



Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California

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Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California

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Abstract

Understanding and predicting biogeographic responses to climate change is fundamental for guiding conservation planning at both local and global scales. Studies of observed biogeographic responses to 20th century climate change have principally examined effects based on increases in mean temperature – collectively termed a warming fingerprint. Although the importance of changes in other aspects of climate – particularly precipitation and water availability – is widely acknowledged from a theoretical standpoint and supported by paleontological evidence, we lack a practical understanding of how these changes interact with temperature to drive biogeographic responses. Here we examine whether recent biogeographic patterns in California are consistent with a warming fingerprint. We describe how various components of climate have changed regionally in California during the 20th century and review empirical evidence of biogeographic responses to these changes. Many responses to climate change do not appear to be consistent with a warming fingerprint, with downslope shifts in elevation being as common as upslope shifts across a number of taxa and many demographic and community responses being inconsistent with upslope shifts. We identify a number of potential direct and indirect mechanisms for these responses, including the influence of aspects of climate change other than temperature (e.g., the shifting seasonal balance of energy and water availability), differences in each taxon's sensitivity to climate change, trophic interactions and land use change. Finally, we highlight the need to move beyond a warming fingerprint in studies of biogeographic responses by considering a more multifaceted view of climate, emphasizing local-scale effects, and including *a priori* knowledge of relevant natural history for the taxa and regions under study.

72 Introduction

73 Climate change is predicted to greatly impact living systems in the coming decades, potentially
74 surpassing habitat loss as the greatest driver of biodiversity change (IPCC, 2007; Leadley *et al.*,
75 2010). The impacts of climate change will be complex and diverse, affecting biological systems
76 at multiple levels, from single organisms to entire biomes (Bellard *et al.*, 2012; Peñuelas *et al.*,
77 2013; Staudinger *et al.*, 2013). Biogeographic responses – spatial changes in the abundance and
78 distribution of populations – are expected to be common (Bellard *et al.*, 2012; Peñuelas *et al.*,
79 2013; Staudinger *et al.*, 2013). Understanding and predicting those responses is fundamental for
80 guiding policy decisions at both local and global scales, and thus is an active field of research.

81 Studies of biogeographic responses to climate change have principally focused on the
82 detection and attribution of responses to increases in mean temperature (McCain & Colwell,
83 2011). Three main reasons are likely to underlie this trend: (i) increases in temperature
84 (minimum, maximum, mean) have been the clearest global signal of ongoing climate change
85 (IPCC, 2007); (ii) for many taxa, the physiological limitations imposed by temperature are better
86 understood than those imposed by other aspects of climate (Buckley *et al.*, 2012); (iii)
87 temperature exhibits a nearly linear decline with both elevation and latitude, facilitating
88 explanations and predictions of broad geographical responses to temperature changes (De Frenne
89 *et al.*, 2013a). As a result, hypotheses based solely on increasing mean temperature – hereafter
90 referred to as a “warming fingerprint” – have been used to find evidence of climate change
91 impacts across the globe, regardless of regional climate trends (Parmesan & Yohe, 2003; Root *et al.*,
92 2003; Hickling *et al.*, 2006; Chen *et al.*, 2011). Nevertheless, reviews of biogeographic
93 responses to climate change consistently report variable population responses within the same
94 region – including both upslope and downslope, poleward and equatorial range shifts (Parmesan

& Yohe, 2003; Chen *et al.*, 2011) – suggesting that a warming fingerprint may be an insufficient explanation for the complexity of biotic responses to climate change (Tingley *et al.*, 2012; Dobrowski *et al.*, 2013; Staudinger *et al.*, 2013).

The influence of additional aspects of climate change on biological systems – particularly changes in precipitation and water availability – is widely acknowledged from a theoretical standpoint (Bellard *et al.*, 2012). Yet, overall efforts to detect recent responses to these changes have been relatively few compared to responses to temperature changes (e.g., Jin & Goulden, 2013). As a result, we lack a practical understanding of how concurrent changes in various aspects of climate interact in a biogeographic context (Bonebrake & Mastrandrea, 2010; McCain & Colwell, 2011; Dobrowski *et al.*, 2013). Considerable evidence indicates that species responded individually to changes in temperature and precipitation during the Pleistocene, producing range shifts more complex than expected solely from temperature changes (Davis & Shaw, 2001). Recent studies also have highlighted how projected precipitation changes likely modify the individual effect of ongoing temperature increase on the distribution and abundance of global biodiversity along latitudinal (Bonebrake & Mastrandrea, 2010) and elevational (McCain & Colwell, 2011; Tingley *et al.*, 2012) gradients.

In this paper, we describe how various aspects of climate have changed regionally in California during the 20th century and review empirical evidence of biogeographic responses to these changes. Specifically, we examine: (i) whether detected responses are consistent with a warming fingerprint (i.e., predominant upslope elevational shifts and/or poleward latitudinal shifts) and (ii) if not, which potential mechanisms of climate change could drive biogeographic responses inconsistent with warming.

California offers a unique opportunity to understand the effects of simultaneous changes in different aspects of climate on the distribution and abundance of populations and communities. First, the climate of California is inherently heterogeneous – including desert, alpine, mediterranean, and temperate rainforest regions – and presents large variation in both temperature and precipitation extremes. In particular, precipitation and associated water availability patterns play a key role in determining species' distributions (Raven & Axelrod, 1978; Stephenson, 1998; Barbour *et al.*, 2007; Jin & Goulden, 2013). Second, California's large latitudinal span and complex topography present a diversity of environments, with the consequence that species can find radically different habitats within short distances (Ackerly *et al.*, 2010). Third, California has experienced substantial spatial and temporal variability in both temperature and precipitation (means and variances) over the 20th century, and the rate of change is predicted to increase in the coming decades (Moser *et al.*, 2012). Fourth, California represents a biologically meaningful region. The state comprises the bulk of the California Floristic Province (CFP), which is listed among the 25 most diverse and endangered terrestrial biodiversity hotspots in the world (Myers *et al.*, 2000). It should be noted, however, that the boundaries of the CFP differ slightly from the state's political boundaries: the Great Basin and deserts east of the Sierra Nevada fall outside the CFP while parts of Oregon, Nevada and Baja California fall inside it. In this paper, we use California's political boundaries due to data constraints. Finally, the extremely diverse flora and fauna of California are among the best-studied in the world, owing to a long tradition of natural history recording and collection dating back to the 18th century. Existing historical surveys, museum specimens, photographs and field notes provide historical baselines against which the current state of biological systems can be compared (Tingley & Beissinger, 2009). Recent efforts to re-survey historical sites and transects

have enabled the detection of significant changes to biological systems in California over the 20th century (Kelly *et al.*, 2005; Kelly & Goulden, 2008; Moritz *et al.*, 2008; Tingley *et al.*, 2009; Crimmins *et al.*, 2011).

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20th century climate change in California: more than warming

The climate of California has experienced dramatic long-term changes during the 20th century that have been linked with both anthropogenic sources and natural climate cycles (Moser *et al.*, 2012). We examined patterns of 20th century climate change in California using interpolated surfaces of monthly mean, minimum, maximum temperature and total precipitation (800-m resolution; Daly *et al.*, 1994, 2000) and two climatic water balance indices (270-m resolution; Flint & Flint, 2012; Flint *et al.*, 2013). For each variable, we calculated differences between means over the years 1900 – 1939 (i.e., historical time period) and 1970 – 2009 (i.e., modern time period) across California (Figure 1; see Appendix S1 for detailed methods). We focused on these six climate variables because they reflect physiological limiting factors that are known to influence the distributional limits of plants at broad spatial scales (Woodward, 1987; Stephenson, 1998). In particular, actual evapotranspiration (AET) and climatic water deficit (CWD) represent the water demand of plants that is either met or not met by water availability, respectively, and reflect the seasonal balance of concurrent water and energy availability (Stephenson, 1990). Flint *et al.* (2013) calculated these variables by integrating seasonal measurements of climate (temperature and precipitation) and meteorological variables (snow melt, solar radiation, vapor pressure deficit, and wind) with soil properties. To better visualize regional patterns of climate change, we grouped individual pixels in California according to Jepson Floristic Regions (Baldwin *et al.*, 2012; Figure 2) – a widely used phytogeographical classification of California. Although this classification was developed from patterns of vegetation (Baldwin *et al.*, 2012), it reflects broad patterns of geology, topography, and climate and therefore is also relevant to animal distributions in California (Parra & Monahan, 2008). Using this classification, we produced scatter plots of three pairs of climate variables: (i) change in annual total precipitation

against change in annual mean temperature (Fig. 2*b*), (ii) change in annual maximum temperature against change in annual minimum temperature (Fig. 2*c*), and (iii) change in mean AET against change in mean CWD (Fig. 2*d*).

