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Plant functional traits predict heterogeneous distributional shifts in response to climate change

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Abstract

1. Climate change is causing the rapid redistribution of vegetation as plant species move to track their climatic optima. Despite a global trend of upward movement in latitude and elevation, there is extensive heterogeneity among species and locations, with few emerging generalizations. Greater generalization may be achieved from considering multidimensional changes in species' distributions as well as incorporating ecologically relevant functional traits into studies of range shifts.
2. To better understand how recent changes in climate are influencing the elevational distribution of plant species and how species' functional traits mediate distributional changes, we resampled a 2438m elevation transect spanning a distance of 16 km which encompasses desert scrub, pinyon-juniper woodland, chaparral and coniferous forest plant communities.
3. Over the last 42 years, total perennial cover and species' average cover increased at lower elevations and decreased at higher elevations while average elevational leading-edge increased 116m and elevational rear edge decreased 84m. Notably, these changes were mediated by species' functional traits, where species exhibiting more conservative traits (lower specific leaf area [SLA], greater $\delta^{13}\text{C}$, larger seed mass) and taller height shifted upward in their leading-edge range limit, average elevation and trailing edge range limit, while declining in abundance at the median and trailing edge of their range. Species possessing more acquisitive traits (higher SLA, lower $\delta^{13}\text{C}$, smaller seed mass) and shorter height shifted downward and increased in abundance at their trailing edge, with increases in their total range size.
4. Our results provide clear evidence that heterogeneous range dynamics under recent climate change can be generalized by considering ecologically relevant plant functional traits, and how they respond to localized climate exposure. Furthermore, by documenting changes across a steep elevational gradient comprising a large aridity gradient, we show divergent patterns for plants occupying contrasting positions along the global spectrum of plant form and function, which

provides critical insight into how trait-mediated changes under increasing aridity will impact ecosystem functioning.

KEYWORDS

aridification, biodiversity change, Boyd Deep Canyon, climate change, drylands, functional diversity, range shifts

1 | INTRODUCTION

Global climate change is causing rapid modifications to terrestrial biodiversity (Díaz et al., 2019). Among plants, there is a global trend of upward movement in latitude and elevation as species track their optimum conditions under accelerated warming (Kelly & Goulden, 2008; Lenoir et al., 2008; Rumpf et al., 2018). However, numerous recent long-term studies have also found either lagged responses of species failing to track their shifting climatic optima (Alexander et al., 2018; Zhu et al., 2012) or unexpected directional changes such as downward elevational and latitudinal shifts (Crimmins et al., 2011; Lenoir et al., 2010; Rumpf et al., 2019). These distributional changes will scale up to influence ecosystem productivity, nutrient cycling, carbon storage and land–atmosphere feedbacks (Anderegg, Anderegg, et al., 2019; Madani et al., 2018; Pecl et al., 2017); however, three major limitations have hindered generalizations. First, most existing studies have only assessed changes to one dimension of species' geographic ranges—typically leading-edge or average elevation (Lenoir & Svenning, 2015). Second, there has been a failure to incorporate ecologically relevant functional differences among species undergoing distributional shifts. Lastly, the majority of long-term studies of plant redistributions have been conducted within temperate alpine and boreal ecosystems, which has limited our understanding of more xeric ecosystems, which as a biome collectively comprise the largest proportion of terrestrial surface (Cherlet et al., 2018).

Despite decades of research, most studies have primarily assessed distributional changes over time at the leading range edge (high elevation or latitudes; Chen et al., 2011; Pauli et al., 2012) or at the centre of the range (Crimmins et al., 2011; Kelly & Goulden, 2008; Lenoir et al., 2008). However, a recent meta-analysis showed that trailing edge range margins have comparable rates of movement (Rumpf et al., 2019). Critically, understanding the response of plant species to changing climate requires examination of change in not only species' range limits, but also changes in abundance across species' entire distributions (Ehrlén & Morris, 2015; Lenoir & Svenning, 2015). Lags in dispersal, establishment and extinction are expected to be widespread among species shifting along elevation gradients, and the magnitude of these lags—captured by range-wide population abundance changes—will likely vary among populations throughout individual species' ranges (Alexander et al., 2018; Peterson et al., 2019). For instance, different life stages and/or locally adapted populations can show divergent demographic responses to the same climate drivers (Hargreaves & Eckert, 2019; Valladares et al., 2014), and the importance of different demographic rates to population growth can vary across a species' range (Oldfather et al., 2021).

