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Research Article

Lagged responses in the composition of small mammal communities to a century of climate change

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Climate change has widespread effects on the distribution, abundance and behavior of species around the world, leading to the reshuffling of ecological communities. However, it remains unclear whether individual species' range shifts scale up to result in communities whose rate of change lag, lead, or track the rate of climate change. We capitalized on a century-old dataset originally collected by Joseph Grinnell and his students, plus modern resurveys, to measure long-term compositional responses of small mammal communities to climate change in historical and modern eras across three regions in the Sierra Nevada of California (Lassen, Yosemite, Sequoia and Kings Canyon National Parks). Across this period, mean annual temperature in each region increased and mean annual precipitation decreased. We tested whether small mammal communities have shifted their composition in favor of species more adapted to hot and dry conditions, processes known as thermophilization and negative mesophilization, respectively. We found positive thermophilization rates (communities composed of more warm-adapted species) in one of three regions, and negative mesophilization rates (communities composed of dry-adapted species) in one of the three regions. We show that region-specific colonization and extinction dynamics of warm-, cool-, wet- and dry-adapted species jointly drive thermophilization and mesophilization rates, highlighting that community change arises from both species gains and losses. Importantly, thermophilization and mesophilization rates within regions lagged behind corresponding rates of climate change on average by 0.39–1.40°C and 154–301 mm. Our results suggest that the net effects of climate change can be directional at the scale of the ecological community, despite variability in individual species responses to environmental change and the varied mechanisms that govern them. Communities, like many individual species, may already be out of equilibrium with ambient climate.

Keywords: biodiversity change, climate change, climate tracking, elevational gradients, mesophilization, thermophilization

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Introduction

Climate change has widespread effects on the distribution (Chen et al. 2011), abundance (Bowler et al. 2017), and behavior (Loe et al. 2016) of species around the world, leading to the reshuffling of ecological communities (Williams and Jackson 2007). The effects of climate change are particularly pronounced in montane ecosystems where compressed environmental gradients lead to rapid turnover in biodiversity across elevation (Sanders and Rahbek 2012, Graham et al. 2014). One prominent hypothesis to explain biodiversity responses to climate change is that species will track their preferred climate conditions by migrating to new areas with suitable climates (Colwell et al. 2008, Pecl et al. 2017). This climate-tracking hypothesis makes two predictions: 1) individual species exhibit range shifts concomitant with their climate preferences, and 2) ecological communities exhibit directional changes in composition, with increases in the relative abundances of species best-adapted to novel climate conditions at a site, and concurrent decreases in less-adapted species. In montane ecosystems, it is generally thought that species will move upslope to track preferred temperature regimes (Thuiller 2007, Feeley et al. 2012, Lenoir and Svenning 2015). However, there is mixed support for upslope climate-tracking in montane ecosystems. While many species have moved to higher elevation in recent decades (Chen et al. 2011, Mamantov et al. 2021, Vitasse et al. 2021), a considerable number have not shifted their elevational distributions or have migrated downslope (Rapacciuolo et al. 2014, Rubenstein et al. 2023). Given the variable responses of individual species to climate change, it remains unclear whether individual species' range shifts scale up to result in directional changes in the composition of entire communities.

Several processes can lead to directional or non-directional responses of montane communities to climate change. First, communities can display directional change despite idiosyncratic range shifts if overall effects of climate on the local community are strong (Devictor et al. 2012, Fadrique et al. 2018). For example, many communities are shifting in composition towards more warm-adapted and dry-adapted species, a process known as thermophilization and negative mesophilization, respectively (Feeley et al. 2012, Duque et al. 2015, Ramón-Martínez and Seoane 2024). These directional changes can result from upslope migration (Morueta-Holme et al. 2015), and selective extirpation of less-adapted species (Freeman et al. 2018). Second, communities can display non-directional change due to variable effects of dispersal limitation or biotic interactions on species range shifts. Dispersal limitation may limit the migration of species, leading to elevational distributions that are decoupled from preferred climate (Wen et al. 2022). Likewise, elevational changes in the strength of local biotic interactions such as competition can result in downslope, upslope, or no change in species ranges (Rubidge et al. 2011, HilleRisLambers et al. 2013, Alexander et al. 2015). If the majority of species respond to different environmental and biotic factors, the signature of climate change at the community-level may be obscured. Lastly, microclimate and behavioral buffering, and changes in the ecological niche, can influence thermophilization and mesophilization rates because species might persist in an environment despite changes in climate. For example, small mammals that burrow can mitigate increases in temperature by inhabiting a cooler and more stable environment (Riddell et al. 2021). Furthermore, local adaptations or environmental plasticity may lead to stable communities, especially for short-lived species (Lavergne et al. 2010, Veloz et al. 2012, DeMarche et al. 2018, Searing et al. 2023).

Three key factors have limited our understanding of how species' range shifts scale up to community-level outcomes. First, there is potential overemphasis on the role of temperature in driving species distributions, when other climatic factors such as precipitation may be important (Tingley et al. 2009, Ackerly et al. 2010). For example, while climate warming is expected to increase upslope migration of species, precipitation and water balance can facilitate downward migration (Lenoir et al. 2010). Second, long-term community assessments are rare. Despite the importance of long-term studies in furthering theory and understanding biodiversity responses to global change (Franklin et al. 1990, Kuebbing et al. 2018), the duration of most ecological research is around five years (Estes et al. 2018). Century-long studies are exceedingly uncommon but offer some of the best evidence for climate change's impact on biodiversity (Tingley et al. 2009, Morueta-Holme et al. 2015). Lastly, most research has focused on single elevational transects, although species have been shown to respond differently throughout their range (Tingley et al. 2012, Rapacciuolo et al. 2014; Rowe et al. 2015). These differences are likely driven by a combination of variable climate forcing and sub-population adaptation to environmental conditions.

