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RESEARCH REVIEW

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

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Abstract

Understanding recent biogeographic responses to climate change is fundamental for improving our predictions of likely future responses and guiding conservation planning at both local and global scales. Studies of observed biogeographic responses to 20th century climate change have principally examined effects related to ubiquitous increases in 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. Further complicating matters, differences in life history and ecological attributes may lead species to respond differently to the same changes in climate. Here, we examine whether recent biogeographic patterns across 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, particularly elevational range shifts. 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.

Keywords: biogeographic responses, California, climate change, climatic water balance, elevation, fingerprint, range shifts, temperature

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Introduction

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

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

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

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 (Figs 1a and 2b). 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. 2b; 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. 1c; 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 (Figs 1d and 2c; 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. 2c; 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. 2b; Table S1) and along the Sierra Nevada rain shadow (Fig. 1d). 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. 1e and f). Across much of the south, particularly the Desert and Southwestern California regions, decreases in AET were matched by large increases in CWD (Fig. 2d; Table S1). Conversely, in the Modoc Plateau and Cascade Ranges, slight increases in AET were matched by decreases in CWD (Fig. 2d; 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. 2d; 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 Fig. 2b. 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. 2b). 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. 2d). These patterns reflect the concurrent large increase in temperature and slight decrease in precipitation (Fig. 2a). Finally, despite

