

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

**Running head:** Beyond a warming fingerprint

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## Abstract

Understanding and predicting biogeographic responses to climate change is fundamental for guiding policy decisions at both local and global scales. Studies of observed biogeographic responses to 20<sup>th</sup> century climate change have principally examined effects based on increases in mean temperature – a warming fingerprint. Although the importance of changes in additional 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 concurrent changes in hydric conditions 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 20<sup>th</sup> century and review empirical evidence of biogeographic responses to these changes. We demonstrate that many responses to climate change across taxa are not consistent with a warming fingerprint. Instead, they may be explained by additional dimensions of climate change, such as the shifting seasonal balance of temperature and water availability. We identify a number of potential direct and indirect climate change mechanisms for these responses of particular relevance to regions with climatic profiles similar to California (e.g. other Mediterranean biomes). We highlight the need to move beyond a warming fingerprint in studies of biogeographic responses by: (i) considering a more multifaceted view of climate, (ii) emphasizing local scale effects, and (iii) including *a priori* knowledge of relevant natural history.

## 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.

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) mean temperature increase has 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 climatic aspects (Buckley *et al.*, 2012); (iii) mean temperature exhibits a nearly linear decline with both elevation and latitude, facilitating explanations and predictions of broad geographical responses to mean temperature compared to other climatic aspects (De Frenne *et al.*, 2013). As a result, hypotheses based solely on increasing mean temperature have been used to find evidence of a climate change fingerprint 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 such a

“warming fingerprint” may not be sufficient to identify the complexity of biotic responses to climate change (Dobrowski *et al.*, 2013; Staudinger *et al.*, 2013).

The importance of additional components of climate change on biological systems – particularly changes in precipitation and water availability – is widely acknowledged from a theoretical standpoint (Bellard *et al.*, 2012), but overall efforts to detect recent responses to these changes have been relatively few compared to responses to temperature changes (but see e.g. Jin & Goulden, 2013). As a result, we lack a practical understanding of how parallel changes in various climatic conditions interact in a biogeographic context (Bonebrake & Mastrandrea, 2010; McCain & Colwell, 2011; Dobrowski *et al.*, 2013). Yet, there is considerable evidence that species responded individually to changes in temperature and precipitation during the Pleistocene, producing range shifts more complex than expectations from temperature changes alone (Davis & Shaw, 2001). Recent studies have also highlighted how projected precipitation changes are likely to modify the individual effect of ongoing temperature increase on the distribution and abundance of global biodiversity along latitudinal (Bonebrake & Mastrandrea, 2010) and altitudinal (McCain & Colwell, 2011) gradients. In this paper, we describe how various components of climate have changed regionally in California during the 20<sup>th</sup> century and review empirical evidence of biogeographic responses to these changes. Specifically, we examine: (i) whether detected responses are consistent with a warming fingerprint; (ii) if not, whether additional components of climate change explain responses that are inconsistent with warming; and (iii) whether we can identify the potential mechanisms through which various components of climate change interact to drive local biogeographic responses.

California offers a unique opportunity to understand the effects of simultaneous changes in different components of climate on the distribution and abundance of populations and

118 communities. First, the mediterranean-type climate of California is inherently heterogeneous and  
119 presents large variation in both temperature and precipitation extremes. In particular,  
120 precipitation and associated water availability patterns play a key role in determining species'  
121 distributions (Raven & Axelrod, 1978; Stephenson, 1998; Barbour *et al.*, 2007; Jin & Goulden,  
122 2013). Second, California's large latitudinal span and complex topography present a diversity of  
123 environments, with the consequence that species can find radically different habitats within short  
124 distances (Ackerly *et al.*, 2010). Third, California has experienced substantial spatial and  
125 temporal variability in both temperature and precipitation (means and variances) over the 20<sup>th</sup>  
126 century, and the rate of change is predicted to increase in the coming decades (Moser *et al.*,  
127 2012). Fourth, California represents a biologically meaningful region. The state comprises the  
128 bulk of the California Floristic Province (CFP), which is listed among the 25 most diverse and  
129 endangered terrestrial biodiversity hotspots in the world (Myers *et al.*, 2000). It should be noted,  
130 however, that the boundaries of the CFP differ slightly from the state's political boundaries: the  
131 Great Basin and deserts east of the Sierra Nevada fall outside the CFP while parts of Oregon,  
132 Nevada and Baja California fall inside it. In this paper, we used California's political boundaries  
133 due to data constraints. Finally, the extremely diverse flora and fauna of California are amongst  
134 the best-studied in the world, owing to a long tradition of natural history recording and  
135 collection. One of the benefits of such long tradition is the existence of historical baselines dating  
136 back to the early 19<sup>th</sup> century – in the form of historical surveys, museum specimens,  
137 photographs and field notes (Tingley & Beissinger, 2009) – against which the current state of  
138 biological systems can be compared. Recent efforts to re-survey historical sites and transects  
139 have enabled the detection of significant changes to biological systems in California over the