In this study, we tested whether the composition of small-mammal communities has changed directionally over a century of climate change in three montane regions, and whether their rate of change tracks the rate of climate change. We capitalized on a century-old dataset originally collected by Joseph Grinnell and his students, plus modern resurveys, to measure long-term compositional responses of small mammal communities to climate change in historical and modern eras across three regions in the Sierra Nevada of California (Lassen, Yosemite, Sequoia, and Kings Canyon National Parks). In a previous study, Rowe et al. (2015; also cf. Moritz et al. 2008) estimated the historical and contemporary elevational ranges for small mammals across the Sierra Nevada of California, USA, using species survey data from sites originally sampled by Joseph Grinnell and his students in the early 1900s (Grinnell and Storer 1924, Grinnell et al. 1930, Sumner and Dixon 1953), and resurveys of the same sites from 2003 to 2011. Notably, the detail with which Grinnell recorded observations of animals, and the modern study design allowed the application of occupancy–detection modeling (MacKenzie et al. 2018) of data from both periods to remove bias from estimates of elevational ranges. Rowe et al. (2015) found no single species shifted their range in the same way across the three regions. We capitalize on this nearly century-old dataset, to explicitly test whether the net effects of climate change on small mammal communities are directional in the face of high variability in individual species' range shifts. We incorporate two aspects of climate, temperature and precipitation, to understand how ecological communities have changed over the past one hundred years. While mean annual temperature has increased, and mean annual precipitation has decreased, in all three regions between historical and contemporary surveys, rates of change have varied by region and elevation (Supporting information). Specifically, we test the prediction that small mammal communities are comprised of more warm-adapted and dry-adapted species after a century of climate warming and drying. We examine whether these shifts are driven by colonization or extinction of warm- and cool-adapted species, and dry- or wet-adapted species. Finally, we test whether community-level change in thermophilization and mesophilization rates has tracked the rate of climate change in temperature and precipitation.

Material and methods

We evaluated compositional responses of small-mammal communities using community-wide climate indices commonly used to study how ecological communities respond to climate change (Devictor et al. 2012, Feeley et al. 2013). To calculate these indices, we first used historical and modern species' elevational range data from three elevational transects to determine species composition at a site. Following other studies on thermophilization, we then averaged the preferred temperature and precipitation values of each species present at a site, estimated using the location of range-wide occurrence records for each species, to calculate a community temperature index (CTI) and community precipitation index (CPI) for historical and modern eras. We detail each of the steps below (Fig. 1).

Small mammal range data

Species' elevational range data for the 34 nonvolant small-mammal species in this study, namely rodents and lagomorphs, come from Moritz et al. (2008) and Rowe et al. (2015), and were generated as part of the Grinnell Resurvey Project (https://mvz.berkeley.edu/Grinnell/index.html) at the University of California's Museum of Vertebrate Zoology (https://mvz.berkeley.edu). Joseph Grinnell and his students surveyed California's small mammal and bird diversity, including sites across three transects spanning the elevational gradient in the Sierra Nevada (Grinnell and Storer 1924, Grinnell et al. 1930, Sumner and Dixon 1953). Oak woodland and chaparral dominate at low elevations, giving way to mixed coniferous forest at intermediate elevations, and alpine conditions at high elevations. Small-mammal composition was recorded from 1911 to 1934 and include 34 sites within and around Lassen National Park and National Forest in the southern Cascade range (northern region, 91–2487 m), 47 sites from Yosemite National Park (central region, 118–3419 m), and 53 sites from Sequoia and Kings Canyon

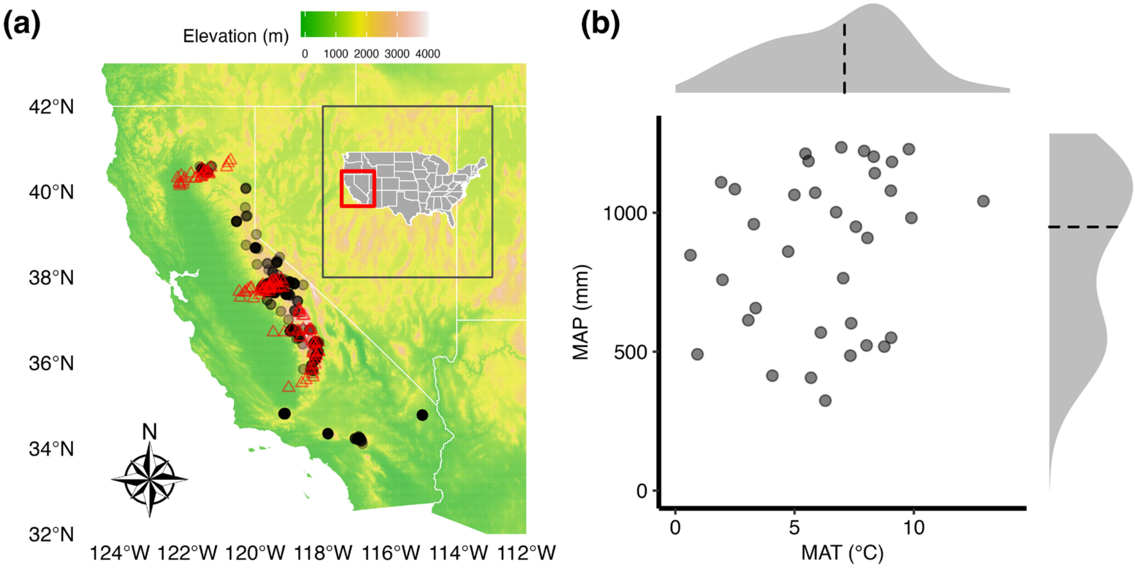

Figure 1. Methodology for calculating the community temperature index (CTI) and community precipitation index (CPI). (a) For each species (data for *Tamius speciosus* depicted here) we collected occurrence records from across the entire species range. Black circles represent occurrence records. Red triangles represent field sites along the three transects. The inset shows the study region within the United States. (b) We measured each species' preferred temperature and precipitation by taking the median mean annual temperature (MAT; dashed vertical line) and mean annual precipitation (MAP; dashed horizontal line), respectively, from the location of each occurrence (16-year averages, the year of plus the 15 years prior to collection). The CTI and CPI of each site, in each era, were measured as the mean of all preferred temperatures and precipitation regimes for each species present. Color shading in panel a) shows elevation (green = lower elevations; yellow/orange = higher elevations).

