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ARTICLE

Contrasting demographic processes underlie uphill shifts in a desert ecosystem

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Abstract

Climate change is projected to cause extensive plant range shifts, and, in many cases such shifts already are underway. Most long-term studies of range shifts measure emergent changes in species distributions but not the underlying demographic patterns that shape them. To better understand species' elevational range shifts and their underlying demographic processes, we use the powerful approach of rephotography, comparing historical (1978–1982) and modern (2015–2016) photographs taken along a 1000-m elevational gradient in the Colorado Desert of Southern California. This approach allowed us to track demographic outcomes for 4263 individual plants of 11 long-lived, perennial species over the past ~36 years. All species showed an upward shift in mean elevation (average = 45 m), consistent with observed increasing temperature and severe drought in the region. We found that varying demographic processes underlaid these elevational shifts, with some species showing higher recruitment and some showing higher survival with increasing elevation. Species with faster life-history rates (higher background recruitment and mortality rates) underwent larger elevational shifts. Our findings emphasize the importance of demography and life history in shaping range shift responses and future community composition, as well as the sensitivity of desert systems to climate change despite the typical “slow motion” population dynamics of perennial desert plants.

KEYWORDS

Boyd Deep Canyon, climate change, demography, desert plants, range shifts, recruitment, rephotography, survival

INTRODUCTION

Species' ranges on average are shifting poleward and upward in elevation in response to warming (Chen

et al., 2011), and many are experiencing contractions in both lower latitudinal (e.g., Zhu et al., 2012) and elevational distributions (e.g., Moritz et al., 2008). However, individual species show idiosyncratic responses

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(Chen et al., 2011; Madsen-Hepp et al., 2023; Moritz et al., 2008), and range shifts are linked to diverse demographic processes (Gibson-Reinemer & Rahel, 2015; Sharma et al., 2022) that are complex and poorly understood. Species ranges delineate locations where population growth is stable or positive over the long term, that is, where birth and immigration rates equal or exceed death and emigration rates. For plants, the components of fitness that together contribute to positive population growth—fecundity, recruitment, growth, and survival—can each be differently sensitive to climatic stressors (e.g., Doak & Morris, 2010; Mclaughlin & Zavaleta, 2012; Sharma et al., 2022).

Knowledge about the demographic processes driving range shifts is critical to improving predictions of future species distributions and informing climate-adaptive management responses. However, for long-lived plants, it is often difficult to directly measure the demographic processes of recruitment and mortality at the timescale of most field research (Cody, 2000). As a result, climate-induced range shifts are often inferred without these measurements, requiring additional assumptions and caveats, and preventing exploration of underlying processes. For example, changes in plant cover over time (e.g., Gottfried et al., 2012; Kelly & Goulden, 2008; Madsen-Hepp et al., 2023) might reflect changes in abundance or individual growth. Inferring range shifts by comparing adult and juvenile distributions requires assuming that juvenile distributions do not include recruitment sinks (Zhu et al., 2012). Studies of changes in presences and absences can obscure instances where long-term persistence is unlikely, such as non-reproductive adult populations (e.g., Mclaughlin & Zavaleta, 2012), or demographic compensation, that is, where vital rates change in opposite directions and thereby compensate for each other (e.g., Doak & Morris, 2010).

Adding to the complexity of range shift dynamics, early stages of range shifts may be detected as changing optima within the range, referred to as a “lean” (Breshears et al., 2008). For long-lived plants in particular, leans are expected in the near-term due to lags in migration and population growth at the leading edge, and long-surviving and/or clonal (but no longer reproductive) individuals at the trailing edge (Davis, 1989; Svenning & Sandel, 2013). In the face of ongoing, directional change, leans in long-lived plants likely represent early stages of range shifts. This can include extinction debts, whereby remnant populations are destined for future extirpation (Dullinger et al., 2012). Eventually, such debts may be “paid off” in abrupt, widespread dieback (Lenoir & Svenning, 2015).

Desert systems are ideal for detecting and studying plant demographic processes underlying climate-induced range shifts, because of their potential vulnerability to climate change (Vale & Brito, 2015), their sensitivity to even small changes in precipitation regime (Brown et al., 1997), and the relatively strong role of abiotic factors in controlling desert plant species distributions (Belnap et al., 2016). In our study region, the Colorado Desert in Southern California, aridity controls vegetation distributions (Belnap et al., 2016) and aridity and drought are already increasing and projected to continue to increase over the next century (Cook et al., 2015; Seager & Vecchi, 2010). Warming minimum temperatures also will decrease freezing (Archer & Predick, 2008), potentially releasing species from cold limitation at high-elevation sites.

To explore plant elevational shifts and the demographic processes underlying these shifts, we took advantage of a unique historical dataset from the Deep Canyon Transect, where a steep climatic gradient compresses many terrestrial inland California vegetation types into a short linear distance. Because a series of landscape photographs were taken across the transect during 1978–1982, we were able to use a powerful alternative to traditional resurveys—rephotography (Bowers et al., 1995; Bullock & Turner, 2010)—to track recruitment, mortality, and growth of individual plants over time. We compared paired historical and modern (2015–2016) photographs at 17 sites along a 1000-m elevational gradient to quantify species demographic rates. With an analysis of 11 species and over 7000 individual plants, we evaluated whether (1) species showed shifts in mean elevation, (2) survival or recruitment varied across the elevational gradient for each species, (3) change in individual size (growth and dieback) varied across the elevational gradient for each species, as evidence of a precursor to an elevational shift, and (4) species’ traits predicted the magnitude of observed range-shift responses.