140 20th century (Kelly *et al.*, 2005; Kelly & Goulden, 2008; Moritz *et al.*, 2008; Tingley *et al.*,  
141 2009; Crimmins *et al.*, 2011).

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## 20<sup>th</sup> century climate change in California: more than warming

The climate of California has experienced dramatic long-term changes during the 20<sup>th</sup> century that have been linked with both anthropogenic sources and natural climate cycles (Moser *et al.*, 2012). We examined patterns of 20<sup>th</sup> 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) to calculate differences between means across the years 1900–1939 (i.e. historical time period) and 1970–2009 (i.e. modern time period) for each variable (Figure 1; see Appendix S1 for detailed methods). We focused on these six climatic variables because they reflect physiological limiting factors that largely determine 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 available water, respectively (Stephenson, 1990; see “*Mechanisms through which various components of climate change interact to drive biogeographic responses*” subsection for a more detailed description). These variables were calculated by integrating seasonal measurements of climate (temperature and precipitation) and meteorological variables (snow melt, solar radiation, vapor pressure deficit, and wind) with soil properties, and reflect the concurrent availability of both water and energy (Flint *et al.*, 2013). To better visualize regional patterns of climate change, we grouped individual pixels in California according to Jepson Floristic Regions (Baldwin *et al.*, 2012; Figure 2a) – a widely used phytogeographical classification of California – and 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, and (iii) change in mean AET against change in mean CWD (Fig. 2*c*).

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 was accompanied by large spatial heterogeneity in change (Fig. 1*a*; Fig. 2*b*). California's deserts, Central Valley and urban areas warmed greatly, while parts of the Cascade ranges and Northwestern California 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 (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 Deserts; 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 Deserts and Southwestern California, 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.

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 in California during the 20<sup>th</sup> century. Three main patterns are evident. First, although mean temperature generally increased across all regions, changes in precipitation patterns separate regions in the climate space of Figure 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, while region-specific trends can be identified, there is great heterogeneity 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 20<sup>th</sup> century in the United States demonstrates huge variation in rates, directions and changes through time (Dobrowski *et al.*, 2013).

## Biogeographic responses to 20<sup>th</sup> century climate change

To provide a composite view of documented biogeographic responses to 20<sup>th</sup> century climate change in California, we reviewed 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 20<sup>th</sup> 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 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, each estimate of elevational shift we report does not necessitate individual dispersal along elevational gradients over time, but could also 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). We accounted for the effect of study time period on the magnitude of shift by quantifying shifts in elevational range (m) relative to the shortest study time period (30 years; Kelly & Goulden, 2008). We used all estimates provided by the underlying studies in our analysis, including shifts for individual

species that were deemed to be statistically insignificant, and indicated whenever their removal 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 higher 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, with the exception 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) have been found to account for a portion of detected 20<sup>th</sup> century biogeographic responses. In California, anthropogenic land-use change has been linked, together with climate, with elevational shifts in Belding's ground squirrels (Morelli *et al.*, 2012), and many species of butterflies (Forister *et al.*, 2010). Furthermore, recent evidence supports a significant influence of competitive species 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

larger number of species co-occur (Millar *et al.*, 2004). On the other hand, 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 a slight but significant increase in the magnitude of downslope shift with historical elevation in plants and birds (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 do not have 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).