California experienced a statewide increase in annual mean temperature of up to 1.68 °C (Table 1) between the historical and modern time periods, but this change was spatially heterogeneous (Fig. 1*a*; Fig. 2*b*). California's Deserts, Central Valley and urban areas warmed greatly, while parts of the Cascade Ranges and Northwestern regions cooled (e.g., Mount Shasta and Lassen regions; Fig. 2*b*; Table S1). The overall increase in annual mean temperature appears to have been driven by a nearly ubiquitous and marked increase in annual minimum temperature (Fig. 1*c*; Table S1). The trend in annual maximum temperature was much more variable, with substantial decreases in northern parts of the state, the southern Central Valley, and Central Western California (Fig. 1*d*; Fig. 2*c*; Table S1). Moreover, minimum and maximum temperatures often had contrasting trends within the same region; increases in minimum temperature were matched by decreases in maximum temperature in the Central Valley, Cascade Ranges, Northwestern, and Central Western California regions (Fig. 2*c*; Table S1).

Precipitation patterns also changed. Although annual total precipitation increased overall (Table 1), there was considerable spatial variation. Increases occurred across much of northern and central California but precipitation mostly decreased in the south (e.g., Southwestern California and Desert regions; Fig. 2*b*; Table S1) and along the Sierra Nevada rain shadow (Fig. 1*d*). The shifting seasonal balance of temperature and precipitation led to changes in both AET and CWD. Both AET and CWD increased slightly overall (Table 1) but changes varied greatly across space (Fig. 1*e, f*). Across much of the south, particularly the Desert and Southwestern California regions, decreases in AET were matched by large increases in CWD (Fig. 2*d*; Table

S1). Conversely, in the Modoc Plateau and Cascade Ranges, slight increases in AET were matched by decreases in CWD (Fig. 2*d*; Table S1). Importantly, large increases in temperature and concomitant but smaller increases in precipitation have led to concurrent increases in both AET and CWD in all other regions (Fig. 2*d*; Table S1).

Figure 2 illustrates the strong heterogeneity in within- and between-region climate change during the 20th century across California. Three main patterns are manifest. First, although mean temperature generally increased across all regions, variation in the direction and magnitude of change in mean precipitation separates regions in the climate space of Figure 2*b*. For instance, although most of Western California warmed, there is strong variation in how precipitation patterns changed, with Northwestern California experiencing substantial increases, Central Western California slight increases and Southwestern California decreases in precipitation (Fig. 2*b*). Second, the three southern California regions – Southwestern California, Mojave Desert and Sonoran Desert – exhibit patterns distinct from other regions. Increases in their mean CWD are larger than for all other regions and are coupled with decreases in mean AET (Fig. 2*d*). These patterns reflect the concurrent large increase in temperature and slight decrease in precipitation (Fig. 2*a*). Finally, despite general region-specific trends, great heterogeneity exists within each region, highlighting the potential for localized biotic responses. The patterns we identified fundamentally agree with recent evidence that the spatial pattern of climate velocity vectors for temperature and climatic water balance during the 20th century in the United States demonstrates huge variation in rates, directions and changes through time (Dobrowski *et al.*, 2013).

Biogeographic responses to 20th century climate change: marked heterogeneity

To provide a composite view of documented biogeographic responses to 20th century climate change in California, we examined published evidence on elevational shifts in birds (Tingley *et al.*, 2012), butterflies (Forister *et al.*, 2010), mammals (Moritz *et al.*, 2008), and plants (Kelly & Goulden, 2008; Crimmins *et al.*, 2011) using data from five of the largest multi-species studies that have identified climate as a potential driver of change during the 20th century (see Appendix S1 for detailed methods). Although we found several relevant high-quality studies of single species, we excluded them from our analysis to minimize positive publishing bias. Studies differed in their approach to quantifying elevational shift (Table S2): some explicitly tested for expansion or retraction of both lower and upper range limits between a historical and a modern time period (Moritz *et al.*, 2008; Tingley *et al.*, 2012), while others compared single estimates of elevational range in each time period such as cover-weighted mean elevation (Kelly & Goulden, 2008), optimum elevation (Crimmins *et al.*, 2011), and mean elevation across all presence sites (Forister *et al.*, 2010).

We derived single estimates of shift in elevational range for each species' population at each independently-analyzed elevational transect, either directly (as reported by the study) or indirectly (by calculating the mean between reported lower and upper limit shifts). Importantly, the estimate of elevational shift we report does not require movement along elevational gradients over time, as it could be the result of population contraction at either range limit or shifts in relative abundance across the elevational gradient. The time between resurveys also differed among studies, ranging from 30 to 98 years (Table S2). To account for the effect of study time period on the magnitude of shift, we calculated shifts in elevational range as meters shifted per 30 years (i.e., the shortest study period; Kelly & Goulden, 2008), and used these estimates in all

exploratory analyses. We used all estimates provided by the original studies, including population shifts that were deemed to be statistically insignificant, but indicate whenever removal of insignificant shifts affected our results.

The direction of relative shift in elevational range was highly heterogeneous among individual populations within each taxonomic group (Fig. 3). Studies of all four groups reported species shifting both upslope and downslope, as well as species not shifting (Fig. 3a). However, there were differences among groups. The proportion of detected upslope shifts was significantly greater than downslope shifts (relative to a null expectation of 0.50) in butterflies (binomial test: observed proportion of upslope shifts = 83/113, $p < 0.05$), while the opposite was true in plants (27/74, $p < 0.05$), and the proportions of upslope and downslope shifts did not differ significantly ($p > 0.05$) in mammals (14/20) and birds (115/205). These results were robust to the removal of insignificant shifts, except that the proportion of plant downslope shifts was no longer significantly greater than that of upslope shifts (24/63, $p > 0.05$).

Heterogeneous elevational shifts may not be exclusively due to climate change. Additional drivers including human-mediated land-use changes (Archaux, 2004), changes in species interactions (Hughes, 2000; Lenoir *et al.*, 2010), and stochastic population variation (Lenoir *et al.*, 2010) could have accounted for a portion of detected 20th century biogeographic responses. In California, anthropogenic land-use change has been linked, together with climate, with elevational shifts in Belding's ground squirrels (*Urocitellus beldingi*, Morelli *et al.*, 2012), and many species of butterflies (Forister *et al.*, 2010). Furthermore, recent evidence supports a significant influence of competitive interactions in mammals (Rubidge *et al.*, 2010) and past disturbance history in plants (Schwilk & Keeley, 2012). The effect of alternative drivers of change can be expected to be higher at low elevations across California, where human-related

landscape modification has been most extensive (Millar *et al.*, 2004; Tingley *et al.*, 2012) and a large number of species co-occur (Millar *et al.*, 2004). It has been suggested that direct and indirect effects of climate change are likely to be disproportionately large at high elevations (Pepin & Lundquist, 2008; La Sorte & Jetz, 2010). Yet, we found no evidence of a significant change in the relative frequency of upslope versus downslope shifts with historical elevation (Fig. 3*b*). Instead, we found that plants and birds shifted more downslope than upslope at higher historical elevations (Fig. 3*b*). Furthermore, bird and mammal elevational shifts were estimated using sites occurring primarily in protected areas (e.g., National Parks) across the entire study period, minimizing the potential impacts of anthropogenic land-use change (Moritz *et al.*, 2008; Tingley *et al.*, 2012). As a result, we lack evidence to indicate that land use change and other non-climate factors are dominant drivers, especially at middle to high elevations in birds, mammals and plants (but see Forister *et al.*, 2010 for butterflies).

301 **Are detected biogeographic responses consistent with a warming fingerprint?**

302 The scarce coverage of biogeographic responses across a number of California's regions
303 precludes attributing patterns of biogeographic change (Figure 3) with regional climate change
304 patterns (Figures 1 and 2). For this reason, we were unable to determine whether biogeographic
305 responses within and among taxa significantly differed among regions experiencing markedly
306 different climatic changes (e.g., Southwestern California and Deserts versus all other regions).
307 Neither were we able to investigate each population's localized response as a function of site-
308 specific changes in climatic variables (e.g., Tingley *et al.* 2012) in the absence of the detailed
309 data underlying each population's response in Figure 3. Instead, we reviewed the published
310 evidence for biogeographic responses to climate change during the 20th century in California and
311 asked whether it is consistent with a warming fingerprint (i.e., predominant upslope and/or
312 poleward shifts; Parmesan & Yohe, 2003; Root *et al.*, 2003) or whether it requires a more
313 complex understanding of the influence of climate change on biological systems.