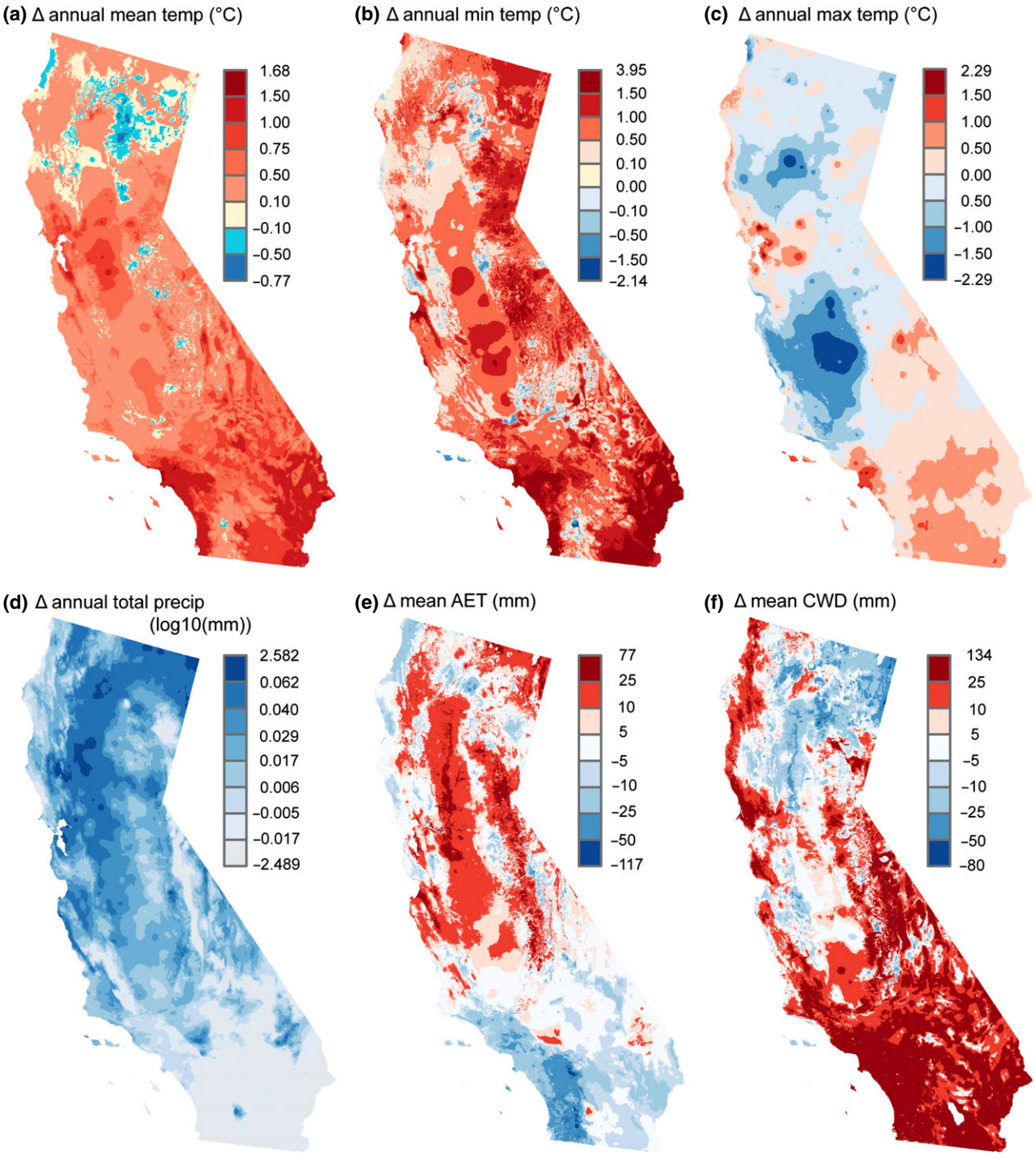

Fig. 1 Changes in mean, minimum, and maximum annual temperature (temp), total annual precipitation (precip), actual evapotranspiration (AET), and climatic water deficit (CWD) across California during the 20th century. Estimates of change for all variables are based on differences between historical (1900–1939) 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.

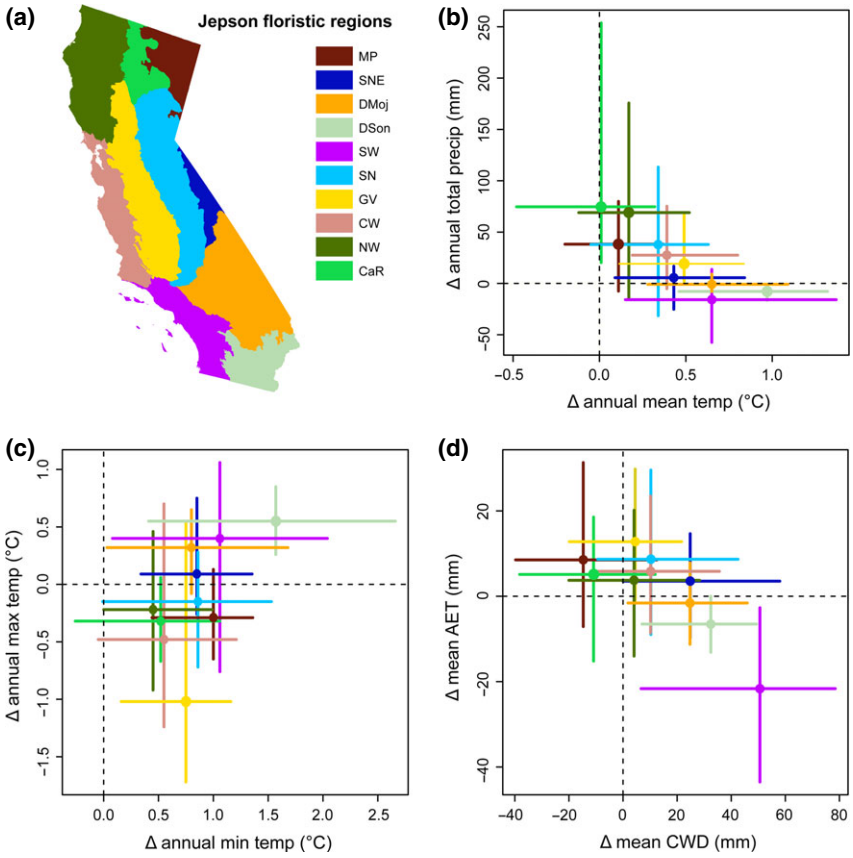

Fig. 2 Regional patterns of 20th century climate change among biogeographic units of California. (a) Map of the 10 Jepson Floristic Regions – a widely used phytogeographical classification of California (Baldwin *et al*., 2012). Scatter plots of (b) change in annual total precipitation (mm) against change 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.

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

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 in 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
Total 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

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 cooccur (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 vs. downslope shifts with historical elevation (Fig. 3b). Instead, we found that plants and birds shifted more downslope than upslope at higher historical elevations (Fig. 3b). 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 nonclimate factors are dominant drivers, especially at middle to high elevations in birds, mammals and plants (but see Forister *et al.*, 2010 for butterflies).