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

A number of biogeographic responses in California are consistent with expectations based solely on the general trend of increasing mean temperature (i.e. 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: mammals (Epps *et al.*, 2004; Larrucea & Brussard, 2008; Moritz *et al.*, 2008), birds (Tingley *et al.*, 2012), butterflies (Forister *et al.*, 2010, 2011), and plants (Kelly & Goulden, 2008; Crimmins *et al.*, 2011; Kopp & Cleland, 2013). These upslope shifts towards cooler higher-elevation locations have been primarily attributed to increases in mean 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 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 (*Uroditellus 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 mean 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 elevational range 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 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 together 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, 2013). 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 20<sup>th</sup> 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). However, the composition of ecological communities during the 20<sup>th</sup> century along parts of the Sierra Nevada has remained largely unchanged in mammals (Moritz *et al.*, 2008) and trees (Dolanc *et al.*, 2013).

**What components of climate change could explain biogeographic responses inconsistent with warming?**

Heterogeneous biogeographic responses to climate change may be partly explained by changes in temperature alone (e.g. Pinsky *et al.*, 2013). Regional patterns suggest that mean temperature has simply not increased everywhere (Fig. 1a; Fig. 2a) and downward shifts in elevation may be expected where temperature has decreased. At local scales, warming temperatures can also lead to downward movement of species into low-lying areas impacted by temperature inversions (see Langan *et al.*, 1997 on physiological effects of freezing events caused by temperature inversions).

Even in warming regions, a portion of biogeographic responses inconsistent with increased temperature may be explained by changes in climate alone if our traditional temperature-centric view is expanded (McCain & Colwell, 2011). In particular, climate change could result in more complex and heterogeneous shifts if changes in precipitation and water availability are considered alongside temperature changes (Crimmins *et al.*, 2011; Stephenson & Das, 2011; Tingley *et al.*, 2012; Dobrowski *et al.*, 2013). While temperature decreases with elevation in montane systems, precipitation generally increases. One consequence of these elevational trends is that numerous subalpine tree species are limited by temperature at their high-elevation range limit and moisture at their low-elevation limit (Salzer *et al.*, 2009). Thus, if species track their climatic niches over time, increased temperature should promote upslope shifts. However, if species are more constrained by their precipitation niche axis, increased precipitation may counteract the effects of temperature and result in a downslope shift (Tingley *et al.*, 2012). Two recent papers suggest that this may explain part of the detected heterogeneity in species' elevational shifts. Tingley *et al.* (2012) showed that the downward shifts they

detected for many bird species were consistent with site-level increases in precipitation shifting precipitation-based niches downslope. Similarly, Crimmins *et al.* (2011) indicated that some of the downward shifts they observed in plant species' optimum elevations may be explained by species tracking regional decreases in climatic water deficit (CWD, explained in detail below) resulting from increased precipitation rather than temperature. Nevertheless, some of the conclusions of Crimmins *et al.* (2011) have been questioned (Dobrowski *et al.*, 2011; Hijmans, 2011; Stephenson & Das, 2011; Wolf & Anderegg, 2011).

There are several important considerations when examining biogeographic responses to changes in precipitation and water availability. First, plant water availability not only depends on precipitation, but also topography, edaphic variables and localized weather conditions (Stephenson, 1990, 1998; Flint *et al.*, 2013). As a result, the general increase in precipitation with elevation does not always translate to an increase in water availability along a given elevational gradient. Second, unlike temperature changes, changes in water availability should not necessarily be expected to cause coordinated directional changes across a large number of species (Stephenson & Das, 2011) – such as primarily downward shifts (Crimmins *et al.*, 2011). This occurs because the effect of a given change in water availability does not counteract that of an equal change in temperature; the two variables have nearly orthogonal effects and should be viewed as interacting, rather than opposing each other, along ecological gradients (Stephenson, 1998). Nonetheless, parallel 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 downward shifts (Crimmins *et al.*, 2011; Dobrowski *et al.*, 2011; Stephenson & Das, 2011; Tingley *et al.*, 2012). In the next section, we explore potential

437 mechanisms through which temperature, precipitation and water availability may interact to  
438 drive individualistic biogeographic responses in plants and animals.

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## **Mechanisms through which various components of climate change interact to drive biogeographic responses**

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). Indeed, it makes little sense to consider changes in energy and water independently. Plants require water in order to use available energy for photosynthesis and growth; otherwise, energy will only contribute to heat and physiologically stress the plants. Similarly, energy must be available for plants to use water for growth, or the water will remain unused (Stephenson, 1990, 1998).