METHODS

Site description

The Deep Canyon Transect spans ~2300 m in elevation over ~16 km in central Riverside County, California, on the slopes of the Santa Rosa Mountains. We studied the lower portion of the Deep Canyon Transect, from ~200 m in elevation (116°21′54.6″ W, 33°40′36.9″ N) to ~1200 m in elevation (116°26′6.0″ W, 33°37′10.5″ N, at which point vegetation becomes too dense for our methods, see below) over ~9 km (Appendix S1: Figure S1 and

Table S1). Moving upslope, minimum, maximum, and mean temperatures and maximum vapor pressure deficit decrease, while annual precipitation, proportion of precipitation falling as snow, and incidence of frost increase (Kelly & Goulden, 2008; Madsen-Hepp et al., 2023; Appendix S1: Table S2). This portion of the Deep Canyon Transect is part of the Colorado Desert, and it encompasses alluvial plain, rocky slopes, and the lower and upper plateaus as defined by Zabriskie (1979) as one moves upslope.

Historical and modern photographs

To overcome typical challenges with the method of rephotography (Vellend et al., 2013), we used permanently marked and relocatable photo sites across our study transect (see example photographs in Figure 1). In this landscape, it was possible to recreate the precise angle and view of historical photographs due to the preponderance of geologic features and sparse vegetation. Almost all of the perennial plant species in the area were



FIGURE 1 Example paired historical and modern photographs from one study site taken (a) May 1978 by Dr. Wilbur Mayhew and (b) March 2015 by study authors. Arrows indicate example demographic processes. From left to right: silver cholla (*Cylindropuntia echinocarpa*) recruitment, palo verde mortality, and creosote survival and change in size.

conspicuous and identifiable from photographs. Spacing between plants was usually sufficient to distinguish, identify, and measure individuals.

We utilized photographs originally taken by Dr. Wilbur Mayhew between 1978 and 1982 (Mayhew, 1981), which we digitized from 35-mm slides stored at Philip L. Boyd Deep Canyon Desert Research Center (doi: 10.21973/N3V66D). We selected 17 photo views out of ~300 available based on several criteria: (1) the photo view encompassed a relatively large and undisturbed area, (2) individual plants in the photograph were close enough to the camera to be identifiable to species, and (3) the final set of photographs spanned the elevation gradient. In addition, to minimize obstructed views, we often selected views that were either relatively higher than the surrounding landscape or facing a slope, and we did not choose any views above ~1200 m elevation (Appendix S1: Figure S1 and Table S1), at which point vegetation became too dense to identify individuals.

We relocated permanently marked sites where historical photographs had been taken (Mayhew, 1981), and we rephotographed them using a Canon 5D Mark II camera and tripod in 2015 and 2016 (Appendix S1: Table S1). We took one additional set of photographs in April 2017 after the end of a multi-year drought so that we could distinguish dormant from dead individuals of two drought-deciduous species (brittlebush, *Encelia farinosa*, and white bursage, *Ambrosia dumosa*). We approximated the view of the original photographs as closely as possible in the modern photographs.

For each photo view, we chose a single historical and modern photograph for analysis based on resolution, contrast, and coloration. The mean timespan between paired historical and modern photographs was 36 years (Appendix S1: Table S1). We perfected the alignment between the paired historical and modern photographs in Photoshop by making one photograph semi-transparent, then rotating and resizing it while maintaining the original aspect ratio.

Data extraction

We extracted data on 11 perennial species that appeared in 5+ sites (Appendix S1: Table S3). We focused on perennials because they integrate climate impacts over a longer period and are visible year-round. We extracted data from the photographs in ArcGIS, arranging the paired photographs as map layers. We created polygons to delimit a survey area close enough to the camera to identify species; these polygons serve as the “sites” in our subsequent analysis. In some cases, we collected data on larger bodied or particularly conspicuous species, such as

ocotillo (*Fouquieria splendens*) and creosote (*Larrea tridentata*), in a larger area including locations farther from the camera than for smaller, less conspicuous species (Appendix S1: Table S1).

We recorded whether each plant underwent recruitment (absent historical, present modern), mortality (present historical, absent modern) or survival (present both), and aggregated these data to determine the number of survivors, recruits, and mortalities for each species at each site. We excluded plants that were dead in the historical period or with main stems outside of the site polygon. In some cases, we consulted other historical and modern photographs of the same site to determine species identity or assess whether an individual was alive. Our methods captured only recruitment events leading to conspicuous individuals visible from a distance and excluded recently recruited small individuals. Our findings are therefore robust to population sinks of new recruits since small or short-lived individuals were not counted. We counted and measured clusters of agave (*Agave deserti*) and Mojave yucca (*Yucca schidigera*) as single individuals. Rarely, we may have misidentified pygmy cedar (*Peucephyllum schottii*) for creosote where these species co-occur on steep slopes, since they have similar morphology and are difficult to distinguish from a distance.

