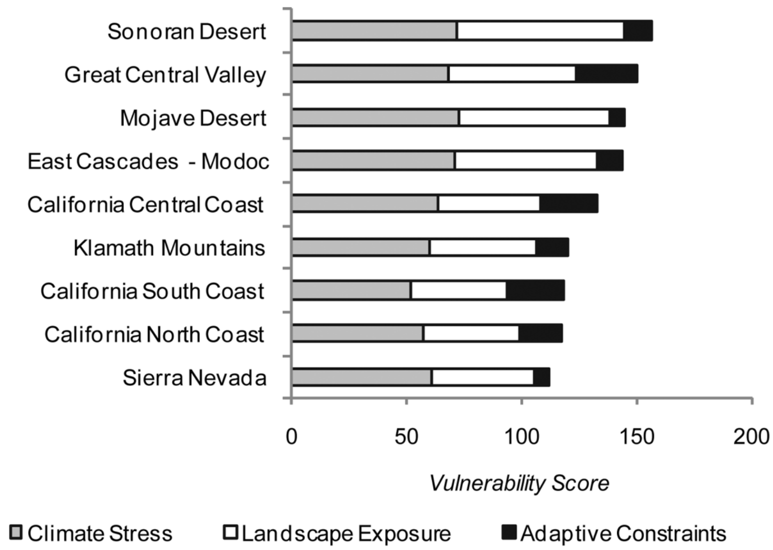


Fig. 5. Average climate stress, landscape exposure, and adaptive constraints values by ecoregion for the natural or semi-natural habitat of the nine largest terrestrial ecoregions in California. Average values do not include the areas in the ecoregion that are >50% cultivated crops or developed. The sum of these three indices is the average vulnerability score for the ecoregion. The ecoregion boundaries are mapped in Fig. 6.

tier 2) to 21% (reduce constraints—tier 2) of the unconverted portions of the state. While each of the categories is represented statewide, the distribution varies significantly by ecoregion. Low stress, exposure, and constraints give the Sierra Nevada, North Coast, Klamath Mountains, and South Coast ecoregions the largest areas in the "current strategies" category. Given the low vulnerability to climate change, new climate change adaptation strategies are likely not needed and managers can continue implementing current conservation strategies and monitor for changes for over one third of these four ecoregions. On the other hand, the East Cascades–Modoc ecoregion has the largest portion (39%) where high stress, exposure and constraints combine, indicating biodiversity managers may have to reassess current conservation goals in these areas. The Great Central Valley also has high vulnerability as 40% is already converted, and one third of the remainder falls in the "reassess goals" category.

The vulnerability map (Fig. 6B) shows the largest drivers of climate change vulnerability throughout the state and thus provides insight for strategies to reduce that vulnerability. Exposure to climate change is the largest component of vulnerability in the inland and arid Mojave, Sonoran, and East Cascades–Modoc ecoregions. Strategies to reduce this exposure could include restoration of riparian vegetation and policies to maintain groundwater levels to prevent springs from drying up. Adaptive constraints are significant in the coastal ecoregions and portions of the Klamath and Sierra Nevada mountains. Strategies to reduce adaptive constraints include enhancing connectivity through fragmented landscapes by encouraging compatible land uses and maintaining or enhancing wildlife corridors. Restoration of habitat on degraded and converted lands will also reduce vulnerability to climate change.

## Discussion

As greenhouse gas emissions continue to rise and climate change is consistently ranked as one of the top threats to the conservation of biodiversity, the need to facilitate species adaptation to climate change is clear. Assessing the vulnerability of individual species may be an important step to develop and prioritize adaptation strategies in some cases, but these assessments are costly, time consuming, and rely on data that in