The climatic water balance summarizes how energy represented by potential evapotranspiration (PET; the evaporative and transpirational water loss from a site supplied with unlimited water) – interacts with available water (W), which is the amount of liquid water usable by plants (see Stephenson, 1990 for a comprehensive review). The interactions between PET and W are described using three parameters: (i) actual evapotranspiration (AET), the evaporative water loss from a site covered by a standard crop, given the prevailing water availability; (ii) climatic water deficit (CWD), the evaporative demand not met by available water; and (iii) climatic water surplus (CWS), the excess water in the environment (Stephenson, 1990). The relationship among water balance parameters can be expressed using two equations:  $W = AET + CWS$ , which describes the conservation of water, and  $PET = AET + CWD$ , which describes the conservation of energy (Stephenson, 1990). These parameters are integrated over the course of the year and therefore, unlike annual means, take into account the shifting seasonal balance of energy and water availability over time.

482           The two climatic water balance parameters AET and CWD have a direct influence on  
483 plant recruitment and mortality, and appear to be better correlates of the elevational distribution  
484 of vegetation types than temperature and precipitation means (Stephenson, 1998). Moreover,  
485 there is growing evidence that changes in these climatic water balance parameters have also been  
486 primary drivers of changes in recruitment and mortality rates of tree species during the 20<sup>th</sup>  
487 century (Lloyd, 1997; Lloyd & Graumlich, 1997; Millar *et al.*, 2004; Guarín & Taylor, 2005;  
488 Van Mantgem & Stephenson, 2007; Lutz *et al.*, 2009; Salzer *et al.*, 2009; Das *et al.*, 2013;  
489 Dolanc *et al.*, 2013). For any given region, the effects of AET and CWD on the demographic  
490 rates of trees depend on whether energy or water have been the most important limiting factors  
491 and whether limiting factors have changed over time (Das *et al.*, 2013). For instance, in  
492 principally energy-limited regions where energy input and water availability have both increased  
493 – such as semi-arid treelines in the Central Sierra Nevada (Fig. 1a, d) – some tree species have  
494 benefitted from an extended growing season, resulting in increased recruitment (Millar *et al.*,  
495 2004; Dolanc *et al.*, 2013) and increased growth rates (Millar *et al.*, 2004; Salzer *et al.*, 2009).  
496 Reduced snow cover due to higher temperatures at high elevations may also have negative  
497 impacts on tree seedlings, as it exposes seedlings to cold early spring air temperatures and earlier  
498 runoff and evaporation of water supplies. Conversely, recruitment has decreased (Lloyd, 1997;  
499 Lloyd & Graumlich, 1997) or remained stable (Van Mantgem & Stephenson, 2007) in  
500 principally water-limited regions where energy input has increased but water availability has  
501 either remained stable or decreased (e.g. low elevation mountainous regions in the Southern  
502 Sierra Nevada; Fig. 1a, d). Regardless of historical limitations, large temperature increases –  
503 even without decreases in precipitation – appear to have induced local increases in CWD during  
504 the 20<sup>th</sup> century (Fig. 1 and Fig. 2), contributing to reduce performance of certain tree species

(Lutz *et al.*, 2010) and increase the mortality of old-growth trees (Guarín & Taylor, 2005; Van Mantgem & Stephenson, 2007; Lutz *et al.*, 2009; Dolanc *et al.*, 2013). Moreover, studies have also reported discordant responses among taxa within regions, providing support towards species-specific tolerances of climatic water balance parameters (Lutz *et al.*, 2009; Dolanc *et al.*, 2013).

The implications of parallel changes in temperature and precipitation on animals are less well known. Animals could be responding to these changes directly, through physiological limiting mechanisms, or indirectly, by tracking climate-induced shifts in vegetation. A growing body of research indicates that the effects of parallel 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) identified a strong link between shifts in bird range limits and climate-induced shifts in net primary productivity during the 20<sup>th</sup> century. In a subsequent paper, Tingley *et al.* (2012) found that traits related to breeding site fidelity, rather than dispersal ability, best predicted range shifts in birds. This suggests that nest-site selection, rather than the physical ability to track climatic conditions, limits 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 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 a number of species (Rubidge *et al.*, 2010). In addition, increases in body size in high elevation ground

squirrels were linked to increased resource availability and a longer feeding season (Eastman *et al.*, 2012).