Ultimately, while multiple factors will influence the rate and direction of range redistributions, a species' ability to respond to changing climate will depend on the extent that its functional traits enable persistence under novel climate regimes or enable movement to favourable climatic conditions (Angert et al., 2011; Damschen et al., 2012; Dawson et al., 2011; MacLean & Beissinger, 2017). Plant functional traits reflect species' morpho-physiological strategies to optimize fitness under a given suite of environmental conditions (Lavorel & Garnier, 2002; Violle et al., 2014) and have strong theoretical support for predicting range dynamics under contemporary climate change (Estrada et al., 2016; Funk et al., 2016). However, functional approaches for predicting range dynamics have historically focused on dispersal traits (Estrada et al., 2016; Zhu et al., 2012) or categorical plant functional types (Lenoir et al., 2008; Rumpf et al., 2018), while largely ignoring that establishment potential and competitive ability in new habitats as well as survival in existing habitats will be dependent on traits relating to resource acquisition and utilization (Griffin-Nolan et al., 2018; Liancourt et al., 2020; MacLean & Beissinger, 2017), which are often orthogonal to dispersal traits (Laughlin, 2014; Westoby et al., 2002). Furthermore, traits within species are often coordinated (i.e. the plant economics spectrum), with global patterns of plant resource-use and acquisition strategies represented by a continuum from 'fast', resource-acquisitive strategies that optimize carbon gain by constructing cheap tissues with shorter life span, taking advantage of brief periods of resource availability, while resource conservative strategies invest more in longer-lived tissues with greater construction costs for enhanced survival in more stressful conditions (Reich, 2014). While resource-use traits conferring tolerance to drought and heat stress (e.g. high water use efficiency (WUE), lower specific leaf area (SLA)) are typically adaptive under the warmer and drier conditions expected with climate change, these conservative strategies become maladaptive under increasing aridity given their susceptibility to hydraulic failure (Bennett et al., 2015; Berdugo et al., 2022; Carvajal et al., 2019).

Finally, while fine-scaled longitudinal data documenting species' range and abundance dynamics have been collected from a variety of ecosystems, most of these studies are confined to temperate alpine and boreal ecosystems. Mountainous regions exhibit high heterogeneity of abiotic factors over short distances, and subsequently host high elevational variation in plant communities (Körner, 2007). Such high rates of turnover along compressed climatic gradients in mountainous systems serve as a natural laboratory for assessing long-term responses to climate change (Sundqvist et al., 2013), especially given that transition zones between habitat types will likely facilitate novel species' interactions and subsequent unexpected

and/or accelerated range dynamics (Beckage et al., 2008; Solarik et al., 2020). Here, we resampled the Deep Canyon Transect, a long-term dataset spanning a steep elevational gradient in Southern California, to understand how recent climate change is influencing the distributions of plants and to ask what role species' functional traits play in mediating their responses. In 2019, we resampled 20,400-m long vegetation sub-transects by identifying all perennial plant species that intercepted each sub-transect at every centimetre (80,000 data points) and compared our findings to surveys in 1977 (Zabriskie, 1979) and 2008 (Kelly & Goulden, 2008). We calculated changes in range edges and abundances across species' entire elevational distributions for all species that were recorded in the original survey. We additionally measured key morphological traits of abundant species and related them to individual species' response to four decades of climate change. Specifically, our goals were to determine the direction and extent of range redistributions of diverse species across multiple ecological zones—including patterns of abundance throughout each species' range—and to assess whether long-term responses are mediated by interspecific functional traits. Given the higher evaporative demand from anomalously dry and warm conditions in our study region throughout the late 20th and early 21st centuries (Overpeck & Udall, 2020; Williams et al., 2020), we predicted that species exhibiting a conservative strategy would show more pronounced upward shifts with decreases in cover at the lower part of their range, while more acquisitive species would show increasing cover and range expansions at their trailing edge margins.