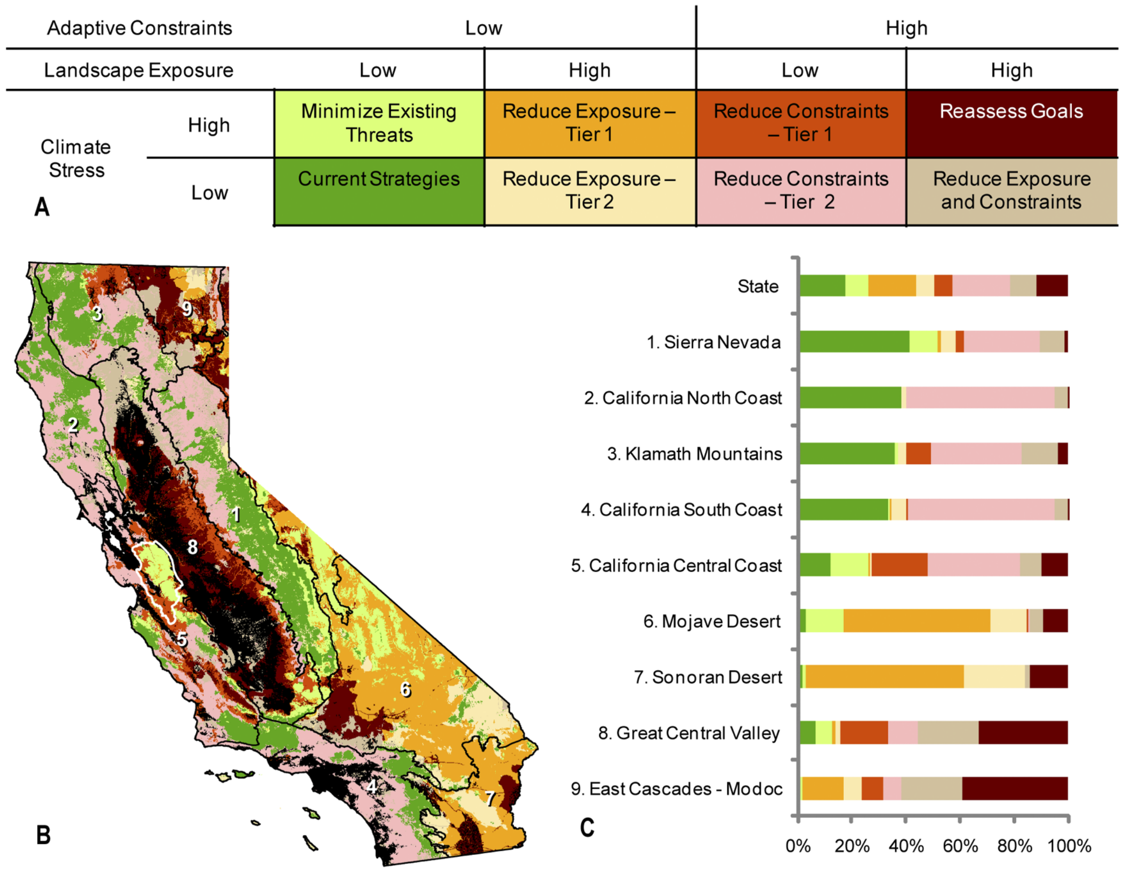


Fig. 6. The categories of vulnerability as defined by relatively high or low climate stress, landscape exposure, and adaptive constraints. The categories in the legend (A) are named by the summary strategy needed to reduce vulnerability. Colors in the map (B) and chart (C) are consistent with the legend. The black areas on the map represent areas that are >50% cultivated crops or developed, black lines represent ecoregional boundaries for the nine largest ecoregions in California, white numbers indicate the ecoregions as numbered in the chart, and the white outline delineates the Mount Hamilton range. Percentages in the chart represent the areas in each category relative to the total area of unconverted land in each ecoregion.

many cases do not exist. We present a cost-effective method to estimate the vulnerability of biodiversity to climate change across broad scales based on landscape-scale indicators. After conducting this assessment, biodiversity managers will be able to (1) compare the vulnerability of biodiversity between areas, (2) screen areas for where vulnerability assessments for individual species are needed, and (3) identify the types of conservation strategies that will likely help reduce vulnerability to climate change across multiple species. We believe this is much needed step forward to efficiently and effectively address the threat of climate change to the conservation of biodiversity.

Without drastic emissions reductions, the GCMs agree that almost all of California will face maximum summer temperatures that have not been experienced in the last century. While fewer of the GCMs project such drastic changes in precipitation patterns, the increase in temperature alone will increase evapotranspiration and likely reduce water availability for plants and animals. While this analysis focuses on the projections for the middle of the 21st century, the climate stress is only projected to worsen by the end of the century. Since these climatic conditions have not been observed in the recent past, we do not know how individual species will react, but the stress on many species will be increased unless they can reduce their exposure or adapt to the change.

Despite the high levels of projected climate stress, California has enduring landscape features that may reduce the exposure of species to climate change. These features include a long coastline, high topographic diversity, abundant perennial water sources, broad elevation and climatic gradients, and long riparian corridors. These features tend to co-occur in the coastal and interior mountain ranges, leaving the areas of low relief in the Central Valley and the interior deserts with the highest potential exposure to change. These areas also have relatively high levels of projected climate stress, indicating the potential impacts to biodiversity are significant.