Nevertheless, there is also evidence of direct physiological effects of parallel changes in temperature and precipitation on animals, although it is scarcer than evidence for the direct effects of temperature. For instance, 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*) and thus largely explain 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. The detected responses of animals to climate change likely stem from a combination of direct and indirect mechanisms, though disentangling the two is notoriously difficult (Morelli *et al.*, 2012). Building direct mechanistic models of physiological constraints (Kearney & Porter, 2009) may help address this problem in the future.

## **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 mean temperature (Parmesan & Yohe, 2003). In particular, individualistic biogeographic responses to 20<sup>th</sup> century climate change in California appear to have been driven by more than just temperature – particularly the shifting seasonal balance of temperature and precipitation – mirroring biotic responses during the Pleistocene (Davis & Shaw, 2001). 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. These mechanisms should be particularly, but not exclusively, relevant to regions with climatic profiles similar to California (e.g. other Mediterranean biomes), where changes in the seasonal balance of energy and water availability are likely to play a major role in controlling biogeographic responses. 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.

First, a fingerprint of *climate* change requires an understanding of climate beyond temperature, because populations respond to concurrent changes in various aspects of climate. Accounting for changes in the shifting balance of temperature and precipitation represents an accessible additional step to broaden our traditional temperature-centric view. For plants, using changes in climatic water balance instead of simple annual means of temperature and/or precipitation appears to be a natural solution for making hypotheses about biogeographic responses to climate change. Stephenson & Das (2011) present a theoretical model for predicting the effects of changes in the climatic water balance parameters AET and CWD on species' elevational ranges. Their model involves mapping elevation onto the environmental space defined by AET and CWD, so that changes in those parameters can be translated into expectations of elevational shift. Although this theoretical model was advanced by Stephenson & Das (2011) – in a comment to Crimmins *et al.*, (2011) – to demonstrate that changes in CWD

cannot result in coordinated directional changes in species' elevations, we believe that it could have a much wider impact and 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 be increasingly important to consider impacts of elevated CO<sub>2</sub> concentrations as well. Increased CO<sub>2</sub> 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, hypotheses should rest on identifying whether study populations are more likely to respond directly or indirectly to parallel 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 it experienced. 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, unlike a climate change fingerprint based exclusively on temperature, a fingerprint based on multiple aspects of climate may lead to alternative, occasionally opposing expectations (e.g. both upward and downward shifts, Tingley *et al.*, 2012). Unfortunately, this can create a situation where each biogeographic response can be construed to be consistent with a climate change fingerprint, as long as the climatic aspect that best explains the response is selected as the main hypothesized driver. To remain *coherent*, a climate change fingerprint should be chosen *a priori* based on aspects of climate of particular relevance to each study, such as the study region's natural and environmental history and the constraints underlying responses in the study system. This will ensure that hypotheses for identifying a climate change fingerprint are falsifiable and that such a fingerprint truly is able to diagnose climate change impacts on a given system within a given region. For example, Dobrowski *et al.* (2011) provide an example of a climate change fingerprint that improves on the widely-used warming fingerprint for each of the three areas we outlined. The authors hypothesize a mechanism which could drive downslope elevational shifts in plants: increases in AET and decreases in CWD may lead to increased survivorship of seedlings/saplings at low elevation sites with deep soils, which in turn may ameliorate regeneration opportunities in these historically water-limited sites. First, their hypothesis is based on a broad, physiologically-relevant view of climate change (i.e. changes in AET and CWD). Second, their hypothesis is local: it only applies to sites with particular features (i.e. low elevation and deep soils). Third, their hypothesis is based on *a priori* knowledge of the climatic factors historically most limiting for their study system and region (i.e. water limitation).