2 | MATERIALS AND METHODS

2.1 | Study site

The Deep Canyon Transect, part of the Boyd Deep Canyon Desert Research Center, is a steep elevational gradient gaining 2438 meters over a distance of 16 km (Figure 1). The gradient encompasses

nine distinctly described plant communities represented by over 600 species documented in the original survey of 1976–1977 (Zabriskie, 1979). In 2008, Kelly and Goulden (Kelly & Goulden, 2008) documented extensive range shifts in the 10 most widely distributed species attributed to recent climate change (although fire history has subsequently been argued as a significant factor [see Schwillk & Keeley, 2012]).

2.2 | Climate data

To determine whether climatic variables in the area have changed significantly, we used local weather station data from stations within 75 km of the study site, representing the elevation range within the transect, and containing nearly continuous records since 1947. For these stations, we analysed changes in the following climatic variables: mean annual temperature, mean annual maximum and minimum temperatures, mean annual precipitation, interannual precipitation variability using the coefficient of variation of monthly precipitation, number of days with maximum temperature less than 0°C, number of days with maximum temperature exceeding 32.2°C, and number of days receiving 2.54 mm in each month. We also analysed site-specific weather station data from the Boyd Deep Canyon Desert Research Center, which is the only climate dataset available from the study site which includes years preceding the first survey in 1977. Furthermore, to compare how climatic variables across the elevation gradient have changed in direction and rate, we analysed changes in 800-m resolution gridded climate data (PRISM; PRISM Climate Group 2014) using the location of transects at the lowest, highest and middle elevations. PRISM data are interpolated from nearby climate station data that are physiographically similar by calculating a local climate-elevation regression that also uses six other topographic predictors; they accurately characterize topoclimate in mountainous areas of the western US (Daly et al., 2008). For these data, we

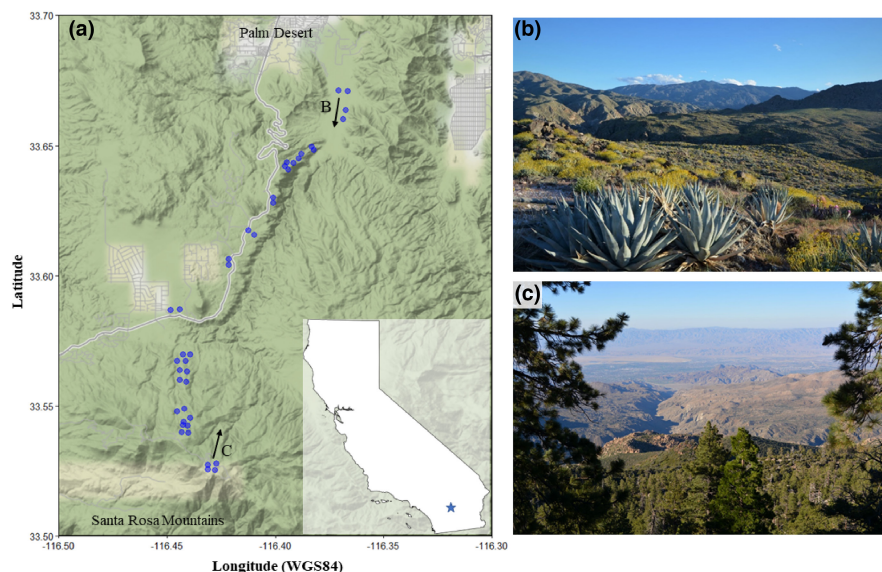


FIGURE 1 Study location of elevation gradient in southern California. (a) elevational distribution of sub-transects where each paired dots represent east and west boundaries of a 400m sub-transect. Inset map depicts general location of the Deep Canyon Transect. (b) View from sub-transect 1 looking to sub-transect 20, marked with a 'B' and an arrow depicting direction of view in a. (c) View from sub-transect 20 looking to sub-transect 1, marked with a 'C' and an arrow depicting direction of view in a.

evaluated trends in annual minimum, maximum and mean temperature, along with annual precipitation and vapour pressure deficit (VPD). Climatic changes across survey intervals were compared between each survey period using *t*-tests.