We measured individual relative change in plant size by measuring the height (perpendicular to the ground) and width (the largest horizontal extent of the plant perpendicular to the camera, i.e., canopy width) of surviving plants in both time periods, using the ruler tool in ArcGIS and focusing on woody biomass. Change in size could have been positive or negative, related to either growth or dieback (e.g., branch dropping), respectively. When dead agave rosettes were surrounded by live rosettes, we did not include the width that was dead if it was >20% the total width (Appendix S1: Section S1). We calculated the relative change in height of each plant as $(H_1 - H_0) / H_0$, where H indicates plant height and the subscripts 0 and 1 indicate the historical and modern periods, respectively. We used an equivalent equation for relative change in width. By using measures of proportional growth, we did not need to calibrate absolute plant size from the photographs.

For some species at some sites, we could not track the fate of individuals between the two time periods. This most often occurred for narrow-bodied and relatively short-lived species (e.g., teddy bear cholla, *Cylindropuntia bigelovii*) in photo pairs that were difficult to perfectly align, thereby making it difficult to tell whether plants either survived, or died and were replaced by recruits. It also occurred when a large plant died and a new plant “appeared” in a spot that was previously hidden, such that

we were unable to determine whether the second plant was a recruit or a surviving plant. We therefore designated two site types for each species: “trackable” sites—those where we could track the fate of at least one third of individuals of a given species over time, and “count-only” sites—those where we could track fewer than one third of individuals, and instead only counted individuals. Count-only sites were retained for analyses of mean elevation shifts but not demographic rates (Appendix S1: Table S3). We chose the one-third cutoff in an attempt to strike a balance between retaining data and only calculating demographic rates where a substantial portion of the population could be included. Our final data set included >7300 plants, including 93 species-site combinations that were trackable (containing 4263 individual plants with demographic outcomes), and 6 that were count-only. Given our unique rephotography methods, we provide additional description of potential bias, accuracy, and detection issues in Appendix S1: Section S2.

Geophysical data

In order to calculate plant densities and changes with elevation, and to account for other topographic factors that impact arid plant distributions (Munson et al., 2015), we gathered data on physical aspects of the sites captured in each photograph. We used Google Earth Pro “ground level view” to draw polygons matching the extent of the site polygons outlined in the photographs. To do so, we first “stood” at the camera’s locality and angle, then used corresponding features (e.g., washes, large creosote, hills) to find the exact site, and finally dropped pins to mark polygon vertices. We used these polygons to extract data on each site’s size, as well as its mean elevation, aspect, slope, and annual solar radiation (from here on “insolation”) using USGS NED Contiguous US 1/3 arc-second digital elevation model (2013) in ArcGIS. We took the cosine of aspect to create linear values ranging from -1 (south) to 1 (north; Appendix S1: Table S1). For details on how we treated five sites that were near (<100 m) another site, see Appendix S1: Section S3.

Statistical analyses

Detecting range shifts

To determine which species showed an overall upward shift within our sample sites, we calculated the change in each species’ density-weighted mean elevation (based on counts) in each time period, using all study sites. We used a one-tailed *t*-test to determine whether the mean shift

across species was statistically greater than zero. To test how sensitive each species’ calculated shifts were to any single site, we did a jackknife analysis, removing each site in turn and recalculating the change in mean elevation with the remaining sites. To test whether the inclusion of count-only sites impacted our results, we also re-ran this analysis using only “trackable” sites.

Statistical models of demographic processes

To explore which demographic processes contributed to uphill shifts, for each species, we created two models to test whether elevation was related to survival and recruitment. We also tested whether elevation was related to change in individual plant size, since dieback and growth can be precursors to mortality and recruitment, respectively. We considered elevation significant if $p < 0.05$.

We modeled species survival and recruitment at the site level. We modeled the number of recruited individuals using generalized linear models and chose between a Poisson or negative binomial distribution and log link using a likelihood ratio test. We also included an offset of $\log(N_0)$ so that recruitment was modeled as a rate relative to the initial population size N_0 at the site. We used generalized linear models to model survival as a binomial response (the number of individuals surviving vs. undergoing mortality at each site) and logit link, and in some cases included a random effect for site to improve model fit (Harrison, 2015). We modeled the relative change in height of individual surviving plants using a linear mixed model with random effect for site, and equivalent methods to model relative change in widths. For all models, we compared models with and without a covariate for insolation and retained insolation if the model including it was within two corrected Akaike information criterion (AIC_c) of the top model. For modeling details, see Appendix S1: Section S4.