Examining recent (e.g. 20<sup>th</sup> century) responses is arguably the most effective way to improve our understanding of the likely impacts of future global climate change on populations and communities. A growing quantity of historical data are 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. Adopting a more multifaceted and local view 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 6 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

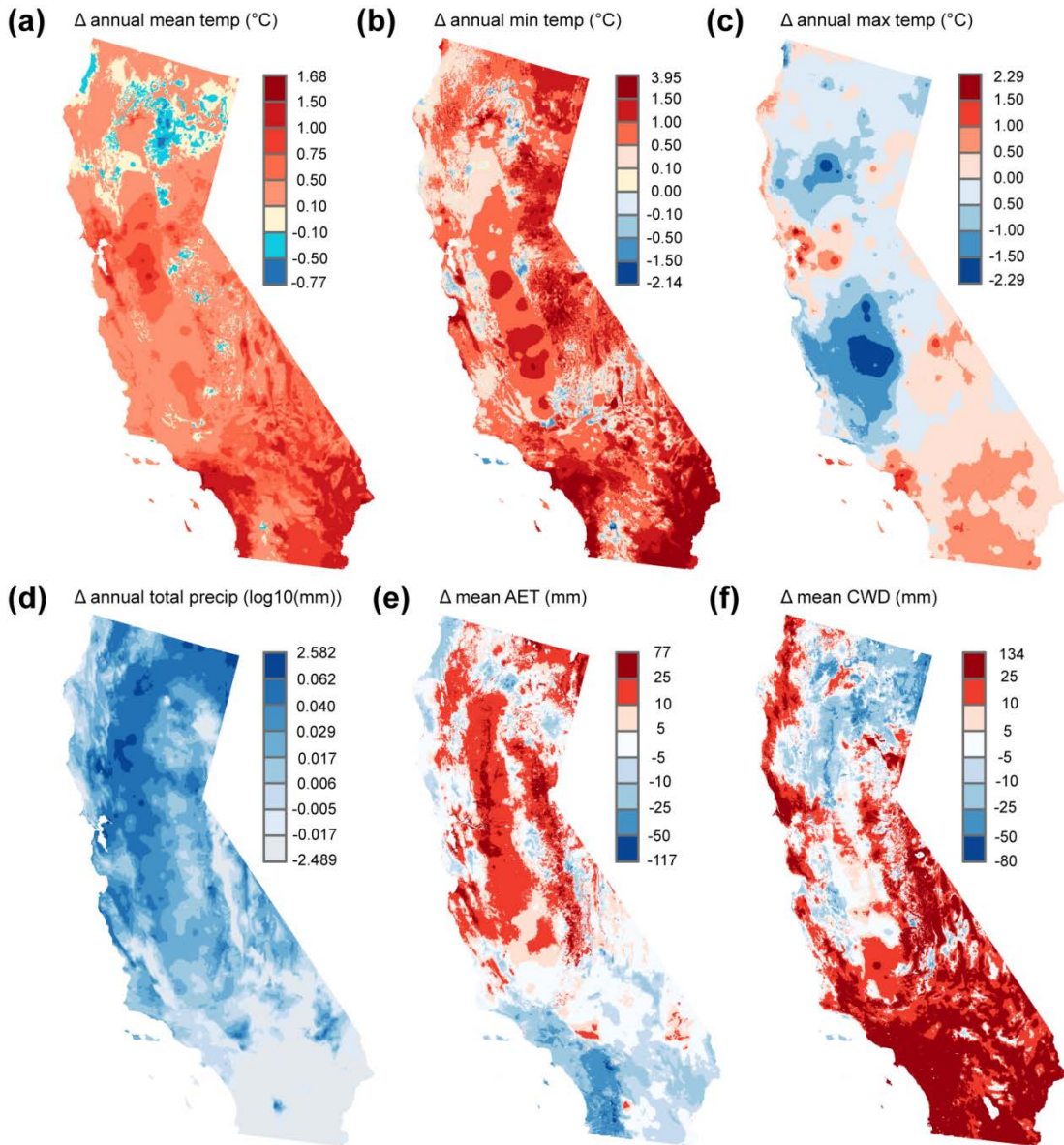
## Figure legends

**Figure 1.** Changes in temperature, precipitation, and climatic water balance parameters across California during the 20<sup>th</sup> 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.