314 A number of biogeographic responses in California are consistent with a warming
315 fingerprint. Significant shifts to higher elevations – particularly contractions of the lower limits
316 of high-elevation species – have been documented across a range of taxonomic groups, including
317 mammals (Epps *et al.*, 2004; Larrucea & Brussard, 2008; Moritz *et al.*, 2008), birds (Tingley *et*
318 *al.*, 2012), butterflies (Forister *et al.*, 2010, 2011a), and plants (Kelly & Goulden, 2008;
319 Crimmins *et al.*, 2011; Kopp & Cleland, 2014). These upslope shifts towards cooler, higher-
320 elevation locations have been primarily attributed to increases in temperature, although studies
321 generally have not explicitly modeled the underlying mechanisms responsible for the shifts.
322 Comparing site occupancy models of historical and modern elevational ranges for 28 small
323 mammal species in Yosemite National Park, Moritz *et al.* (2008) showed that half of these

species shifted or contracted their ranges upslope in a manner consistent with warming across the study area but did not provide a direct test of this relationship. Subsequent studies, however, have identified a clear effect of temperature increase for a subset of these mammal species. Morelli *et al.* (2012) showed that persistence of the Belding's ground squirrel (*Urocitellus beldingi*) was negatively correlated with increased winter temperature. Similarly, Rubidge *et al.* (2010) found a strong correlation between increased minimum temperatures and the contraction of the lower elevational range limit in the alpine chipmunk (*Tamias alpinus*). For birds, Tingley *et al.* (2012) found that about half of all significant elevational shifts were upslope, and the magnitudes of the shifts were consistent with predictions from rising temperatures. Forister *et al.* (2010) also detected upslope shifts in the elevational ranges of high-elevation butterfly species from long-term monitoring data, and linked those with average daily minimum and maximum temperatures and concurrent habitat change. Comparing two vegetation surveys in Southern California's Santa Rosa Mountains over a 30-year period, Kelly & Goulden (2008) detected an increase in the mean elevation – based on abundance-weighted distributions across transects – of 9 out of 10 dominant plant species in the region, and suggested increases in mean and minimum temperature as the main underlying drivers (but see Schwilk & Keeley, 2012 for evidence of the possible importance of fire history). Although less common, there are also accounts of species shifting to higher latitudes (i.e., lower temperatures). For instance, Karban & Strauss (2004) reported a northward shift in the latitudinal range of the meadow spittlebug (*Philaenus spumarius*). They provided evidence of a strong link between this geographical shift and physiological tolerance to temperature based on laboratory experiments and field censuses.

Several studies provide evidence of demographic responses consistent with upslope shifts in elevational range (i.e., population decline at the lower elevational limit and/or population

increase at the higher elevational limit). Kopp & Cleland (2013) observed significant declines in abundance at the lower elevation range limit of three alpine cushion plants (*Trifolium andersonii*, *Phlox condensata* and *Eriogonum ovalifolium*) between 1961 and 2010. Van Mantgem & Stephenson (2007) found that the decreases in mortality rates reported for a number of *Abies* and *Pinus* species were highest at lower elevations but were not significant at the highest elevation. Lutz *et al.* (2009) indicated that proportional decreases in large-diameter tree density for three *Pinus* species were greatest in the lower-elevation portions of their ranges but found no species for which decreases were greatest in high-elevation zones. Thorne *et al.* (2008) reported the replacement of large *Pinus ponderosa*-dominated areas by vegetation types typically found at lower elevations on the west slope of the Central Sierra Nevada. Forister *et al.* (2010) observed increases in abundance at the highest elevation site within their study area for most butterfly species, except for two species that specialize on the alpine environment.

Finally, some changes in community structure were also consistent with expectations from temperature increase (i.e., communities shifting upslope leading to the progressive replacement of higher elevation communities by lower elevation communities). Kopp & Cleland (2013) found that shifts in individual plant species could be leading to the transition of an alpine plant community to subalpine sagebrush steppe. Similarly, lower montane forest herb communities in the Siskiyou Mountains now resemble those found on steep south-facing slopes (Harrison *et al.*, 2010). Forister *et al.* (2010) also reported that low-elevation butterfly assemblages have acted as sources for migrants recolonizing higher elevations, although they suggested a strong effect of habitat change on this pattern.

Nevertheless, many populations and communities have not followed expectations based solely on increased mean temperature. Despite being the main focus of many studies, upslope

shifts in elevational range have been far from ubiquitous in predominantly warming regions. All multi-species studies also detected many species whose ranges have shifted downslope or remained stable (Kelly & Goulden, 2008; Moritz *et al.*, 2008; Forister *et al.*, 2010; Crimmins *et al.*, 2011; Tingley *et al.*, 2012). The two studies that included the greatest number of species found that downslope shifts occurred more frequently (plants, Crimmins *et al.*, 2011) or as frequently (birds, Tingley *et al.*, 2012) as upslope shifts. Heterogeneity in responses also exists among populations of the same species. For instance, Tingley *et al.* (2012) found that only 5 of 53 (9.4%) bird species shifted in the same direction across three different regions of the Sierra Nevada. Similarly, the elevational range of two evergreen tree species (*Abies concolor* and *Quercus chrysolepis*) shifted upslope in Southern California's Santa Rosa Mountains (Kelly & Goulden, 2008) but downslope across Northern California's mountain ranges (Crimmins *et al.*, 2011). Heterogeneous responses have also been identified among populations of the same species occurring on different mountain slopes (Yang *et al.*, 2011) or substrates (Kopp & Cleland, 2014). Moreover, certain demographic responses also appear to be in contrast with upslope elevational shifts, with two studies detecting increases in the density of younger cohorts of tree species at lower elevations during the 20th century (Millar *et al.*, 2004; Eckert & Eckert, 2007). Finally, some ecological communities may be responding to climate change in a manner more complex than simple thermal zone shifts, with the result that old ecological assemblages are disappearing and new ones are being created (Urban *et al.*, 2012). Bird communities of the Sierra Nevada appear to be responding in such a way: overall, species composition has changed by 35% and species turnover has been highest at low and high elevation extremes, providing little evidence that communities have shifted in the same direction (Tingley & Beissinger, 2013).

Therefore, it would appear that a more complex understanding of the influence of climate change on biological systems, which goes beyond the effects of ubiquitous warming, is required to explain recent biogeographic responses in California. In the next section, we investigate potential mechanisms of climate change that may explain complex biogeographic responses inconsistent with a warming fingerprint.

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Mechanisms of climate change that could explain biogeographic responses inconsistent with warming

A complete assessment of the mechanisms through causing populations (or species) to respond to climate change should consider four main factors (reviewed by Williams *et al.*, 2008; Dawson *et al.*, 2011; Huey *et al.*, 2012; Foden *et al.*, 2013): (i) exposure – how much the climate has changed across a population’s range and the degree to which local microhabitat buffers change; (ii) sensitivity – the degree to which persistence and performance of the population depends on the climate it experiences; (iii) adaptive capacity – how the population responds to changes in climate by either persisting *in situ* or migrating to more suitable regions; and (iv) indirect effects – the influence of climate change via changes in assemblage composition and biotic interactions with other species. Below we discuss each mechanism as it relates to the heterogeneous biogeographic responses we have documented in California.

Exposure

Exposure reflects the direction, rate, and magnitude of change in various climate components that a population is likely to experience over the habitats and regions it occupies (Dawson *et al.*, 2011). Heterogeneous biogeographic responses to climate change may be partly explained by differences in exposure to temperature changes alone (e.g., Pinsky *et al.*, 2013). Regional patterns suggest that mean temperature has not increased everywhere in California (Fig. 1a; Fig. 2a), and downward shifts in elevation may be expected where temperature has decreased. Biogeographic responses inconsistent with increased temperature may be better explained by expanding our traditional temperature-centric view of climate change (McCain & Colwell, 2011)

to include concurrent changes in precipitation and water availability (Crimmins *et al.*, 2011; Stephenson & Das, 2011; Tingley *et al.*, 2012; Dobrowski *et al.*, 2013).

It has long been recognized that both temperature and precipitation – the main determinants of a system's energy and water supply, respectively – are climatic aspects of direct physiological importance to plants and largely control vegetation distribution (Holdridge, 1967; Whittaker, 1975). The climatic water balance summarizes how the energy available to plants interacts with available water over the course of the year (see Stephenson, 1990 for a comprehensive review). In particular, two climatic water balance parameters, actual evapotranspiration (AET; the evaporative water loss from a site given the prevailing water availability) and climatic water deficit (CWD; the evaporative demand not met by water availability), have a direct influence on plant recruitment and mortality, and appear to be better correlates of the elevational distribution of vegetation types than atmospheric temperature and precipitation (Stephenson, 1998).