Comparing detected shifts to species traits

To test the expectation that faster life histories on the fast-slow life-history continuum (Salguero-Gómez et al., 2015) will lead to more sensitive climate change responses, we developed a life-history rate index value for each species. We first quantified background annual per capita mortality and recruitment rates for each species across all sites. We then calculated the life-history rate index by taking the mean of the rescaled log of the recruitment rate and the rescaled mortality rate (Appendix S1: Table S4). We then used linear regression

to test whether the life-history rate index was predictive of log mean elevation shifts. To confirm that our results were robust to the potentially confounding effect of more extreme values at high and low elevation sites being incorporated into species demographic rates, we repeated these methods after removing the highest and lowest elevation sites for each species; results were virtually identical (not shown). We also used linear regression to test whether any of historical minimum elevations, historical maximum elevations, or elevational ranges (extracted from Zabriskie, 1979) were predictive of log mean elevation shifts. Finally, we used *t*-tests to test whether photosynthetic pathway or leaf habit (for species with leaves) were predictive of log mean elevational shifts (Appendix S1: Table S4).

RESULTS

We documented survival of 2378 plants, mortality of 986 plants, and recruitment of 899 plants of 11 species across 17 sites between the periods 1978–1982 and 2015–2016, over a 1000-m elevational gradient (Appendix S1: Table S1 and Figure S5). All species showed an increase in mean elevation, and across species, there was an average upward shift of 45 m ($t = 3.11$, $df = 10$, $p < 0.01$) (Figure 2; Appendix S1: Table S3). Seven species showed an upward shift in mean elevation of >20 m, and the extent of shifts ranged widely, from 2 to 134 m (Appendix S1: Table S3). The positive shifts in

mean elevation for white bursage and palo verde were sensitive to the removal of specific sites (Appendix S1: Figure S2). Limiting our analysis to only trackable sites did not change our overall results (average upward shift of 51 m, $t = 2.75$, $df = 10$, $p = 0.01$; Appendix S1: Table S3).

Out of 99 species-site combinations, we detected two local colonization events, in which a species that had not been recorded in the site during the first survey was detected in the second survey (palo verde at 269 m and ocotillo at 834 m). We also detected two local extinction events, in which a species was fully extirpated from a site (Mojave yucca at 836 m and beavertail cactus at 677 m). All other species-site combinations showed population persistence.

Three species showed higher recruitment with increasing elevation (creosote, ocotillo, and white bursage, Figure 3a; Appendix S1: Table S3). Three species showed increases in survival with increasing elevation (brittlebush, teddy bear cholla, and Mojave yucca; Figure 3b; Appendix S1: Table S3). Two species had increasing relative change in height with increasing elevation (creosote and Gander's cholla; Figure 3c; Appendix S1: Table S3), and creosote also showed increasing relative width with increasing elevation (Figure 3d; Appendix S1: Table S3). We did not detect any species in which recruitment, survival, or change in plant size decreased with elevation. One of our findings, for ocotillo recruitment, was sensitive to the inclusion of a single site (see Appendix S1: Section S4).

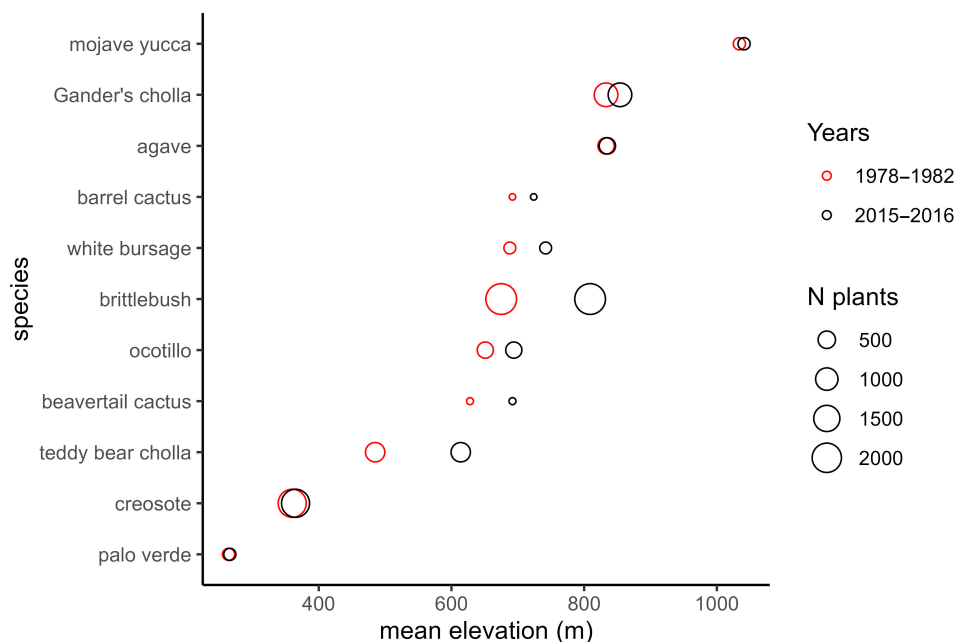


FIGURE 2 Species' mean elevation in 1978–1982 (red) and 2015–2016 (black). Point size is scaled by the number of plants in all study sites (both count-only and trackable).