National Parks (southern region, 63–3292 m). Because east and west slope sites represent different habitats, we restricted our analyses to those sites on the western slope resulting in 26 sites in the northern region, 40 sites in the central region, and 40 sites in the southern region. Moritz et al. (2008) and Rowe et al. (2015) resurveyed these transects between 2003 and 2010, including 38 sites in Lassen, 81 sites in Yosemite, and 47 sites in Sequoia and Kings Canyon. Modern resurveys represent both successfully relocated historical plots and additional sites used as proxies for inaccessible historical locations. Using these data, Moritz et al. (2008) and Rowe et al. (2015) estimated the elevational range shifts (hereafter range shifts) of nonvolant, non-game small mammals across these three regions using occupancy-detection modeling to correct for the problem of non-detection (Moritz et al. 2008, Rowe et al. 2015). Details of the statistical analysis are presented in Rowe et al. (2015), but in summary form, elevational ranges were estimated by calculating the model-averaged probability of false absence at a site, conditional on presence of the species, within each site where a species was detected in one era but not the other (Supporting information). This method provides a robust estimate of the probability of elevation-dependent extirpation or colonization, while accounting for uncertainty in detectability parameterizations. Range shifts (i.e. colonization or extirpation) were considered to have occurred if the probability of false absence was less than or equal to 0.05 (Moritz et al. 2008, Rowe et al. 2015). We used the modeled historical and modern elevational ranges of nonvolant mammals in northern, central, and southern regions. Across sites, species richness ranged from a minimum of 1 species to a maximum of 17 species, with an average of 11.9 species per site.

Species climate preferences

We estimated the thermal and precipitation preferences for the 34 small-mammal species using occurrence data downloaded from the Global Biodiversity Information Facility (data DOI: 10.15468/dl.7x7sex). Thermal and precipitation preferences were estimated across the entire range of each species using climate data at the location of each occurrence record. Previous research using these methods typically use 30-year climate normals when assigning climate values to each record (Fadrique et al. 2018). We improve upon these methods by considering the exact year each record was collected, plus preceding years, which allows us to account for changes in climate at any given location. We first filtered all occurrences to those recorded as 'occurrence', or those representing collected specimens, and collected between 1901 and 2021. All records without latitude and longitude were removed. To remove spurious records, we used species' range maps from the IUCN (2018). For a given species, specimens located outside a buffer of 240 km around its range map were excluded. We chose a 240 km buffer because visual inspection indicated it provided a good balance of excluding outliers and including parts of distributions not reflected in range polygons. If coordinate uncertainty was not reported, occurrences were discarded unless the occurrence was found within the IUCN range map. All occurrences with coordinate uncertainty greater than 1000 m were excluded. Lastly, we excluded any occurrences with any remaining geospatial issues. Mean annual temperature (MAT) and mean annual precipitation (MAP) from 1901 to 2021 were extracted for each occurrence using ClimateNA software ver. 7.30 (Wang et al. 2016, Supporting information). The recorded temperature and precipitation for each occurrence was measured as the 16-year average (the year of collection, plus −15 years prior). We took the average of available years for occurrences without 15 years of available climate data (e.g. for records collected < 15 years after 1901). To remove biases resulting from uneven collection efforts we thinned the occurrences by keeping only one occurrence per 1 × 1-km grid. Species' thermal and precipitation preferences were estimated as the median temperature and precipitation of the 16-year averages of each record (Fig. 1). To account for outliers, we used the median temperature and precipitation of the inner 90th percentile to measure species' preferences. The final dataset used to measure species' thermal and precipitation preferences included 7465 occurrences across all species. Preferences varied considerably across species (Supporting information).

Community climate indices

For each historical site originally surveyed by Grinnell, we created a species-by-site matrix using presence/absence data for historical and modern eras. A species was deemed present if the site's elevation overlapped with the species' elevational range for each respective era. We measured the historical and contemporary community temperature index (CTI) and community precipitation index (CPI) at each of these sites as the mean of species' thermal and precipitation preferences, respectively, for all species present. Because our analysis utilized species presence/absence data (Rowe et al. 2015), changes in the community climate indices (CCI) at each site are the result of changes in species composition (as opposed to abundance). Thermophilization and mesophilization rates were calculated for each region separately by dividing the net change in the CTI and CPI by the average number of years spanning historical and modern surveys (northern = 80 years, central = 85 years, southern = 94 years). We used ClimateNA (Wang et al. 2016) and the same time spans to calculate changes in mean annual temperature (MAT) and mean annual precipitation (MAP) at each site (−15 years from historical and modern censuses, northern = 1929–2009, central = 1920–2005, southern = 1916–2010).

The role of colonization and extinction

We partitioned changes in community climate indices into colonization and extinction (Borderieux et al. 2024). Furthermore, we assessed whether colonization and extinction dynamics were governed by cool- or warm-adapted species for the CTI, and whether colonization and extinction dynamics were governed by wet- or dry-adapted species for the CPI. We applied a sequential two-step procedure: 1) an extinction step that removes historical species that are absent in contemporary sites, and 2) a colonization step that adds species absent historically but present in contemporary sites. The extinction contribution was calculated as the CCI (CTI and CPI) of persisters minus the CCI of historically present species (including persisters and those that were extirpated), while the colonization contribution was calculated as the CCI of the colonists minus the CCI of persisters. By construction, extinction plus colonization equals the total change in CCI. We defined species as cool- or warm-adapted and wet- or dry-adapted relative to the historical community at each site. Specifically, species were classified as warm-adapted if their temperature preferences were higher than the historical CTI for that site, and cool-adapted if it was lower. Likewise, species with precipitation preferences above or below the historical CPI were classified as wet- or dry-adapted, respectively. For each partition, we recomputed means after selectively removing (extinction) or adding (colonization) only the focal group, defining group-specific contributions as the difference from the historical (for extinction) or persister (for colonization) community mean.