The ability of species to adapt to climate changes depends both on the intrinsic adaptive capacity of the species and the extrinsic constraints of the landscape that limits that capacity (Klausmeyer and Shaw 2009). Roads, development and cultivated crops reduce the extent of native habitat to patches and break potential connections between those patches. The remaining habitat and connectivity will be essential as species need to move through the landscape to minimize exposure to extreme climate changes and migrate to areas of more suitable climate. After combining climate stress, landscape exposure, and adaptive constraints and masking out lands that are already converted, we can map biodiversity's vulnerability to climate change based on landscape-scale indicators (Fig. 4D) and provide insight to what categories of conservation strategies will help to reduce this vulnerability (Fig. 6).

To provide an example of how land managers could use this information, we focus in on the Mount Hamilton range south and east of San Francisco Bay (outlined in white in Fig. 6B). The area of lower elevation falls in the summary category of "Reduce Constraints—Tier 1" meaning that it has high climate stress, high adaptive constraints, and low landscape exposure. The primary constraint is fragmentation so a manager could look for ways to reduce fragmentation and enhance connectivity by building wildlife friendly road crossings, restoring corridors, and linking existing protected areas. This area is threatened by future habitat loss from new homes, agricultural expansion, and transportation infrastructure. Managers should look for ways to minimize future loss by encouraging urban growth boundaries, influencing local plans, and purchasing parcels that are the most threatened by conversion and support the most species. The higher elevation areas fall into the "Minimize Existing Threats" category because adaptive constraints are less but the climate stress is still high. Here, managers should focus on reducing the existing threats like invasive species and exurban development. If existing threats are controlled, species will have a better chance to adapt to the projected climate stress given the low adaptive constraints and landscape exposure. The specifics of these strategies will depend on site-specific factors, but this example shows how land managers can use this method to convert a complex set of data on landscape-scale indicators that influence climate change vulnerability into targeted strategy guidelines to reduce the vulnerability of biodiversity to climate change.

While this method to estimate vulnerability from landscape-scale indicators provides important information, managers should consider some limitations when interpreting it. This method is based on vulnerability factors for terrestrial species, and a map of vulnerability for aquatic biodiversity could be significantly different. Mapping vulnerability for aquatic biodiversity based on past and projected future hydrological conditions and landscape features is an important avenue for future research. In addition, the results presented here are designed to apply across a wide range of species, so individual species may be highly vulnerable in areas where the mapped vulnerability is low. This could result from a species being at the edge of its climatic range, so even a small change in climate would stress the species. A species may not be able to utilize landscape features that limit exposure like north facing slopes and river corridors if it has very limited dispersal capacity or requires a localized habitat feature like a rare soil type. On the other hand, some species may not be vulnerable to climate change in the areas of high vulnerability because they can tolerate large changes in climate, utilize exposure buffering features not included in this analysis (like caves or rock outcrops) or migrate across converted and fragmented landscapes. Given these limitations, biodiversity managers should attempt to complete species-specific vulnerability assessments using a framework like the one presented by Dawson et al. (2011) for iconic and well-known species to complement the results of this assessment.

Another key assumption of this method is the estimation of the coping range in the calculation of climate stress. We were unable to comprehensively test the accuracy of the coping range method because the climate tolerances of most species in California are not known, nor are detailed records of presence and absence during historical climate extremes. For example, in order to test this method, we would have to have results from laboratory controlled studies of the climate limits of species and records that show local population declines when the climate exceeded those limits. Furthermore, changes in climate can alter interactions between species and thus cause stress that would not be revealed even if the above test were possible (Hellmann 2002, Suttle et al. 2007). Finally, many conditions that actually stress species (e.g., soil moisture, stream temperature) depend on local conditions and are thus not adequately characterized in GCMs. The field work and historical research needed to test this method will be an important area for future research, but is beyond the scope of this analysis.

The potential impact of climate change on biodiversity is well established in the scientific literature, but there is much less research on what managers can do to reduce the impacts and help biodiversity adapt to climate change (Heller and Zavaleta 2009). Researchers are highlighting the importance of identifying and protecting landscape-scale features such as topographic and climatic heterogeneity, elevation gradients, solar insolation, soil types, geology, and riparian corridors to aid species' adaptation to climate change (Peterson 2003, Seavy et al. 2009, Ackerly et al. 2010, Anderson and Ferree 2010, Beier and Brost 2010, Dobrowski 2011). Our method combines this information with climate change stress and potential constraints to adaptation to provide a map of climate adaptation strategies. The method we present here to assess the vulnerability of biodiversity based on landscape-scale indicators can be modified based on regional considerations and repeated elsewhere using readily available data. Given the uncertainty of how species will respond to climate change and the costs associated with reducing that uncertainty, this method is a much needed contribution to help biodiversity managers identify and implement strategies to help species adapt to climate change.

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