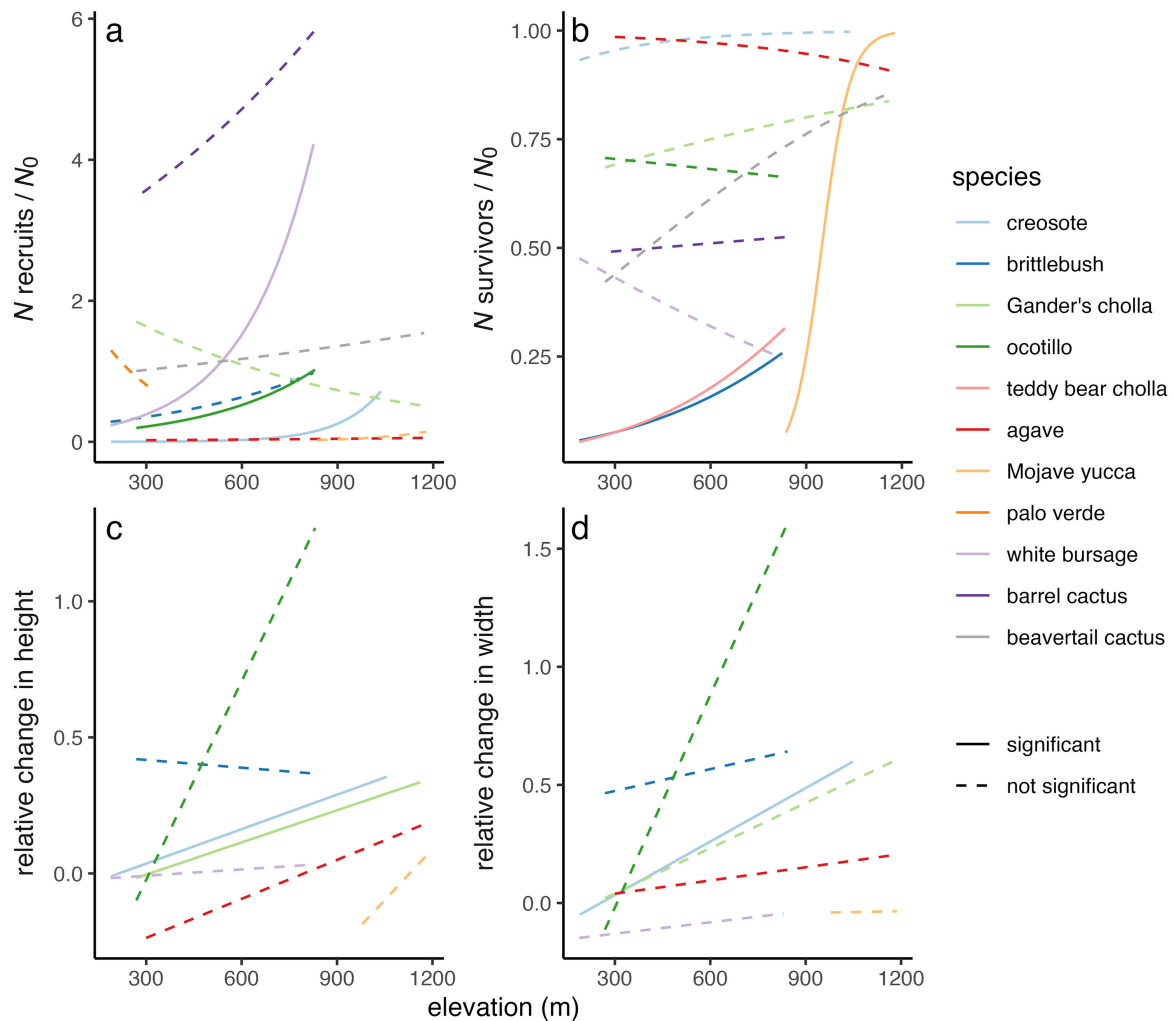


FIGURE 3 Modeled predictions of (a) recruitment, (b) survival, (c) relative change in height, and (d) relative change in width, across elevations, for each species (colors). Solid and dashed lines indicate that elevation was and was not statistically significant ($p < 0.05$), respectively. Where relevant, predictions are calculated with insolation and N_0 set to their mean value from that model’s data. Species are listed from the largest to smallest sample size. For model details, see [Methods](#) and [Appendix S1](#).

Species that were faster along the fast-slow life-history continuum (with higher life-history rate index values) had significantly larger shifts in mean elevation ($p = 0.01$; [Figure 4](#)). We did not detect relationships between mean elevational shifts and species’ minimum elevations, maximum elevations, elevational range, photosynthetic pathway, or leaf habit ([Appendix S1](#); [Figure S3](#)).