There is growing evidence that changes in AET and CWD have been primary drivers of changes in recruitment and mortality rates of tree species in California during the 20th century (Lloyd, 1997; Lloyd & Graumlich, 1997; Millar *et al.*, 2004; Guarín & Taylor, 2005; Van Mantgem & Stephenson, 2007; Lutz *et al.*, 2009; Salzer *et al.*, 2009; Das *et al.*, 2013; Dolanc *et al.*, 2013). For any given region, the effects of AET and CWD on demographic rates of trees appear to depend on whether energy or water have historically been the most important limiting factor and whether limiting factors have changed over time (Das *et al.*, 2013). For instance, in principally energy-limited regions where energy input and water availability have both increased (e.g., semi-arid treelines in the Central Sierra Nevada; Fig. 1a, d), some tree species have benefitted from an extended growing season, resulting in increased recruitment (Millar *et al.*,

2004; Dolanc *et al.*, 2013) and increased growth rates (Millar *et al.*, 2004; Salzer *et al.*, 2009). Conversely, recruitment has decreased (Lloyd, 1997; Lloyd & Graumlich, 1997) or remained stable (Van Mantgem & Stephenson, 2007) in principally water-limited regions, where energy input has increased but water availability has either remained stable or decreased (e.g., low elevation mountainous regions in the Southern Sierra Nevada; Fig. 1a, d). Regardless of historical limitations, large temperature increases – even without decreases in precipitation – appear to have induced local increases in CWD during the 20th century (Fig. 1 and Fig. 2), reducing performance of certain tree species (Lutz *et al.*, 2010) and increasing mortality of old-growth trees (Guarín & Taylor, 2005; Van Mantgem & Stephenson, 2007; Lutz *et al.*, 2009; Dolanc *et al.*, 2013). Climate change feedbacks may mediate these general patterns. For instance, increased temperatures and/or reduced precipitation are likely to reduce snow cover at high elevations, negatively impacting tree seedlings by exposing them to cold early spring air temperatures and earlier runoff and evaporation of water supplies (Wipf *et al.*, 2009).

There is also evidence that changes in precipitation can interact with changes in temperature to affect animals, although this has been much less of a focus than in plants. Karban & Strauss (2004) showed that simple deviations from optimum conditions of humidity and temperature can interact to increase the risk of desiccation in the meadow spittlebug (*Philaenus spumarius*), which largely explained past population dynamics. Pereyra (2011) found that heavy precipitation and snowfall in the spring can delay egg laying in dusky flycatchers (*Empidonax oberholseri*), leading to reduced productivity for both individual females and entire populations.

Complex shifts in the seasonal balance of energy and water availability over time may explain part of the heterogeneity in elevational shifts of populations in Figure 3. This occurs because precipitation generally increases while temperature decreases with elevation in montane

systems. A consequence of these elevational trends is that numerous tree species are limited by temperature at their high-elevation range limit and water at their low-elevation limit (Salzer *et al.*, 2009). Thus, if populations track their climatic niches over time, increased temperature should promote upslope shifts. However, if populations are more constrained by precipitation and water availability, increased precipitation may counteract the effects of temperature and result in a downslope shift (Tingley *et al.*, 2012). Tingley *et al.* (2012) showed that downslope shifts detected for many bird species were consistent with site-level increases in precipitation and may have been the consequence of these species tracking their precipitation-based niches downslope. Similarly, Crimmins *et al.* (2011) argued that some downslope shifts in plant species' optimum elevations were explained by species tracking regional precipitation-driven decreases in CWD rather than temperature. Nevertheless, it should be noted that some of the conclusions of Crimmins *et al.* (2011) have been challenged, primarily because they may be affected by spatial bias and because they rest upon an incomplete test of the causal relationship between CWD and downslope shifts (Hijmans, 2011; Stephenson & Das, 2011; Wolf & Anderegg, 2011; but see Dobrowski *et al.*, 2011 for a response). Similarly,

There are several important considerations when comparing biogeographic responses to concurrent changes in temperature and precipitation. First, the microclimate experienced by an individual organism at ground level can vary markedly from the regional climate due to variation in local land cover and terrain. For instance, the water locally-available to a plant not only depends on atmospheric precipitation, but also topography, edaphic variables, water use by competing plants, and localized weather conditions (Stephenson, 1990, 1998; Flint *et al.*, 2013). Thus, the general increase in precipitation with elevation does not always translate to increased water availability along a given elevational gradient. Topography can also complicate the

gradient of temperature with elevation: localized temperature inversions occasionally occur within low-lying areas of warming regions and result in downward movements of populations within those areas (see Langan *et al.*, 1997 on physiological effects of freezing events caused by temperature inversions). It is important to consider such microclimatic variation because it may buffer populations from the full magnitude of regional climate change, making biogeographic responses of individual populations hard to predict based on large-scale temperature and precipitation changes (Williams *et al.*, 2008; De Frenne *et al.*, 2013b). Second, changes in water availability should not always be expected to cause coordinated directional changes across a large number of species (Stephenson & Das, 2011), such as primarily downslope shifts (Crimmins *et al.*, 2011). This is because, at local scales, water availability and temperature do not oppose each other and should be viewed as nearly orthogonal interacting variables (Stephenson, 1998). Stephenson & Das (2011) argue that increased precipitation will allow trees to shift to shallower or more exposed soils, but not necessarily to shift downslope. Nonetheless, at regional to continental scales, water availability and temperature are inextricably linked by the dynamics of heat transfer within Earth's global energy balance (Trenberth & Shea, 2005), as illustrated by the negative correlation between changes in mean AET and mean CWD (Fig. 2d). It may be unfeasible to decouple them into independent components. As a result, concurrent changes in temperature and water availability may sometimes cause individual populations to shift in ways that are not consistent with expectations based solely on increased temperature, including downslope shifts (Crimmins *et al.*, 2011; Dobrowski *et al.*, 2011; Stephenson & Das, 2011; Tingley *et al.*, 2012).

Sensitivity

Exposure alone does not determine how populations and species respond to climate change. Many studies report discordant responses among taxa experiencing comparable changes in climate within the same region (e.g., Moritz *et al.*, 2008; Lutz *et al.*, 2009; Dolanc *et al.*, 2013) or even single sites (e.g., Tingley *et al.*, 2012; Kopp & Cleland, 2013). A number of intrinsic factors determine how sensitive populations and species are to climatic changes. These factors reflect the degree to which population persistence and resilience depend on climate (Williams *et al.*, 2008; Dawson *et al.*, 2011).

One factor determining a species' sensitivity to climate change is its physiological tolerance to various aspects of climate (Huey *et al.*, 2012). For instance, populations of thermal specialists, which have limited capacity to acclimatize to changing temperatures, are likely to be most sensitive to temperature increases (Stillman, 2003; Calosi *et al.*, 2008; Huey *et al.*, 2012). For similar reasons, ectothermic organisms are also likely to be more vulnerable to climate change than endothermic organisms (Aragón *et al.*, 2010). Much less is known about which physiological traits determine sensitivity to concurrent changes in temperature and precipitation. A hydraulically-based theory, focused on the piñon–juniper woodlands of southwestern USA, indicates that the survival of plant species during extreme drought events will depend on their evolved hydraulic strategies (McDowell *et al.*, 2008). Furthermore, when changes in both temperature and precipitation are considered, tree (Das *et al.*, 2013) and bird (Tingley *et al.*, 2009) populations are more likely to track changes in the climatic variable that has limited them historically.

Life history traits are also likely to influence sensitivity to climate change. Sensitivity is likely to be higher for species with multiple life stages (e.g., migration, breeding, seed germination, hibernation and spring emergence), each of which depends on environmental

triggers or cues and requires different habitats and/or microclimates (Foden *et al.*, 2013). Few life history traits have been successfully linked with recent biogeographic responses to climate change in California. However, birds that are year-round California residents, strongly territorial species, dietary specialists, with small clutches were more likely to shift their elevational limits (Tingley *et al.*, 2012).

Adaptive Capacity

The sensitivity of a species to climate change will be mediated by its adaptive capacity, at least over long time scales. Adaptive capacity refers to the capacity of a species or constituent populations to cope with climate change by persisting *in situ*, or by migrating to more suitable regions (Williams *et al.*, 2008; Dawson *et al.*, 2011). Adaptive capacity depends on a variety of intrinsic factors, including phenotypic plasticity, genetic diversity, life history, and dispersal and colonization ability (Foden *et al.*, 2013). For instance, poor dispersers with a low genetic diversity are less likely to be able to adapt to the climate change to which they are exposed (Huey *et al.*, 2012; Foden *et al.*, 2013). In California, short-lived mammal species that lay more litters per year (i.e., shorter generation time and higher fecundity) were more likely to expand their range upward than were their long-lived, less fecund counterparts (Moritz *et al.*, 2008). Furthermore, non-ruderal butterfly species (i.e., less dispersive species with more localized population dynamics) appeared to be in more severe decline at several sites in the Central Valley compared to ruderal, more dispersive species (Forister *et al.*, 2011b), although the opposite was true at a number of sites near but not in the Central Valley (Forister *et al.*, 2010).

Indirect effects

The realized impacts of climate change on given species, driven by their particular combination of exposure and sensitivity, will lead to additional indirect impacts on interacting species, including mutualists, predators and competitors (Williams *et al.*, 2008). These indirect effects may be as, or even more, important as direct effects in determining population declines and extinctions related to climate change (Cahill *et al.*, 2012).