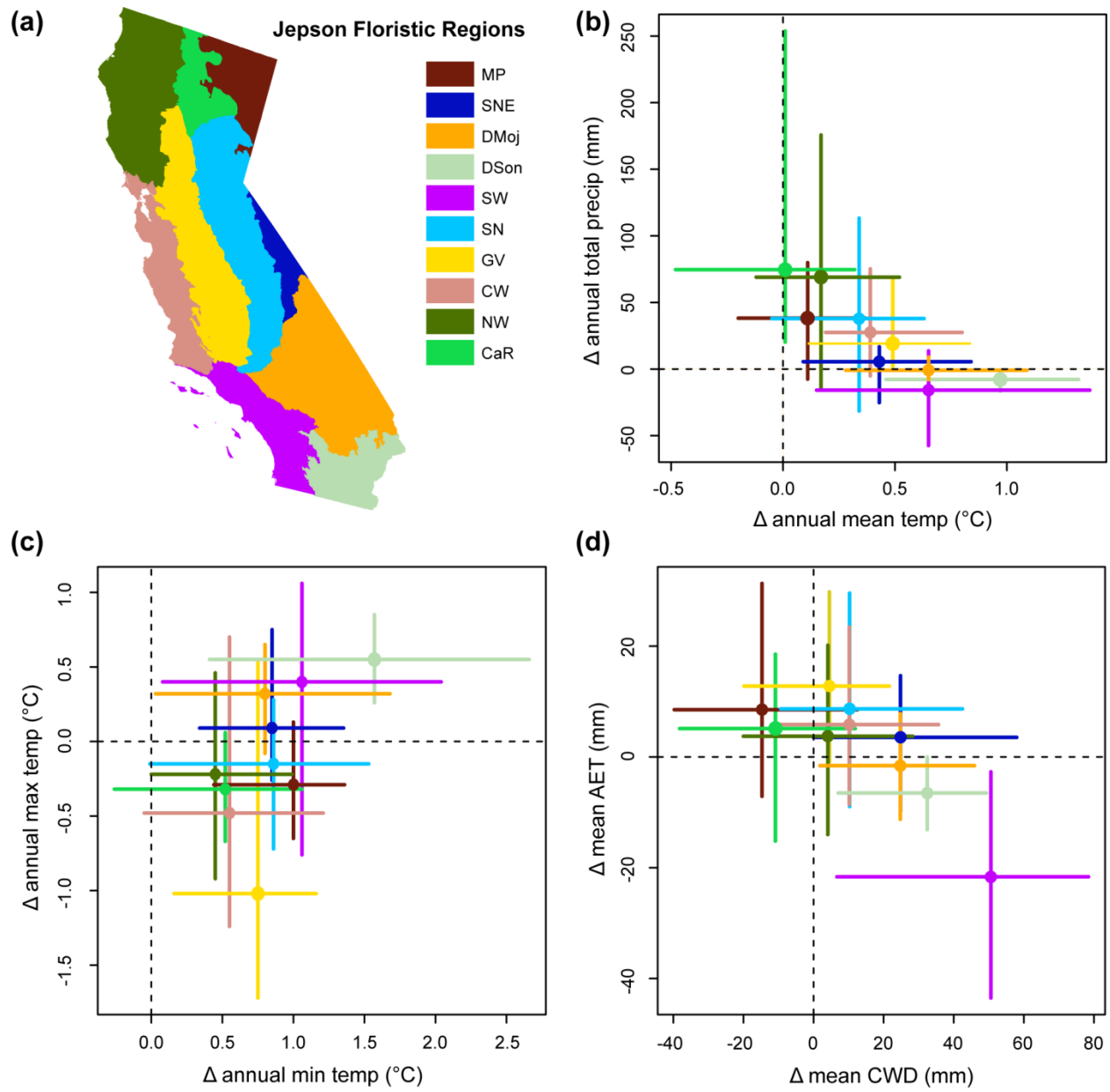
**Figure 2.** Regional patterns of 20<sup>th</sup> century climate change among biogeographic units of California. (a) Map of the 10 Jepson Floristic Regions – a widely used phytogeographical classification of California (Baldwin *et al.*, 2012). Scatter plots of (b) change in annual total precipitation (*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 AET (*mm*) against change in mean CWD (*mm*) across each Jepson Floristic Regions. Symbols represent the medians of all points falling within each Jepson Floristic Region, while arrows indicate 5<sup>th</sup>–95<sup>th</sup> 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 20<sup>th</sup> 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). 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 among (30 years; Kelly & Goulden, 2008). Analysis was limited to relative shifts between -500 and 500 m/30 years, which excluded 7 (5%) butterfly populations which shifted more than 500 m/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. All icons were obtained from the University of Maryland Center for Environmental Science ([www.ian.umces.edu/imagelibrary](http://www.ian.umces.edu/imagelibrary)). (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,  $t_{72} = -2.098$ ,  $p < 0.05$ ).