DISCUSSION

Plant elevational shifts track climate change

Our finding of an overall uphill shift in woody plants and cacti at the Deep Canyon Transect ([Figure 2](#),

[Appendix S1](#); [Table S3](#)) supports a growing body of evidence that underscores the climate change responsiveness of desert systems (e.g., [Félix-Burrueal et al., 2024](#); [Kelly & Goulden, 2008](#); [Madsen-Hepp et al., 2023](#)), despite the frequent “slow motion” population dynamics of desert perennial species ([Cody, 2000](#)). Our finding of an average uphill shift of 45 m in elevation over ~36 years (1978–1982 to 2015–2016, 12.5 m per decade) is similar in magnitude to the 56 m upward shift in mean temperature in the area between 1947–1976 and 1977–2006 ([Kelly & Goulden, 2008](#)). Our observed species’ elevational shifts coincide with local increases in temperatures since recording began in 1961, including increases in mean minimum and maximum temperatures of 1.7 and 2.2°C, respectively, between the historical and modern photo periods ([Appendix S1](#); [Figure S4](#)), and an increase in extreme

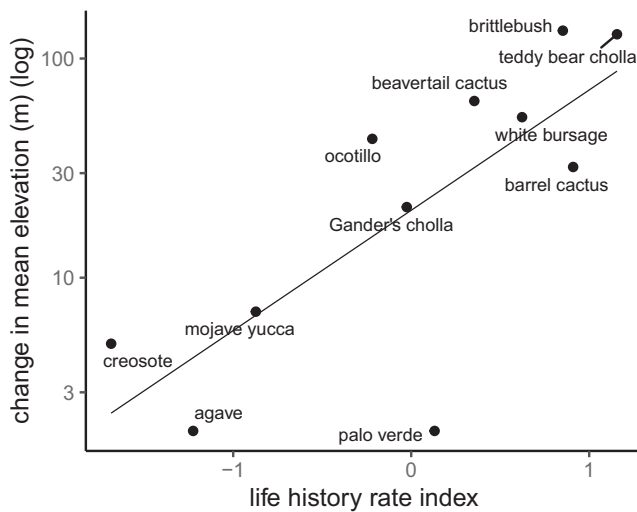


FIGURE 4 Species' life-history rate index against mean elevational change (log). We show the significant linear regression between life-history rate index and elevational change ($p < 0.05$).

drought years in the region since the first set of photographs was taken (Muth et al., 2023).

The mean elevational shifts we observed were slightly higher, on average, but generally within the range of the reported mean global shifts across taxa of 11 m per decade (Chen et al., 2011). Locally, our findings align with other research in our study region, including a 37-m average uphill shift reported for conifer species following a 2002–2004 drought (Fellows & Goulden, 2012) and average uphill shifts reported in trees and shrubs of 65 m between 1977 and 2006–2007 (Kelly & Goulden, 2008). Studies in the Deep Canyon Transect have also documented upward shifting range minima and maxima for some plants (Madsen-Hepp et al., 2023) and rapid upward shifts of birds (Hargrove & Rotenberry, 2009). Overall, our results, combined with those of Kelly and Goulden (2008) and Fellows and Goulden (2012), suggest a general pattern of plant species moving upward in elevation in this landscape (however, see Madsen-Hepp et al. (2023), which reported multidirectional responses).

The response of cacti to climate change has been relatively understudied compared to other plant groups. We documented mean uphill shifts of >20 m in four cactus species (Figure 2; Appendix S1: Table S3). For three of these species—teddy bear cholla (*C. bigelovii*), barrel cactus (*Ferocactus cylindraceus*), and beavertail cactus (*Opuntia basilaris*)—to our knowledge, climate change responses have not been previously studied. It has been suggested that climate change may benefit cacti because more xeric climates and increased atmospheric CO₂ will favor the crassulacean acid metabolism (CAM) photosynthetic pathway of most succulents (Reyes-García & Andrade, 2009), and cacti are frequently adapted to

drought and high temperatures (Seal et al., 2017; Smith et al., 1984). Moreover, dispersal of fruits or clonal joints via animals (e.g., Bobich & Nobel, 2001) might support cactus's ability to track favorable climates. However, other work suggests that climate change may be an important driver of cactus decline and extinction risk (Félix-Burrueal et al., 2024; Pillet et al., 2022). Our study indicates that certain species of cacti are responsive to climate change through already shifting elevational ranges.

It is unlikely that the species elevational shifts we detected are due to other non-climatic, confounding drivers. There has been very limited land use change along the Deep Canyon Transect over the study period. Most of the sites we photographed have been under strict protection as part of the University of California Natural Reserve System since the 1960s, with the remainder jointly managed by the US Forest Service and Bureau of Land Management as part of the Santa Rosa/San Jacinto National Monument. In addition, we focused on relatively low-elevation sites that have not been subject to historical fire, thereby avoiding the potentially confounding drivers of fire and fire suppression in the region (Schwilk & Keeley, 2012).

Contrasting demographic processes underlie elevational shifts

Our results underscore the importance of both broad patterns and underlying demographic processes to understanding plant community response to climate change. Our tracking of individuals over time demonstrated that similar overall patterns in species mean elevational shifts can be underlain by contrasting demographic processes: increased recruitment or decreased survival with elevation (Figure 3a,b; Appendix S1: Table S3). These varying demographic responses could lead to different ecological outcomes and have different management implications. For example, changes in recruitment with elevation could indicate early stages of an uphill range expansion (if higher recruitment at higher elevations eventually leads to colonization of new sites), and/or declining recruitment at low elevations, indicating that conditions in the lower elevation sites are becoming less suitable for reproduction. Alternately, changes in survival with elevation could indicate early stages of lower elevation range contraction (if lower survival at lower elevations eventually leads to local extinctions) and/or improved survival in the upper elevation parts of the range. A “conveyor belt” response, with both higher losses at lower elevations and increased recruitment at higher elevations could portend an overall range shift with little total range loss; however, we did not detect such a response in any

of our study species. Percent cover surveys or those that rely on mean elevational shifts could miss varying demographic signals at lower versus higher elevations. Attention to these dynamics could improve climate-adaptive management.