A growing body of research indicates that the effects of concurrent changes in temperature and precipitation on animals during the 20th century in California may have been largely mediated by changes in vegetation rather than, or in addition to, direct physiological effects. Tingley *et al.* (2009) suggested a link between shifts in bird range limits and climate-induced shifts in net primary productivity during the 20th century. In a subsequent paper, Tingley *et al.* (2012) found that traits related to breeding site fidelity best predicted range shifts in birds, suggesting that nest-site selection, rather than the physical ability to track climatic conditions, may limit the magnitude of elevational shift. McLaughlin *et al.* (2002) indicated that growing season precipitation can affect the population dynamics of the checkerspot butterfly (*Euphydryas editha bayensis*) by determining the suitability of host plants for larval growth and survival. Similarly, Forister *et al.* (2011) suggested that the positive relationship between winter precipitation and butterfly abundance may be a consequence of the increased availability of nectar resources in the spring. In mammals, accounting for changes in vegetation as well as climate improved predictions of range change from correlative species distribution models for several species (Rubidge *et al.*, 2010). In addition, increases in body size of high elevation ground squirrels were linked to increased resource availability and a longer feeding season (Eastman *et al.*, 2012).

Conclusions: towards a new fingerprint of climate change

Using California as a case study, we have demonstrated that recent biogeographic responses to climate change across a wide range of taxa have been more complex than expected from a ‘globally coherent fingerprint’ based solely on increases in temperature (Parmesan & Yohe, 2003; Root *et al.*, 2003; Chen *et al.*, 2011). In particular, individualistic biogeographic responses to 20th century climate change in California appear to have been driven by exposure and sensitivity to more than just temperature – particularly the shifting seasonal balance of temperature and precipitation – mirroring biotic responses during the Pleistocene (Davis & Shaw, 2001; Moritz & Agudo, 2013). We identified a number of potential direct and indirect mechanisms through which these additional climatic aspects may determine the biogeographic responses of plants and animals. Perhaps more importantly, this review highlights the need to move beyond a fingerprint of climate change based on global monotonic increases in temperature to identify a more nuanced fingerprint better suited to diagnosing past biogeographic responses and predicting future ones. We believe a new fingerprint of climate change should: (i) capture a more complex understanding of climate, (ii) be capable of producing local, site-level predictions of biogeographic change, and (iii) include *a priori* knowledge of relevant natural history for the species and region under study.

First, a fingerprint of *climate* change requires an understanding of climate beyond temperature, because organisms respond to concurrent changes in multiple aspects of climate. Using changes in water balance instead of simple annual means of temperature and/or precipitation appears to be a natural solution for making more realistic hypotheses about biogeographic responses to climate change in plants. Stephenson & Das (2011) presented a theoretical model for predicting the effects of changes in climatic water balance on species’

elevational ranges, which involves mapping elevation onto the environmental space defined by AET and CWD, so that changes in those parameters can be translated into expectations of shifts along elevational or soil moisture gradients. This and similar models could form the basis for defining new hypotheses of climate change impacts. The challenge lies in understanding how environmental space maps onto geographical variables, such as elevation or latitude, which is not easily resolved because these relationships are not inherently linear or monotonic (Dobrowski *et al.*, 2011). For future projections, it will also be increasingly important to consider impacts of elevated CO₂ concentrations. Increased CO₂ levels interact with freezing tolerance (Dole *et al.*, 2003) and lead to enhanced water use efficiency for many plants (Wullschlegel *et al.*, 2002); the latter effect is expected to partially offset the impacts of increased climatic water deficit in some cases. For animals, climate change impacts are likely to be more complex and should rest on identifying whether study populations are more likely to respond directly or indirectly to concurrent changes in temperature and precipitation, acknowledging that responses may well be driven by both physiological limiting mechanisms and climate-induced habitat changes.

Second, populations respond to climate *locally* and local patterns of climate change often differ substantially from global patterns. As a result, we are unlikely to diagnose local climate change impacts using a global fingerprint. Instead, a fingerprint should be determined for each locality (e.g., individual sites, study transects, or biogeographic regions) based on its geography and the particular pattern of climate change exposure. In this context, we see great potential in approaches that can scale to meaningful site-level measures of climate change, such as the estimation of changes in realized environment (Ackerly *et al.*, 2010), vectors of climate velocity (Loarie *et al.*, 2009; Ackerly *et al.*, 2010; Dobrowski *et al.*, 2013; Pinsky *et al.*, 2013), measures

of site-level shifts in relation to species' climate niche centroids (Tingley *et al.*, 2009), and nearest neighbor elevations (Tingley *et al.*, 2012).

Finally, hypotheses about biogeographic responses to climate change should be chosen *a priori* based on aspects relevant to each particular study, such as the study region's natural and environmental history and the study species' sensitivity to the climate variables undergoing change. This is necessary to prevent post-hoc hypotheses in which the climate variable that relates most strongly to the response is selected as the causal driver. Choosing hypotheses *a priori* will ensure that they are falsifiable and that the climate change fingerprint derived from them truly is able to diagnose climate change impacts on a given system within a given region.

Examining recent biotic responses to climate change is a key step towards improving our understanding of how future change will impact populations and communities. A growing quantity of historical data is becoming available for this purpose as institutions focus their efforts on finding innovative ways to rescue and digitize information contained in museum specimens, field notes, and photographs (Sparks, 2007; Drew, 2011). A major challenge for researchers now is to devise effective approaches to make the best use of these historical baselines (Tingley & Beissinger, 2009; Moritz & Agudo, 2013). Adopting a more multifaceted and finer-scale understanding of climate change impacts is both a necessary and attainable step in the right direction.

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Tables

Table 1. Summary statistics (mean, minimum, and maximum) of change in six climate variables in California based on differences between historical (1900-1939) and modern (1970-2009) means derived from interpolated climate surfaces (see Appendix S1 for detailed methods). Estimates of temperature (annual mean, minimum, and maximum) and precipitation change were derived from the Parameter-elevation Regression on Independent Slopes Model (PRISM) climate dataset (Daly *et al.*, 1994, 2000). Estimates of change actual evapotranspiration (AET) and climatic water deficit (CWD) were derived from the Basin Characterization Model (BCM; Flint & Flint, 2012; Flint *et al.*, 2013).

Variable	Mean change	Minimum change	Maximum change
Mean temperature (°C)	0.447	-0.770	1.680
Minimum temperature (°C)	0.792	-2.140	3.950
Maximum temperature (°C)	-0.118	-2.290	2.290
Annual precipitation (mm)	26.543	-308.421	381.691
Mean AET (mm)	2.548	-116.940	76.763
Mean CWD (mm)	14.320	-79.523	133.895

Figure legends

Figure 1. Changes in mean, minimum, and maximum annual temperature, total annual precipitation, actual evapotranspiration (AET) and climatic water deficit (CWD) across California during the 20th century. Estimates of change for all variables are based on differences between historical (1900-1939) and modern (1970-2009) means derived from interpolated climate surfaces (Daly *et al.*, 1994, 2000; Flint & Flint, 2012; Flint *et al.*, 2013; see Appendix S1 for detailed methods). Maps (a) to (d) are based on 800-m resolution and (e) and (f) on 270-m resolution layers. Values of change in precipitation (mm) in (d) were logged (to the base 10) before mapping to aid visualization.

Figure 2. Regional patterns of 20th century climate change among biogeographic units of California. (a) Map of the 10 Jepson Floristic Regions – a widely used phytogeographical classification of California (Baldwin *et al.*, 2012). Scatter plots of (b) change in annual total precipitation (*mm*) against change in annual mean temperature (°C), (c) change in annual maximum temperature (°C) against change in annual minimum temperature (°C), and (d) change in mean actual evapotranspiration (AET, *mm*) against change in mean climatic water deficit (CWD, *mm*) across each Jepson Floristic Region. Symbols represent the medians of all points falling within each Jepson Floristic Region, while arrows indicate 5th–95th percentile intervals. Colors in scatter plots (b), (c) and (d) correspond to colors in (a). Abbreviations: NW = Northwestern California Region; CaR = Cascade Ranges Region; SN = Sierra Nevada Region; GV = Great Central Valley Region; CW = Central Western California Region; SW =

Southwestern California Region; MP = Modoc Plateau Region; SNE = East of the Sierra Nevada Region; DMoj = Mojave Desert Region; DSon = Sonoran Desert Region.

Figure 3. Relative elevational shifts during the 20th century from published studies of birds (Tingley *et al.*, 2012), butterflies (Forister *et al.*, 2010), mammals (Moritz *et al.*, 2008) and plants (Kelly & Goulden, 2008; Crimmins *et al.*, 2011) in California. Estimates of elevational shift and historical elevation (either as a mean or an optimum) were derived from individual studies. Relative shifts in elevational range across the four groups are calculated relative to the shortest study time period (30 years; Kelly & Goulden, 2008). Analysis was limited to relative shifts between -500 and 500 m per 30 years, which excluded 7 (5%) butterfly populations that shifted > 500 m per 30 years. (a) Violin plot of relative elevational shift (m/years) for the four taxonomic groups. Violins are scaled to have the same area across the four groups. Numbers adjacent to violins indicate the number of individual population shifts for each group. Bold horizontal lines represent the median relative elevational shift for each group. (b) Scatter plot of relative elevational shift (m/years) against mean historical elevation (m) for the four taxonomic groups. Closed symbols refer to significant shifts and open symbols refer to non-significant shifts, as assessed by the individual studies. Trend lines illustrate the results of the two significant linear models of relative elevational shift as a function of historical elevation: birds (slope = -0.022, $t_{227} = -2.216$, $p < 0.05$) and plants (slope = -0.039, $t_{72} = -2.098$, $p < 0.05$). Data on mammals, birds, and historical occurrence of most plants included in this figure can be accessed via <http://ecoengine.berkeley.edu>. All icons were obtained from the University of Maryland Center for Environmental Science (www.ian.umces.edu/imagelibrary).