Statistical analyses

All analyses were performed in R ver. 4.3.1 (www.r-project.org). Data tidying and formatting were performed using 'tidyverse' packages (Wickham et al. 2019). All spatial procedures used in cleaning the occurrence data utilized functions from the 'sf' package (Pebesma 2018). Code for the analysis is available at: https://github.com/EthanAbercrombie/Lagged-responses-in-the-composition-of-small-mammal-communities-to-a-century-of-climate-change.git. We used a two-tailed t-test to test whether communities in each region have thermophilization and mesophilization rates different from zero. To better meet assumptions of normality for these t-tests (Supporting information), we applied a composite sine-log transformation to thermophilization rates for the central region and to mesophilization rates in the northern and southern regions. To test for differences in thermophilization and mesophilization rates between regions, we used a one-way ANOVA (Supporting information). We evaluated whether small mammal communities were tracking climate by comparing changes in site MAT and MAP with changes in the CTI and CPI, respectively, using a paired Wilcoxon signed-rank test for each region. To evaluate whether the magnitude of site warming had an effect on the magnitude of change in the CTI, we used an ANCOVA with CTI change as the response variable, and MAT change, region, and the interaction between MAT change and region as predictor variables (Supporting information). To evaluate whether the magnitude of site drying had an effect on the magnitude of change in the CPI, we used an ANCOVA with CPI change as the response variable, and MAP change, region, and the interaction between MAP change and region as predictor variables (Supporting information). We used Wilcoxon signed-rank tests to assess whether extinction and colonization contributions differed significantly from zero. Tests were conducted separately for cool- and warm-adapted species in the CTI, and for wet- and dry-adapted species in the CPI.

Results

Climate change across regions and elevation

Over the past ~ 100 years mean annual temperatures have risen in all three regions (Fig. 2). On average, northern sites have risen 0.93°C, central sites 1.45°C, and southern sites 1.53°C. Temperature rose faster at higher elevations than lower elevations in all regions (Supporting information). Mean annual precipitation has decreased 255 mm on average in northern sites, 328 mm in central sites, and 171 mm in southern sites (Fig. 2). All sites showed elevation-dependent drying, with higher elevations experiencing the largest decreases in precipitation (Supporting information).

Community responses to climate warming and drying

Mean thermophilization rates differed significantly from zero in the northern region (Fig. 3, Supporting information). In the northern region, the mean thermophilization rate across sites was significantly greater than zero (6.80×10^{-3} °C year^{-1}, $t = 3.88$, $p < 0.001$) and positive in 85% of sites. In the central region, the mean thermophilization rate was not significantly different than zero (5.84×10^{-4} °C year^{-1}, $t = -0.95$, $p = 0.35$) and positive in 63% of sites. In the southern region, the mean thermophilization rate was not significantly greater than zero (3.20×10^{-3} °C year^{-1}, $t = 1.81$, $p = 0.08$) and positive in 63% of sites. Mean thermophilization rates did not differ significantly between regions (ANOVA, $F_{2,103} = 2.83$, $p = 0.06$).

Mean mesophilization rates only differed significantly from zero in the central region (Fig. 3, Supporting information). In the northern region, the mean mesophilization rate was not significantly different from zero (0.15 mm year^{-1}, $t = -0.99$, $p = 0.33$) and was positive in 69% of sites. In the central region, the mean mesophilization rate was significantly less than zero (−0.31 mm year^{-1}, $t = -3.45$, $p = 0.001$) and negative in 75% of sites. In the southern region, the mean mesophilization rate was not significantly different than zero (-0.01×10^{-3} mm year^{-1}, $t = -0.22$, $p = 0.83$) and was positive in 58% of sites. Mean mesophilization rates did not differ significantly between regions (ANOVA, $F_{2,103} = 2.50$, $p = 0.09$).

To evaluate whether negative mesophilization rates might be explained by high thermophilization rates (and vice versa), we examined correlations between species' climate preferences and between community climate-change responses (Supporting information). We found a weak negative correlation between species' temperature and precipitation preferences ($r = -0.32$, $p = 0.065$) and a stronger negative correlation between thermophilization and mesophilization rates across sites ($r = -0.50$, $p < 0.001$). Sites that thermophilized also experienced negative mesophilization.

Lagged responses of community composition to climate change

We observed significant lags in the CTI compared with changes in site MAT in all three regions (Fig. 4, Supporting

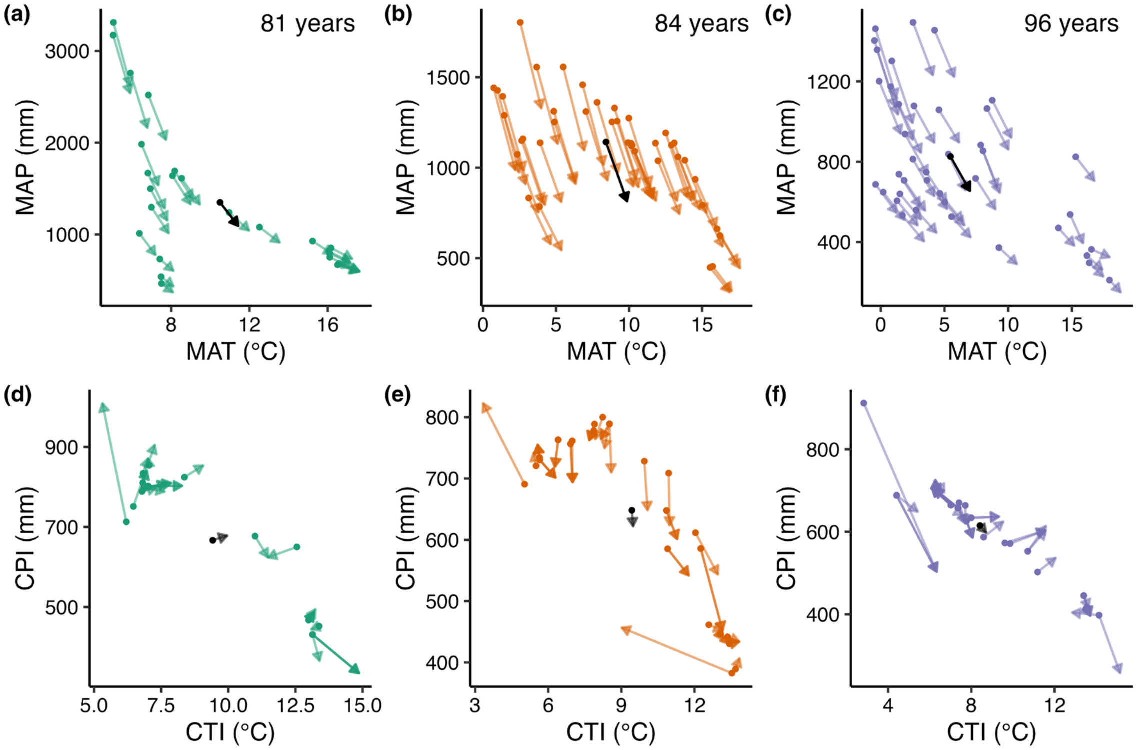

Figure 2. Climate vectors for site mean annual temperature (MAT) and mean annual precipitation (MAP) (a–c), and the community temperature index (CTI) and community precipitation index (d–f). (a, d) Northern sites (Lassen National Park and National Forest; 80 years: 1929–2009), (b, e) central sites (Yosemite National Park; 85 years: 1920–2005), (c, f) southern sites (Sequoia and Kings Canyon National Parks; 94 years: 1916–2010). Points represent historical values for each site while arrow tips represent contemporary climate. Black points represent the mean historical value while black arrow tips represent mean contemporary values. Nearly all climate vectors indicate sites have become hotter and drier.