The uphill shifts we observed in ocotillo, white bursage, and creosote were associated with higher recruitment with increasing elevation (Figure 3a; Appendix S1: Table S3). These findings suggest that each species' reproductive capacity is responsive to climate change (Hedhly et al., 2009) or that one or more of the phases associated with juvenile recruitment (e.g., seed germination, seedling establishment, or seedling survival into size classes detectable by our study) are sensitive to climate change. Our findings on recruitment are consistent with reports that in many plants, including desert species, juveniles are more susceptible to climatic stress than adults (e.g., Félix-Burrueel et al., 2024; Lloret et al., 2009; Miriti et al., 2007). The decoupling of climate sensitivity across plant life stages might occur when juveniles and adults have different drought response capacities or strategies. For example, juveniles and adults might depend on different water sources. In the exceptionally long-lived creosote (Vasek, 2006), recruitment is precipitation-limited (Woods et al., 2011), but adults have deep roots (Hamerlynck et al., 2002) and access to sub-surface water sources that can be less coupled to local precipitation (McLaughlin et al., 2017), allowing mature individuals to persist after local climate conditions are no longer suitable for reproduction. Accordingly, the recruitment-driven elevational shift that we observed in creosote could reflect higher precipitation and higher soil moisture at upper-elevation sites. In contrast, in species such as the relatively shallow-rooted ocotillo (Schwinning & Ehleringer, 2001), juveniles likely have lower water storage capacity and higher resource requirements than adults (Bobich & Huxman, 2009). These differences could make juveniles more sensitive to xeric conditions and suggest another mechanism that could underlie a recruitment-driven elevational shift. Finally, a recruitment-driven shift could also relate to changes in the community that affect recruitment, such as a decline in nurse-plant species. For relatively long-lived species experiencing recruitment-driven shifts, climate change adaptation or restoration efforts with the goal of conserving the species in situ for the foreseeable future could focus on managing young life stages through climate-sensitive periods. "Relict" stands of adults could be prioritized for seed collection to conserve threatened genetic resources (McLaughlin et al., 2022).

The elevational shifts we observed in teddy bear cholla, brittlebush, and Mojave yucca were associated with higher survival at higher elevations (Figure 3b;

Appendix S1: Table S3). This kind of survival-driven shift indicates that for such species, mature individuals are more sensitive to climate change than young recruits (Bennett et al., 2015), potentially because of juveniles' lower water or other resource needs, or their capacity to establish in the shade of nurse plants (Rebman & Pinkava, 2001). A survival-driven shift where species' lower survival at low elevations is not met with corresponding higher recruitment at high elevations, could lead to an overall range contraction rather than a range shift. Such species might be prioritized for climate-adaptation strategies such as helping to establish juveniles in or near the expanding parts of the species distribution. Our finding of greater teddy bear cholla survival with higher elevation aligns with drought-induced mortality patterns in this species described by Bobich et al. (2014), who attributed increased adult survival at higher elevations to milder temperatures and greater precipitation at those elevations.

For three species, we found an upward shift in mean elevation >20 m but did not detect survival or recruitment varying with elevation (Gander's cholla, barrel cactus, and beavertail cactus; Figure 3a,b; Appendix S1: Table S3). For these species, weaker demographic processes across the gradient could have combined to create a mean elevational shift despite being undetectable by our analyses. Moreover, two of these three species (beavertail cactus and barrel cactus) had the lowest sample sizes in the study, which could have contributed to low detectability of responses.

Change in individual size varies with elevation

Two species, creosote and Gander's cholla, showed trends in individual plant growth or dieback with elevation (Figure 3c,d; Appendix S1: Table S3), with larger increases in plant size at higher elevations than at lower elevations. Negative changes in crown size could portend future mortality—for example, in creosote, individuals that experienced crown dieback in one drought were more likely to die in a subsequent drought (Miriti et al., 2007). Conversely, increased growth in higher elevation sites could signify improved overall plant performance, leading to higher survival, reproductive capacity and eventual new recruitment. The lack of detected growth or canopy dieback response in other species could be due to recent extreme drought events in the region that could have triggered mortality rather than partial dieback in vulnerable individuals (i.e., in those species for which we found a survival response with elevation) or to the relatively slow growth of desert species. Our

findings of both demographic and plant size responses suggest that documented uphill shifts in species' percent cover at this site (Kelly & Goulden, 2008) might have been driven by demographic changes as well as changes in individual size. Demographic responses suggest a more robust pattern of long-term directional change than do size responses alone.