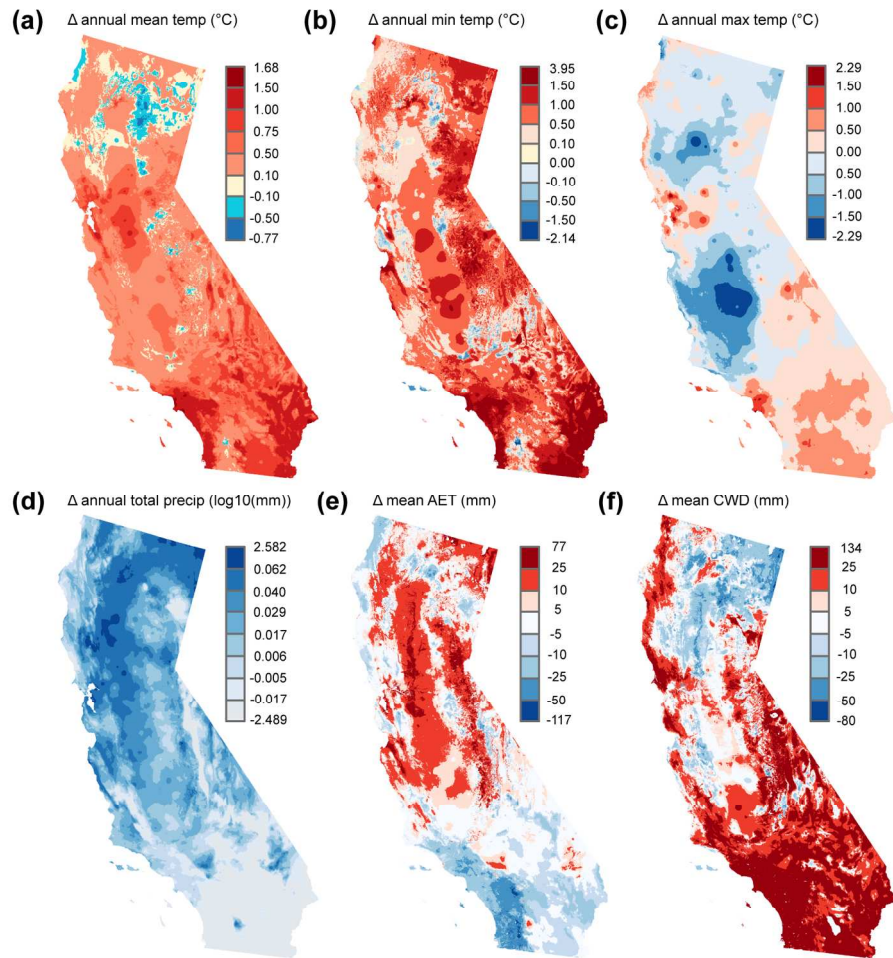


Figure 1
163x169mm (300 x 300 DPI)

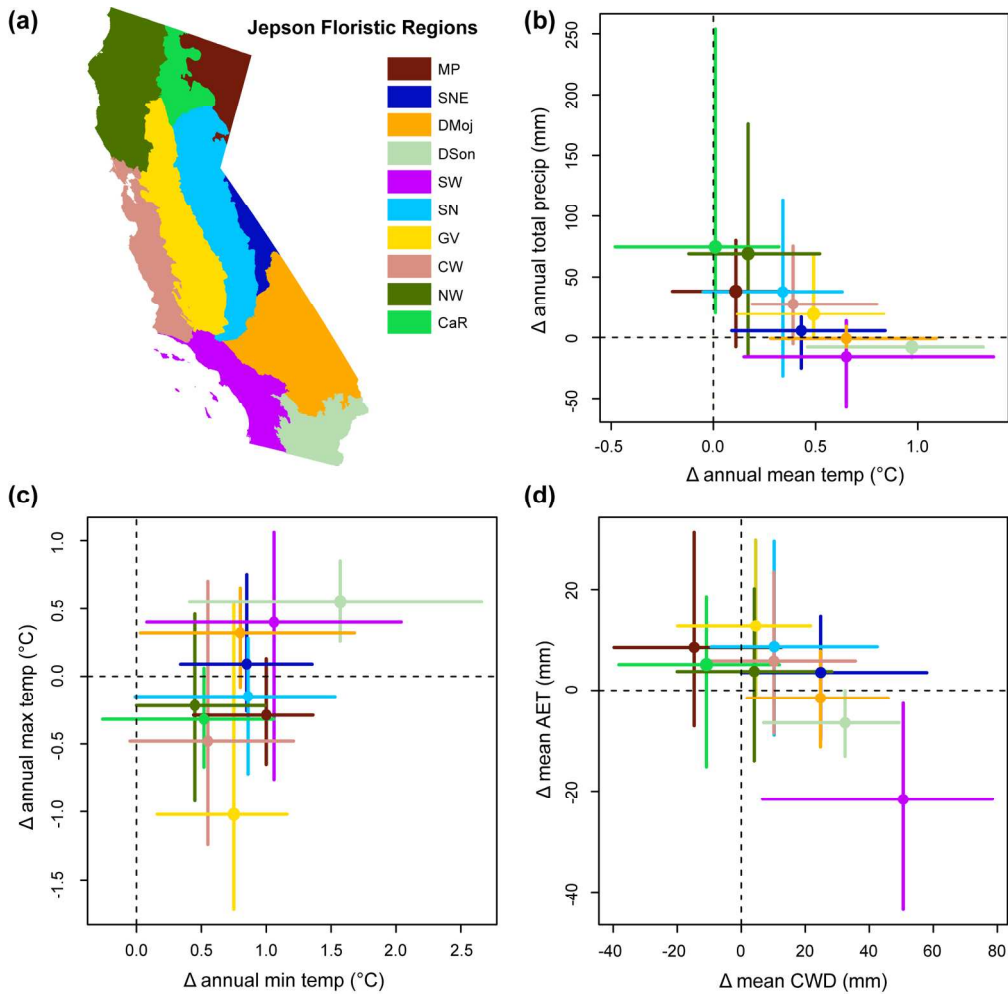


Figure 2
169x166mm (300 x 300 DPI)