information). In the northern region, the mean value of MAT changed by +0.93°C while the mean change in the CTI was +0.54°C ($V=276$, $p < 0.01$). In the central region, the mean change in MAT was +1.45°C while the mean change in the CTI was 0.05°C ($V=820$, $p < 0.001$). In the southern region, the mean change in MAT was +1.53°C while the mean change in the CTI was +0.30°C ($V=770$, $p < 0.001$). We observed no significant effect of region (ANOVA, $F_{2,100} = 1.27$, $p=0.29$), and no significant effect of MAT change ($F_{1,100} = 0.06$, $p=0.81$), or the interaction between MAT change and region on the change in the CTI ($F_{2,100} = 1.36$, $p=0.26$).

We observed significant lags in the CPI compared with changes in site MAP in all three regions (Fig. 4, Supporting information). In the northern region, the mean change in MAP was −255 mm while the mean change in the CPI was +11.64 mm ($V=8$, $p < 0.001$). In the central region, the mean change in MAP was −328 mm while the mean change in the CPI was −26.36 mm ($V=0$, $p < 0.001$). In the southern region, the mean change in MAP was −171 while the mean change in the CPI was −17.49 mm ($V=44$, $p < 0.001$). We observed a significant effect of region (ANOVA, $F_{2,100} = 4.49$, $p=0.01$), MAP change ($F_{1,100} = 9.44$, $p < 0.01$), and the interaction between MAP change and region on the change in the CPI ($F_{2,100} = 3.73$, $p=0.03$).

Relative contributions of colonization and extinction to thermophilization and mesophilization

We observed region-specific contributions of colonization and extinction dynamics to changes in the community temperature index and community precipitation index (Fig. 5, Supporting information). In the northern region, positive thermophilization rates were primarily driven by warm-species colonization and cool-species extirpations. CPI dynamics in this region were dominated by dry-species extirpation, and countered by dry-species colonization and wet species extirpation. In the central region, opposing cool- and warm-affinity processes contribute to low thermophilization rates. Negative mesophilization rates in this region were caused by the extinction of wet-adapted species, and colonization of dry-adapted species. In the southern region, thermophilization rates were caused by opposing extinction dynamics of cool- and warm- adapted species, and a positive effect of warm-species colonization. Mesophilization rates in this region were not significant, but we observed opposing extinction dynamics of wet- and dry-adapted species.

Discussion

Species range shifts in response to recent climate change has led to significant positive thermophilization rates in the