Are detected biogeographic responses consistent with a warming fingerprint?

The scarce coverage of biogeographic responses across a number of California's regions precludes attributing patterns of biogeographic change (Fig. 3) to regional

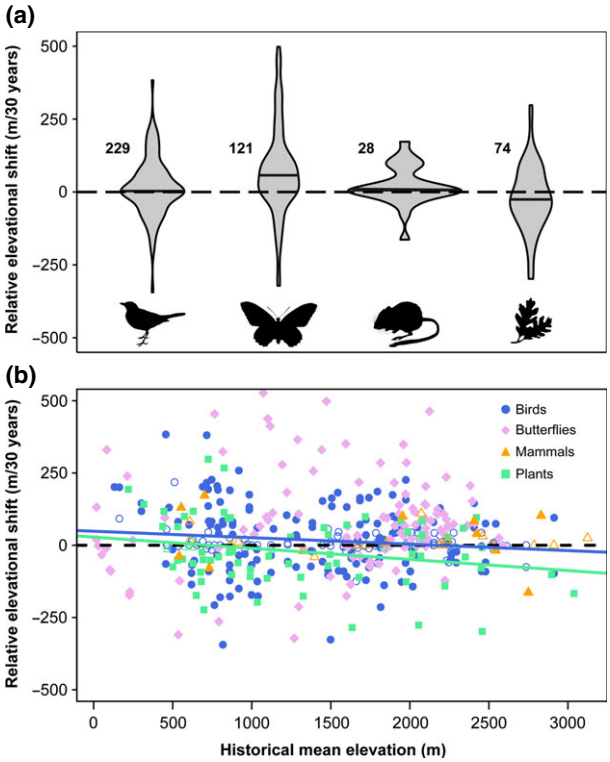

Fig. 3 Relative elevational shifts during the 20th century from published studies of birds (Tingley *et al.*, 2012), butterflies (Forister *et al.*, 2010), mammals (Moritz *et al.*, 2008) and plants (Kelly & Goulden, 2008; Crimmins *et al.*, 2011) in California. Estimates of elevational shift and historical 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 yr^{-1}) 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 yr^{-1}) against mean historical elevation (m) for the four taxonomic groups. Closed symbols refer to significant shifts and open symbols refer to nonsignificant 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 Integration and Application Network at the University of Maryland Center for Environmental Science (www.ian.umces.edu/imagelibrary).

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

A number of biogeographic responses in California are consistent with a warming fingerprint. Significant shifts to higher elevations – particularly contractions of the lower limits of high-elevation species – have been documented across a range of taxonomic groups, including mammals (Epps *et al.*, 2004; Larrucea & Brussard, 2008; Moritz *et al.*, 2008), birds (Tingley *et al.*, 2012), butterflies (Forister *et al.*, 2010, 2011a), and plants (Kelly & Goulden, 2008; Crimmins *et al.*, 2011; Kopp & Cleland, 2014). These upslope shifts toward cooler, higher-elevation locations have been primarily attributed to increases in temperature, although studies generally have not explicitly modeled the underlying mechanisms responsible for the shifts. Comparing site occupancy models of historical and modern elevational ranges for 28 small 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, although they did not test for this relationship statistically. Subsequent studies 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 (2014) 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 (2014) 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.

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

A complete assessment of the mechanisms 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. Regional patterns suggest that mean temperature has not increased everywhere in California (Figs 1a and 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., semiarid treelines in the Central Sierra Nevada; Fig. 1a and 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 and 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 (Figs 1 and 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 Fig. 3. This occurs because precipitation generally increases while temperature decreases with elevation in temperate 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 statistical relationship between CWD shifts and elevational shifts (Hijmans, 2011; Stephenson & Das, 2011; Wolf & Anderegg, 2011; but see Dobrowski *et al.*, 2011 for a response).

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, 2014). 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. For instance, 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). Furthermore, mammals with large body sizes and short activity times are more likely to respond to climate change (McCain & King, 2014). 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, nonruderal 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*. (2011a) 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: toward 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 CO_2 concentrations. Increased CO_2 levels interact with freezing tolerance (Dole *et al.*, 2003) and lead to enhanced water use efficiency for many plants (Wullschleger *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), 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 toward 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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Supporting Information

Additional Supporting Information may be found in the online version of this article:

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.