Life-history rates predict individual elevational shifts

Whether ecological communities track climate change in tandem or individualistically will shape future community compositions and ecosystem functioning. The range of species responses we observed, which spanned an order of magnitude in elevational shifts, emphasizes the Gleasonian prediction that members of ecological communities will move individualistically with climate change instead of in tandem (Gleason, 1926). While past responses of these species to the Earth's previous epochs of climate change may also have been individualistic, and any given species may benefit from such shifts, the rate of current climate change and timescale of conservation management make current individualistic responses potentially highly disruptive. Differences in individual species' movement responses could disrupt community dynamics, with cascading effects on species limited by their positive interactions with slower species. For example, in our study system, trees and shrubs can perform essential ecosystem functions such as acting as nurse plants by providing shade, nutrients, and protection from herbivory and freezing temperatures (Braun & Lortie, 2020; Withgott, 2000) and creating animal habitat (Deacon et al., 1966). These functions could be disrupted as climate changes and communities shift (Miriti et al., 2007). Palo verde, an important nurse plant for many cacti species (Withgott, 2000), showed the smallest elevational shift of all species we studied (2 m; Figure 2; Appendix S1: Table S3). If this trend continues, its key functions may be absent from future plant communities at higher elevations. Such foundational species with observed slow responses to climate change could be promising candidates for interventions that assist with tracking climate. Where data on climate change response of individual species are not available, species' life history and functional traits could be useful proxies.

Range shift responses to climate change can be related to species' life history (Madsen-Hepp et al., 2023; Vásquez-Valderrama et al., 2022). In our study system, Madsen-Hepp et al. (2023) found that species with more conservative (as opposed to acquisitive) functional traits on the leaf economic spectrum (Wright et al., 2004), such

as lower specific leaf area and larger seed size, were more likely to show upward elevational range expansion and to shift their ranges overall. However, we found that faster species along the fast-slow life-history continuum (Salguero-Gómez et al., 2015), with a higher life-history rate index, showed more pronounced elevational shifts (Figure 4), indicating that these species may track climate change more readily. Logically, species with faster life-history rates have greater potential to respond to climate change given their ability to disperse more quickly into newly available environments and the shorter time-scales over which relict adult populations would be likely to survive. Our finding is aligned with Wolf et al. (2016), who, in contrast to Madsen-Hepp et al. (2023), found that for >4000 plant taxa in California, smaller seed size was associated with a higher likelihood of upward elevational range shifts. Our finding that species with faster life-history rates had larger range shifts is also generally consistent with those of Perry et al. (2005) for plants and Lenoir et al. (2008) for fishes. The discrepancies in our study results and those of Madsen-Hepp et al. (2023) may be explained by the different suites of species and taxa evaluated (e.g., Madsen-Hepp et al. included many tree species while our study focused on shrubs and cacti), and/or by the different parts of the Deep Canyon Transect that the two studies covered.

Study limitations

Our analyses did not include soils or geology, which can have strong effects on desert species' responses to climatic drought (Hamerlynck et al., 2002). Further, our data came from a single transect that did not necessarily capture the full elevational range of the individual study species, and we could have missed threshold effects that might have occurred at such distributional edges (e.g., Madsen-Hepp et al., 2023). Likely due to our relatively small number of sites, our finding of upward elevation shifts for two species (white bursage and palo verde) was sensitive to the removal of specific sites (Appendix S1: Figure S2). Therefore, we have lower confidence in the results for those species. Rephotography can create unique detection issues (Appendix S1: Section S2); for example, we may have missed recruitment responses for species that are often hidden by nurse plants (e.g., agave; Franco & Nobel, 1988). Future studies should corroborate our life-history rate findings with independent data on mortality and recruitment rates, which is currently lacking across the full set of species in our study. The analysis of data from additional time points or locations would help relate our findings to background demographic rates and contribute to models

of population dynamics (Drees et al., 2023), thereby further resolving patterns of demographic change and informing climate-adaptive conservation strategies for individual species.

Rephotography for detecting climate change responses

Rephotography provides a powerful alternative to traditional field resurveys of transects or quadrats. In traditional field surveys, quantification of demographic rates would require the original collector to have permanently marked or geolocated each plant. In contrast, rephotography allows historical photographs to be used opportunistically, since demographic rates can be extracted without the foresight of the original photographer. Moreover, a single photographic view can be used to capture data on hundreds of individuals in much larger and steeper areas than would be practical to survey repeatedly using conventional methods. Our use of rephotography allowed us to track the fate of >4200 individual plants over ~36 years and thereby document both uphill shifts and the varying demographic processes that underlie them. This large sample would have been exceedingly difficult using traditional field methods such as permanently tagging individual plants. Rephotography requires a careful consideration of potential issues of bias, accuracy, and detection (Appendix S1: Section S2), and its use in demographic studies is likely limited to arid and semi-arid climates with well-spaced, conspicuous vegetation to allow the tracking of individuals. Nevertheless, as more than one third of the Earth's land surface is arid or semi-arid, often harboring discontinuous vegetation (Maestre et al., 2021; Wickens, 1998), it is likely that many sources of quantifiable data are currently locked up in historical photographs. Given the importance of historical data for understanding responses to climate change (Vellend et al., 2013), efforts to unlock these additional data sources will be increasingly valuable in the future.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Skikne et al., 2024) are available in Dryad at <https://doi.org/10.5061/dryad.pk0p2ngz6>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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