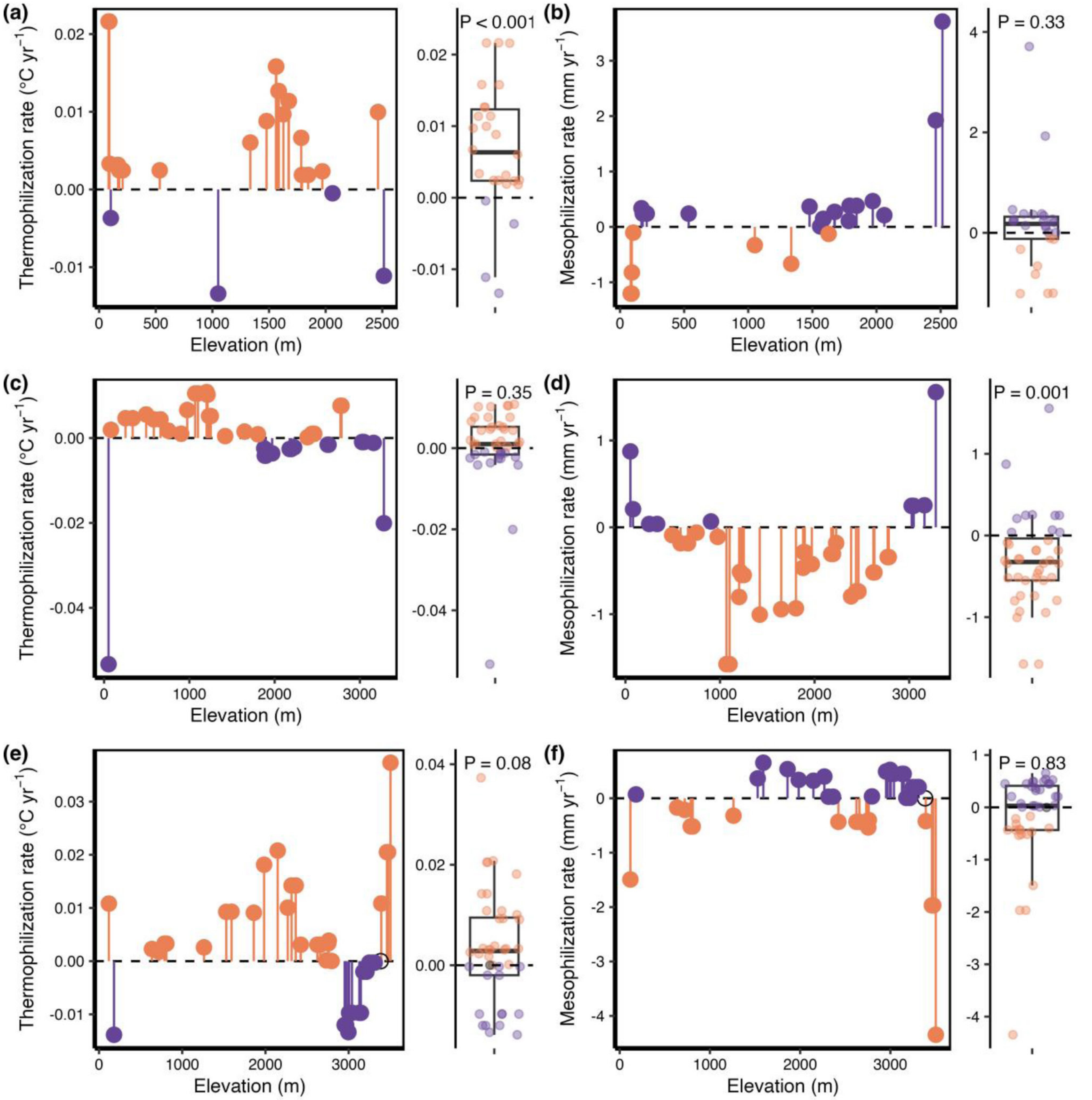

Figure 3. Thermophilization rates (°C year^{-1}) and mesophilization rates (mm year^{-1}) of small mammal communities at sampled sites in the three study regions across elevation. (a–b) Northern region (Lassen National Park and National Forest); (e, f) Central region (Yosemite National Park); (c–d) Southern region (Sequoia and Kings Canyon National Parks). Box plots show region-wide trends in thermophilization and mesophilization rates and p-values from two-tail t-tests. Each point in the boxplot corresponds to a point in the graph to the left of it. Colors represent communities displaying warming and/or drying (orange), cooling and/or wetting (purple), or no change in community climate indices (black open circle). Communities with thermophilization and mesophilization rates of 0 represent communities whose composition has not changed since original surveys.

northern region, and negative mesophilization rates in the central region. Importantly, the only region showing significant negative mesophilization did not show significant thermophilization, and vice versa, suggesting that while the two processes are partially correlated (Supporting information), distinct ecological factors are also driving regional patterns of community change. The composition of small mammal communities in the Sierra Nevada are not changing at a pace required to track climate change (Fig. 4). MAT increased, and MAP decreased, at all sites in our study (Fig. 2). Decomposing

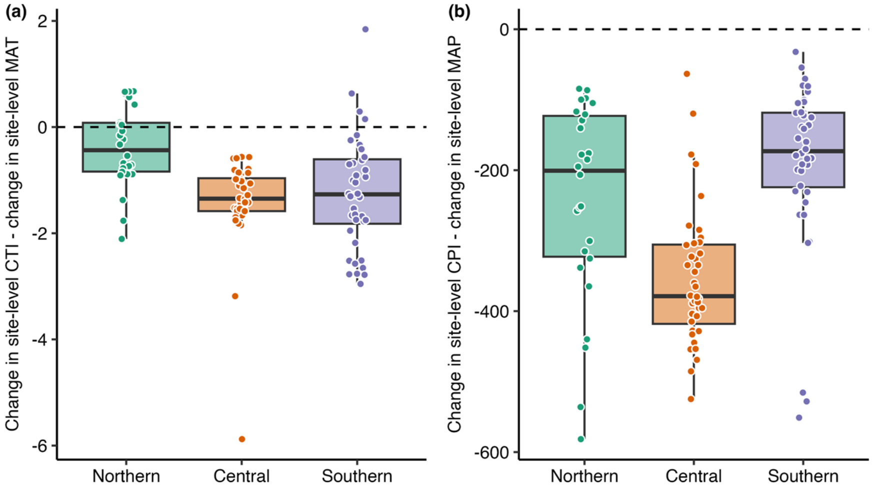

Figure 4. Lags between change in climate and community compositional change. (a) The difference between site temperature change (°C) and change in the CTI (°C). (b) The difference between site precipitation change (mm) and change in the CPI (mm).

changes in CTI and CPI into contributions from colonization and extinction, we found insignificant changes arose due to counterbalancing effects of these processes, whereas significant changes occurred when they operated in conjunction. Our study demonstrates that communities, like many individual species, may already be out of equilibrium with ambient climate.

Compared to the past, small mammal communities in the northern region of the Sierra Nevada are comprised of more warm-adapted species. Thermophilization rates for this region were comparable to previous research in other ecosystems (Table 1) on birds (Devictor et al. 2012, 2.6×10^{-3} °C year^{-1}), butterflies (Devictor et al. 2012, 9.3×10^{-3} °C year^{-1}), and plants (Cuesta et al. 2023, 7×10^{-3} °C year^{-1}, Fadrique et al. 2018, 6.6×10^{-3} °C year^{-1}). Furthermore, mesophilization rates were negative in the central region. These results suggest decreases in precipitation across the Sierra Nevada have also contributed to directional shifts in community composition. Two mechanisms can contribute to positive thermophilization and negative mesophilization rates: range expansions and range contractions. For example, high-elevation (cool/wet-adapted) species in the southern region including the alpine chipmunk *Tamius alpinus* and the Belding's ground squirrel *Urocitellus beldingi* have shown range contractions at the lower edge of their ranges (Rubidge et al. 2011, Morelli et al. 2012), while low-elevation (warm-/dry-adapted) species like the Californian pocket mouse *Chaetodipus californicus* show range expansions at their upper edges (Rowe et al. 2015). Both mechanisms, the expansion of low-elevation species and the contraction of high-elevation species, contribute simultaneously to the high thermophilization rates in the northern region and negative mesophilization rates in the central region at mid-elevations (Fig. 3).

Thermophilization and mesophilization rates were highly variable across sites within regions (Fig. 3). Biotic interactions, vegetation dynamics, and behavioral buffering are three mechanisms that can increase variation in thermophilization and mesophilization rates. For example, low- and mid-elevation species in Yosemite expanded their ranges by tracking suitable vegetation (Santos et al. 2015). The slow rates of thermophilization found in the central region might be due to the inability for mammals to shift their ranges because of a lack of suitable vegetation. Furthermore, low rates of thermophilization and mesophilization might be due to the behavioral buffering capacity of mammal species at a site, delaying extirpation. For instance, small-mammal communities in California's Mojave Desert were found to be largely stable over the past century (with only moderate turnover, ~ 2 species), despite increases in temperature, because of low physiological exposure to climate change through burrowing (Riddell et al. 2021). If mammals across elevation can behaviorally thermoregulate through microhabitat selection, species may not shift their ranges and thermophilization and mesophilization rates will be low.