**Figures**

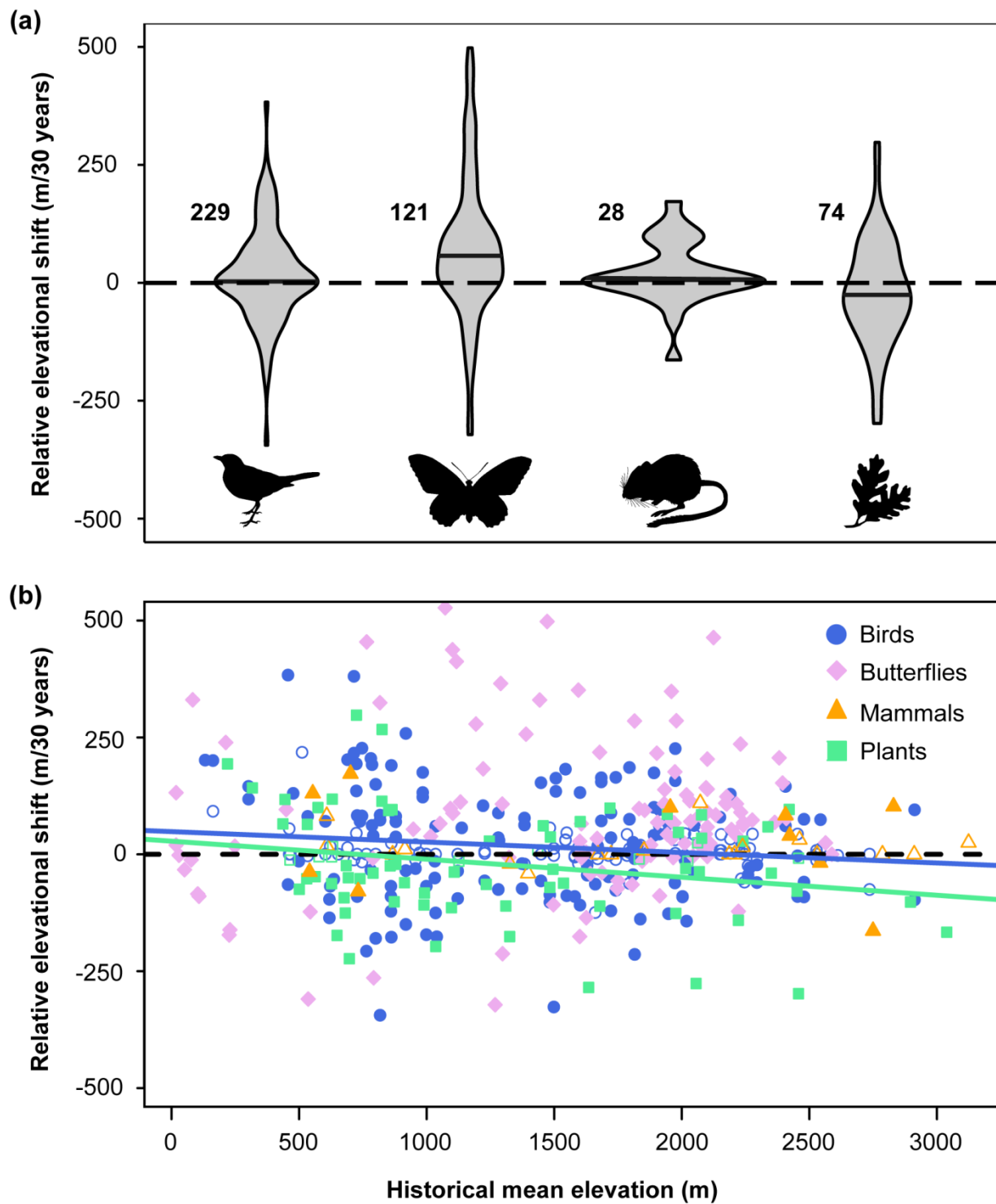


**Figure 1**



**Figure 2**





**Figure 3**