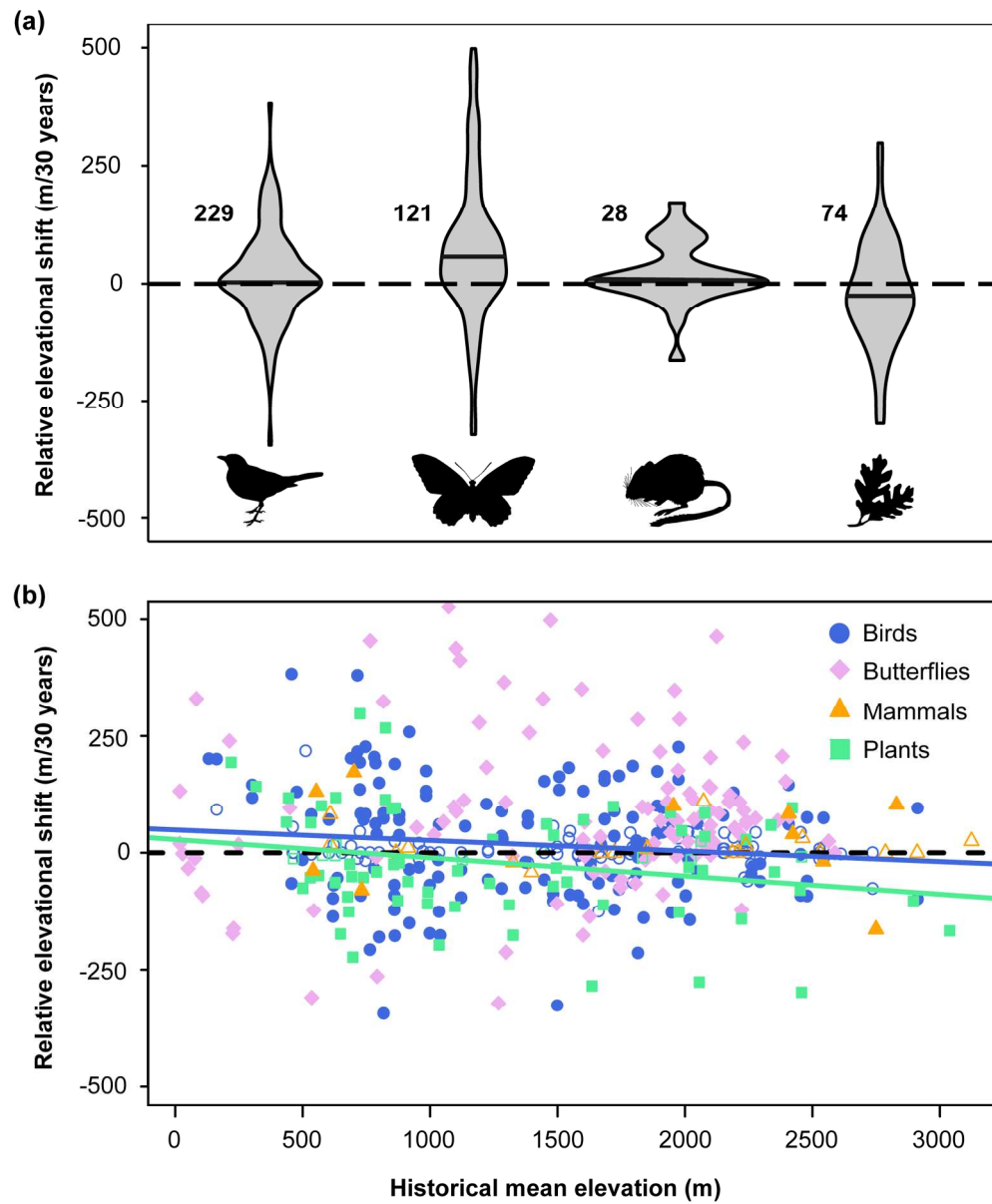


Figure 3
161x194mm (300 x 300 DPI)

Supporting Information

Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California

Giovanni Rapacciuolo *et al.*

The following Supporting Information is available for this paper:

Appendix S1. Detailed methods for analyses of climate change and biogeographic responses

Table S1. Summary statistics of change in climate variables during 20th century in California across the 10 Jepson Floristic Regions and overall

Table S2. Characteristics of the studies included in the analysis of biogeographic responses to 20th century climate change in California.

Appendix S1: Detailed Methods

Changes in temperature, precipitation and climatic water balance during the 20th century

Temperature and precipitation data

We used 30-arcsec (~800-m) resolution climate layers of monthly minimum, maximum and mean temperature and precipitation derived from the parameter-elevation regression on independent slopes model (PRISM) for the years 1900 – 2009 (Daly *et al.* 1994, 2000). A detailed description of how the PRISM data set was developed and assembled is available in Daly *et al.* (2000, 2002, and 2004; see also <http://www.prism.oregonstate.edu>), so here we limit ourselves to a brief description of the methods used to develop the PRISM climate layers with a focus on aspects relevant to the climate over California during the time periods we used. PRISM is a statistical model built on the assumption that, locally, elevation is the most important factor in the distribution of temperature and precipitation. The climatic factor of interest (temperature or precipitation) was thus calculated using linear climate-elevation relationships developed from climate observations supplied by weather stations in the local area and a digital elevation model. PRISM continually changes its frame of reference by calculating a separate climate-elevation regression for each grid cell, selecting stations falling within a user-defined moving window around the grid cell. In building each regression, climate observations are weighted by their horizontal and vertical distance to the target cell, as well as their similarity in aspect (calculated at multiple spatial scales), atmospheric layer in which they reside (boundary layer or free atmosphere), coastal proximity, terrain, and clustering among stations. By weighting stations according to their similarity in coastal effects and aspect, PRISM accounts for the maritime influences on climate and rain shadow effects. These are especially relevant to the climate of California as it is characterized by the influence of the Pacific Ocean in the west and a complex

topography. The PRISM dataset was then converted to bioclimatic variables to summarize trends (see Smith *et al.*, 2013 for details).

Actual evapotranspiration and climatic water deficit data

We also obtained 270-m climatic water balance layers of monthly actual evapotranspiration (AET) and climatic water deficit (CWD) derived from the Basin Characterization Model (BCM; Flint & Flint, 2012; Flint *et al.*, 2013) – a regional water balance model – for the years 1900 – 2009. The BCM mechanistically models the pathways of precipitation into evapotranspiration, infiltration into soils, runoff, or percolation below the root zone based on data inputs for topography, soil composition and depth, underlying bedrock geology, and spatially-explicit values (measured or estimated) of air temperature and precipitation. The model begins with the calculation of potential evapotranspiration (PET), which relies on an hourly energy-balance calculation, based on solar radiation, air temperature, and the Priestley-Taylor equation (Priestley & Taylor, 1972). Using PET, gridded precipitation, maximum and minimum air temperature and estimates of snow accumulation and melt the model calculates available water (W). Based on the soil-water storage and permeability of the underlying bedrock, the BCM then quantifies the proportion of available water that results in AET, runoff or recharge. This permits the subsequent calculation of CWD as $PET - AET$. Values of CWD and AET are encapsulated by summing monthly values over water years, which begin in October and end in September.

Calculating and presenting changes in climate variables

We derived estimates of change in temperature, precipitation and climatic water balance variables by averaging estimates across the years 1900 to 1939 (i.e., historical time period) and

1970 to 2009 (i.e. modern time period), inclusive, and subtracting historical from modern values. We chose these time periods because: (i) 40-year periods should enable reliable estimates of long-term changes that are discernible from short-term climatic fluctuations, especially for the modern time period (Otto *et al.*, 2013); (ii) they provide the most overlap with historical and modern time periods for which biogeographic data were available. Although it is generally assumed that recent accelerated warming started around 1980, we do not believe that including the years 1970-1979 in our modern time period led to bias in our analyses; on the contrary, excluding this decade would have biased the analysis towards a higher degree of warming. As a result, our choice of modern time period leads to conservative estimates of climate change during the 21st century. Because weather stations were online in different years and some had missing data, it is likely that a different set and number of stations underlie the climate layers we obtained for each time period. Nevertheless, there are indications that the overall set of stations was roughly stable within each time period, providing approximately 2300 stations for the 1900–1939 period and 8900 for the 1970–2009 period (Smith *et al.*, 2013). As a result, we expect historical climate records to be less accurate than modern records (Smith *et al.*, 2013).

In Figure 1, we present maps of change in the six climate variables at the resolution of the original interpolated surfaces (i.e., 800-m for temperature and precipitation variables and 270-m for AET and CWD). We log-transformed (on a base scale 10) precipitation change values (*mm*) to normalize their distribution before mapping them in Figure 1*d* but present untransformed estimates of precipitation change in Figure 2 and Table 1.

In order to better examine regional associations and differences across the topographic complexity and climatic and habitat diversity of the large state of California, we grouped the individual sites of Figure 1 (i.e., single 800-m or 270-m cells) according to Jepson Floristic

Regions (Baldwin *et al.*, 2012). This classification was developed for The Jepson Manual (1993) – and slightly modified in the second Edition – to enhance the effectiveness of geographic data in predicting plant occurrences and combines features of topography, climate and vegetation to delimit units, as opposed to using the often arbitrary and unnatural boundaries of counties. The Jepson geographic system is organized hierarchically, starting with broadly defined provinces, then regions, subregions, and ending with districts, for a total of 50 geographic units. In this paper, we used the 10 Jepson Floristic Regions, as defined in The Jepson Manual II (Baldwin *et al.*, 2012): the Northwestern California Region (NW), the Cascade Ranges Region (CaR), the Sierra Nevada Region (SN), the Great Central Valley Region (GV), the Central Western California Region (CW), the Southwestern California Region (SW), the Modoc Plateau Region (MP), the East of the Sierra Nevada Region (SNE), the Mojave Desert Region (DMoj), and the Sonoran Desert Region (DSon). Figure 2a in the main body of this paper provides a map of those regions' boundaries. In Figure 2, we provide scatter plots of pairwise comparisons of climate change variables across the 10 Jepson Floristic Regions.

Biogeographic responses to 20th century climate change

We reviewed the literature for data on biogeographic responses to climate change in California. Our methodology was modified from Parmesan & Yohe (2003). We did not conduct an exhaustive review but identified a set of studies that comprise the bulk of 20th century biogeographic responses in California studied with respect to climate change hypotheses. We reviewed only but not all climate change biogeography studies that met one or more of the following criteria: a) at least two time periods of data (i.e. historic and modern), b) more than 20 years apart, c) the modern time period ending in 1990 or later, d) data on presence-absence

and/or abundance of populations in both time periods, and e) data gathered in an unbiased manner for a multi-species assemblage. Only data reported in terms of change per individual species were included. This precluded use of studies that only report mean change across a set of species. Although we identified several relevant high-quality studies of single species, these mostly reported significant positive shifts of single species in congruence with warming trends (e.g. Epps *et al.*, 2004; Larrucea & Brussard, 2008). Therefore, we excluded these studies from our analyses to minimize the positive publishing bias associated with them. Given the final set of papers and the difficulty of combining spatial responses along both latitudinal and elevational gradients, we chose to focus on studies of shifts in elevational range and excluded studies of latitudinal range changes (e.g. Karban & Strauss, 2004). We also excluded studies that considered climate change as a potential driver but ruled out its influence based on their analyses (e.g. Davidson *et al.* 2002). Finally, we excluded studies that did not provide estimates of shifts in elevational range (i.e. in terms of presence-absence) for all study populations but focused on changes in abundance along localised portions of whole elevational gradients (e.g. Kopp & Cleland, 2013).