Despite decreased species richness in the majority of sites (Supporting information), we observed a dynamic interplay between of both species colonization and extirpation in generating thermophilization and mesophilization rates (Fig. 5). Across sites, we observed a significant effect of cold-species extirpation and warm-species colonization on thermophilization rates. We observed a similar pattern for mesophilization rates whereby the extirpation of wet-adapted species and the colonization of dry-adapted species had negative effects. These findings illustrate that community change cannot be interpreted solely as colonization by warm- and dry-adapted species but also involve losses of cold- and wet-adapted specialists. Importantly, thermophilization rates lag behind temperature changes, and mesophilization rates lag behind precipitation change in all three regions (Fig. 4). Our analyses revealed a significant interaction between MAP change and region in models of region-wide mesophilization rates ($F_{2,100} = 3.73$, $p = 0.03$). These results suggest that varying responses across regions may be attributed to different climatic buffering capacities between regions, or may be more evident in systems

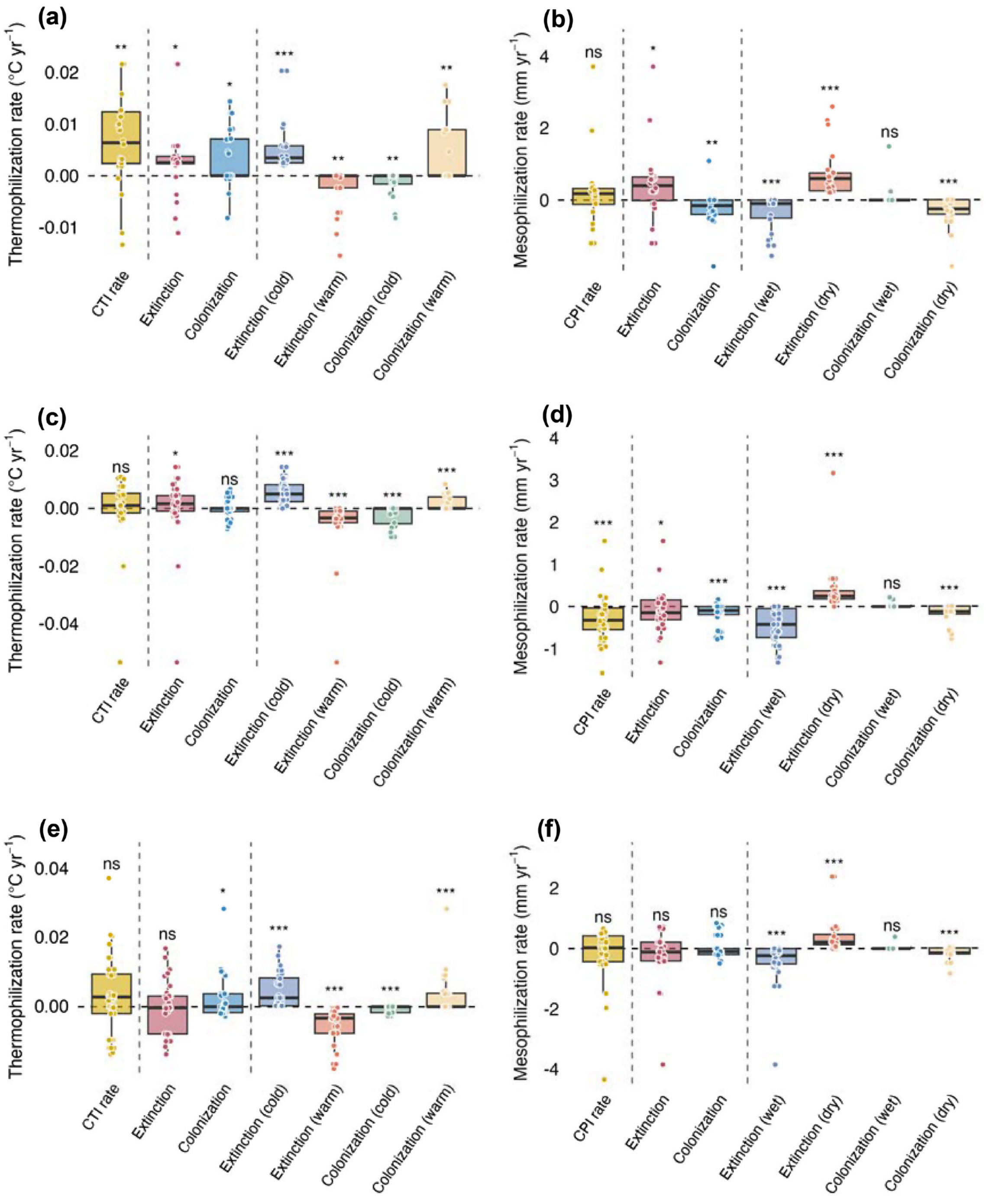

Figure 5. Contribution of colonization and extinction to thermophilization (a, c, e) and mesophilization (b, d, f) across the northern (a, b), middle (c, d), and southern (e, f) regions. In each subpanel, the leftmost boxplot represents the observed change in CTI or CPI (same bars as in Fig. 4). 'Extinction' and 'colonization' decompose the change in CTI or CPI into these processes. The remainder of the boxplots show how extinctions and colonization of warm-adapted or cold-adapted species contributed to changes in CTI or CPI. Significance levels are from Wilcoxon signed-rank tests against zero: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = not significant.

with greater variation in climate change. While differences between thermophilization and mesophilization rates and compositional change can be explained through microhabitat selection, they can also occur from the inability for species to respond to climate change fast enough. If small mammal communities across the Sierra Nevada cannot keep pace with climate change, they are at risk of population collapse.

The use of community-wide averages carries some caveats. These averages assume stable niches; however, low thermophilization or mesophilization rates could instead reflect

Table 1. Twenty-one selected studies that have measured thermophilization and/or mesophilization rates. Articles were compiled through personal knowledge, and through a Web of Science search on 24 November 2024 using the following Boolean phrase: 'thermophilization OR thermophilisation OR mesophilization OR mesophilisation'. * NS = rates not significantly different from zero. ** Thermophilization and mesophilization rates weighted by species abundance or basal area.

Reference	Organism(s)	Thermophilization rate (°C year^{-1})*	Thermophilization variable used	Mesophilization rate (mm year^{-1})*	Mesophilization variable used	Time interval	Abundance weighted**
This study	small mammals	1.83×10^{-3} (northern, NS); -8.79×10^{-4} (central, NS); 8.31×10^{-3} (southern)	Mean annual temperature	0.34 (northern, NS); 0.05 (central, NS); −0.27 (southern)	Mean annual precipitation	multiple: 1916–2010	no
Bergamin et al. 2024	trees	3.6×10^{-2} (Atlantic forest); 3.4×10^{-2} (Araucaria Forest)	Mean annual temperature	NA	NA	10 years: 2009–2019	no
Borderieux et al. 2024	understorey plants	1.2×10^{-2}	Mean annual temperature	NA	NA	multiple: 2005–2021	no
Brice et al. 2019	trees	3.0×10^{-2}	Mean annual temperature	NA	NA	multiple: 1970–2016	yes
Comte et al. 2021	riverine fish	3.0×10^{-3}	Mean annual water temperature	NA	NA	multiple: 1951–2010	yes
Cuesta et al. 2023	alpine plants	7.0×10^{-3}	Monthly mean air temperatures	NA	NA	multiple: 2008–2019	yes
Cuni-Sanchez et al. 2024	tropical trees	3.2×10^{-3} (Rwanda-Uganda-Democratic Republic of the Congo); 8.6×10^{-3} (Uganda); 2.3×10^{-3} (Tanzania)	Mean annual temperature	0 (NS)	Mean annual precipitation	multiple: 2010-2022	yes
De Frenne et al. 2013	herbaceous plants	4.1×10^{-2}	Mean temperature (April–September)	NA	NA	multiple (34.5 year average)	no
Devictor et al. 2008	birds	6.0×10^{-3}	Mean temperature (March–August)	NA	NA	multiple: 1989–2006	yes
Devictor et al. 2012	birds and butterflies	2.6×10^{-3} (birds), 9.3×10^{-3} (butterflies)	Mean annual temperature	NA	NA	multiple: 1990–2008	yes
Dietz et al. 2020	understory pants	1.1×10^{-2}	Mean annual temperature	NA	NA	16 years: 2002–2018	yes
Duque et al. 2015	Andean trees	1.1×10^{-2} for adults, 2.7×10^{-2} for juveniles	Mean annual temperature	NA	NA	multiple: 2006–2014	yes
Fadrique et al. 2018	Andean trees	6.6×10^{-3}	Mean annual temperature	NA	NA	multiple: 1990-2012	yes
Feeley et al. 2020	plants	1.7×10^{-2}	Mean annual temperature	0.81 (NS)	Total annual precipitation	multiple: 1970–2011	yes
Haase et al. 2019	stream invertebrates	2.2×10^{-2}	Mean temperatures	NA	NA	25 years: 1990–2014	yes
Lajeunesse and Fourcade 2023	multiple	9.9×10^{-3}	Multiple	NA	NA	5 years: 1992–2017	no
Ramón-Martínez and Seoane 2024	birds	2.0×10^{-2}	Mean temperature (April–July)	NA	NA	~ 15 years: 1998–2018	no
Richard et al. 2021	herbaceous plants	9.0×10^{-3}	CATMINAT and EcoPlant Datasets	NA	NA	20 years; 1995–2015	no
Rosenblad et al. 2023	trees	3.9×10^{-3}	Mean annual temperature	NA	NA	10 years: 2000–2008, 2010–2018	yes
Zellweger et al. 2020	understory plants	1.0×10^{-2}	Mean temperature (April–September)	NA	NA	multiple: 1937–2017	no
Zhu et al. 2024	grassland plants	2.16×10^{-2}	Mean annual temperature	−3.04	Total annual precipitation	multiple: 1983–2021	yes

phenotypic plasticity, local adaptation, behavioral shifts, or rapid evolutionary change. Geometric constraints at upper elevations could bias high-elevation species toward downhill shifts (Iseli et al. 2023). Finally, because climate change has accelerated in recent decades (Supporting information), community responses may primarily reflect recent trends, which could inflate estimates of climate lags. Nonetheless, in a post hoc analysis, we observed that changes in CTI precipitation and temperature preferences calculated from early and late collections were similar (Supporting information).

Our analyses highlight the importance of variation in how species and communities respond to climate change (Rapacciuolo et al. 2014). Previous studies of species-level responses to climate change in the Sierra Nevada suggest no universal explanation for species' range shifts (Rowe et al. 2015, Santos et al. 2015). We observe a similar complex pattern of community dynamics, with only one region responding to ongoing warming, and one region drying in the expected way. This highlights how the net effects of climate change are not uniform across the Sierra Nevada. Understanding this variability is necessary for developing region-specific conservation strategies.

The lags between community-wide responses and climate change indicate that these communities are already out of equilibrium with ambient climate change. Compared to future forecasts (Cayan et al. 2008) only moderate warming and drying has occurred in the Sierra Nevada. Hence, we should expect that the degree of disequilibrium between these communities and their environments will only increase into the future. In an influential study, Colwell et al. (2008) draw attention to 'lowland biotic attrition' in the tropics, which they expect to occur because the warmest places in those regions will become intolerably warmer, while there are no nearby sources of species that can tolerate these extended conditions. Analogously, we suggest a similar dynamic, but not necessarily restricted to the lowlands of tropical ecosystems. Rather, our work demonstrates that lags between climate and communities can occur across elevations, leading to declines in richness (Supporting information). Even if the species pool of a particular location contains species that could reside there, the accelerating pace of climate change may disallow them from shifting their ranges to match climate change. As a result, entire elevational gradients may eventually suffer from a low-grade biotic attrition. Additional to climate, other factors are also stressing biological communities of the Sierra Nevada, including shifts in vegetation (Santos et al. 2017), disturbance regime (i.e. fire; Taylor et al. 2016), air pollution (Fenn et al. 2019), and increases in ultraviolet radiation (Barnes et al. 2019), any of which would only exacerbate biotic attrition.

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Author contributions

Ethan Abercrombie: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Jonathan A. Myers**: Conceptualization (equal); Investigation (supporting); Methodology (supporting); Resources (supporting); Supervision (supporting); Writing – review and editing (equal). **Richard L. Usdin**: Investigation (supporting); Visualization (supporting); Writing – review and editing (equal). **Adam B. Smith**: Conceptualization (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Resources (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.15468/dl.7x7sex (Abercrombie et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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