Table S2 lists the four studies we selected for our analysis. Tingley *et al.* (2012) – our only source for bird data – report data from three independent transects in the Sierra Nevada; we considered each species' elevational shift estimate at each transect as an independent data point in our analysis. This meant that each bird species had up to three alternative estimates of change depending on how many transects it had been adequately recorded in. Studies differed in their approach to quantifying elevational shift (Table S2); some explicitly tested for expansion or retraction of both lower and upper range limits between a historical and a modern time period (Moritz *et al.*, 2008; Tingley *et al.*, 2012), while others compared single estimates of elevational

range in each time period (cover-weighted mean elevation, Kelly & Goulden, 2008; optimum elevation, Crimmins *et al.*, 2011; mean elevation across all presence sites, Forister *et al.*, 2010). We used single estimates of shift in elevational range for each independent data point (i.e. study population). We obtained those directly whenever reported by the study (i.e. Kelly & Goulden, 2008; Forister *et al.*, 2010; Crimmins *et al.*, 2011). For studies exclusively reporting estimates of shift in upper and lower range limits, we first calculated historical and modern elevation as the mean of historical and modern lower and upper range limits and then subtracted historical from modern mean elevation to derive a single shift estimate. It is important to note that the estimates of elevational shift we report in Figure 3 and Table 2 do not necessitate individual dispersal along elevational gradients over time, but could simply be the result of population contraction at either range limit, or shifts in relative abundance across the elevational gradient. The time between historical and modern time periods differed among studies, ranging from 30 to 98 years (Table S2). Comparing estimates of absolute elevational shift among these varying timescales would be misleading, so we accounted for the effect of study time period on the magnitude of shift by quantifying shifts in elevational range relative to the shortest study time period (30 years; Kelly & Goulden, 2008). In the violin plots of Figure 3a, we therefore present these as shifts in m/30 years.

We used all estimates provided by the underlying studies in our analysis, including population shift estimates that were deemed to be statistically insignificant by each study. In the scatter plot of Figure 3b, we identified which shifts were not statistically significant under each study's assessment – if this was assessed – by using open symbols. We tested for significant differences in the proportion of upslope shifts (shift > 0) versus downslope shifts (shift < 0) in each major taxonomic group (i.e. birds, butterflies, mammals, plants) using a binomial test with a

null expectation of proportion of upslope shifts = 0.5. For Figure 3b, we also used estimates of each study population's elevation in the historical time period as reported the underlying studies. We produced linear models of relative elevational shift (m/years) as a function of historical elevation (m) separately for each major taxonomic group and tested for significance of the model's slope term using a t-test with a significance threshold of $p < 0.05$. We only report the trendlines from the two significant linear model slopes (i.e. birds and plants). To test for differences in the proportion of upslope versus downslope shifts along different elevations, we grouped individual study populations of each taxonomic group in three categories based on their historical elevation (low elevation: historical elevation $< 900\text{m}$; middle elevation: $900\text{m} < \text{historical elevation} < 1800\text{m}$; high elevation: $1800 < \text{historical elevation}$). The three categories were loosely based on a coarser classification of Grinnell's life zones (Hall & Grinnell, 1919). For each group, we assessed whether the proportion of upslope shifts differed among the three elevation categories using a test of equal proportions and identified which pairs of proportions differed using pairwise comparisons of proportions using a Bonferroni-Holm adjustment.

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Table S1. Summary statistics (mean, minimum, and maximum) of change in 6 climate variables across the 10 Jepson Floristic Regions and overall based on differences between historical (1900-1939) and modern (1970-2009) means derived from interpolated climate surfaces. Abbreviations: NW = Northwestern California Region; CaR = Cascade Ranges Region; SN = Sierra Nevada Region; GV = Great Central Valley Region; CW = Central Western California Region; SW = Southwestern California Region; MP = Modoc Plateau Region; SNE = East of the Sierra Nevada Region; DMoj = Mojave Desert Region; DSon = Sonoran Desert Region.

	Mean temp	Min temp	Max temp	Tot Precip	Mean AET	Mean CWD
Mean						
MP	0.10	0.96	-0.27	37.15	9.65	-14.10
SNE	0.44	0.85	0.16	2.46	3.01	26.19
Dmoj	0.67	0.81	0.30	-1.04	-1.65	24.63
Dson	0.95	1.52	0.54	-8.50	-6.89	31.60
SW	0.70	1.05	0.32	-19.50	-22.68	47.40
SN	0.32	0.82	-0.18	37.85	9.36	12.63
GV	0.49	0.72	-0.81	26.30	13.56	3.51
CW	0.42	0.55	-0.41	30.22	6.24	11.23
NW	0.18	0.47	-0.23	71.47	3.70	4.33
CaR	-0.03	0.48	-0.32	94.19	4.04	-11.24
Overall	0.45	0.79	-0.12	26.54	2.55	14.32
Minimum						
MP	-0.55	-0.49	-1.15	-27.41	-25.98	-73.25
SNE	-0.19	-0.60	-0.43	-157.75	-38.79	-26.57
Dmoj	-0.17	-1.02	-0.70	-30.34	-34.25	-39.13
Dson	0.03	-0.88	0.04	-55.58	-69.06	-26.10
SW	-0.25	-2.14	-1.24	-140.90	-116.94	-27.51
SN	-0.76	-1.24	-1.43	-308.42	-61.17	-62.54
GV	-0.18	-1.28	-2.29	-27.36	-23.25	-68.98
CW	-0.10	-0.61	-1.49	-98.42	-34.38	-53.14
NW	-0.40	-0.86	-1.75	-190.59	-40.04	-79.52
CaR	-0.77	-0.91	-1.41	-84.01	-46.49	-71.68
Overall	-0.77	-2.14	-2.29	-308.42	-116.94	-79.52
Maximum						
MP	0.69	1.63	0.25	265.24	67.71	51.21
SNE	1.17	1.85	1.38	27.82	32.04	86.80
Dmoj	1.50	2.84	0.94	46.96	23.30	71.53
Dson	1.68	3.95	1.06	15.22	17.32	79.10
SW	1.66	2.61	1.88	99.89	26.49	133.89
SN	1.05	2.46	1.17	314.64	66.94	92.51
GV	1.16	1.61	1.84	88.94	76.16	57.32
CW	1.22	2.00	2.07	198.46	65.59	56.31
NW	1.01	2.04	2.29	362.54	76.76	74.73
CaR	0.77	1.86	0.46	381.69	58.11	25.52
Overall	1.68	3.95	2.29	381.69	76.76	133.90

Table S2. Characteristics of the studies and regions included in the analysis of biogeographic responses to 20th century climate change in California.

Study	Taxon	N	Study region	Latitudinal range	Elevational range	N sites	Historic time period	Modern time period	Measures of elevational shift
Tingley <i>et al.</i> , (2012)	Birds	78	Lassen (Northern and Central Sierra Nevada)	40.0 – 40.9	80 – 2751	26	1924–1928	2006–2007	Shift in upper range limit; shift in lower range limit
Tingley <i>et al.</i> , (2012)	Birds	78	Yosemite (Northern Sierra Nevada)	37.5 – 38.2	65 – 3226	24	1915–1919	2003–2004	Shift in upper range limit; shift in lower range limit
Tingley <i>et al.</i> , (2012)	Birds	73	Southern Sierra Nevada	34.8 – 36.8	61 – 3356	27	1911	2008–2009	Shift in upper range limit; shift in lower range limit
Forister <i>et al.</i> , (2010)	Butterflies	121	Central Valley, Northern Sierra Nevada	38.2–39.8	18–2775	4	1977–1986	1998–2007	Shift in mean elevation
Moritz <i>et al.</i> , (2008)	Mammals	28	Yosemite (Northern Sierra Nevada)	37.5 – 38.2	60–3300	56	1914–1920	2003–2006	Shift in upper range limit; shift in lower range limit
Kelly & Goulden, (2008)	Plants	10	Santa Rosa Mountains (South Coast Range)	33.2–34.0	244–2560	20	1977	2006–2007	Shift in cover-weighted mean elevation
Crimmins <i>et al.</i> , (2011)	Plants	64	Most of the major mountain ranges north of 35° latitude (North Coast, Cascade Ranges, Sierra Nevada, and Central Coast)	35–42	0–3500	8747	1932–1936	2000–2005	Shift in optimum elevation