2.3 | Vegetation surveys

To understand how vegetation has responded to ongoing climatic changes, we resurveyed the plant communities following the same protocol used in the original surveys by Zabriskie (1979) also followed by Kelly and Goulden (2008). The original survey consisted of 22 linear transects along the elevation gradient, equally spaced at 122-meter intervals beginning at 24 meters elevation and following 400m isocontours. Due to urban development in the Coachella Valley, the lowermost transect was lost forever beneath an irrigated golf course subdivision, and therefore we only resurveyed 21 of the original transects. We surveyed all transects at peak biomass across the elevational gradient, from March 2019 at the lowest elevation, to August 2019 at the highest elevation. At each 400-m transect, we identified all perennial plant species, and abundance was estimated as the amount of foliage intercepted by the tape to the nearest centimetre. Permits were obtained for sampling on the Boyd Deep Canyon reserve and no permits were needed at other locations.

2.4 | Functional trait data

Since the raw transect data were not available for the 1977 survey, we retained the 36 species with published abundance values (Zabriskie, 1979) for subsequent analyses assessing long-term elevational trends. The 36 species were chosen by the original author to be published given their widespread distribution and dominance across the ecological communities spanning the gradient. From 10 individuals of each of these 36 species, we collected functional trait data but only collected leaf trait data on the 31 non-CAM species following standard protocols (Pérez-Harguindeguy et al., 2013; Table S2). For species spanning multiple habitat types, we collected 10 individuals from each habitat type to account for intraspecific trait variation along the gradient. We focused on 10 commonly measured traits that reflect well-documented trade-offs in plant ecological strategies and are all known to affect the ability of plants to establish, persist and reproduce in variable environments (Westoby et al., 2002) including plant height, SLA, leaf dry matter content (LDMC), leaf area (LA), leaf water content (LWC), seed mass, chlorophyll content, foliar $\delta^{13}\text{C}$, leaf nitrogen content and foliar $\delta^{15}\text{N}$. Plant height is related directly to growth rates and resource availability, and along with SLA has been shown to reflect biotic interactions in dryland communities (Gross et al., 2013). Additionally, plant height influences the extent of decoupling between free air temperature and leaf or canopy temperature (De Frenne et al., 2021; Körner, 2007). SLA, chlorophyll content and LDMC are traits related to a plant's ability to acquire and use nutrients,

while LA and LWC are related to light availability and water use (Pérez-Harguindeguy et al., 2013). Seed mass influences a plant's dispersal potential and establishment success (Moles & Westoby, 2004). Intrinsic water use efficiency (WUEi), measured as $\delta^{13}\text{C}$, reflects the relative efficiency of carbon gain through photosynthesis, in regard to water transpired (Farquhar et al., 1989), and can capture site water availability (Livingston & Spittlehouse, 1996). Leaf nitrogen content is associated with higher photosynthetic capacity (Evans, 1989) and foliar $\delta^{15}\text{N}$ can shed light on short-term dynamics of the N cycle (Craine et al., 2015).

Upon collecting leaves in the field, we placed them in water picks to hydrate for 24 h before processing. We measured LA (cm^2) by scanning fresh leaves with a flat-bed digital scanner and then calculated LA using ImageJ (Schneider et al., 2012). After scanning, fresh leaf mass (g) was determined using a digital balance, and subsequently dried at 60°C for at least 72 h prior to determining dry mass (g). LDMC was calculated as dry mass divided by fresh mass. Chlorophyll content was measured using a digital chlorophyll meter (Konica Minolta) and averaged across three measurements per leaf. We measured plant height as the distance from the ground to the highest photosynthetically active tissue. We used seed mass data retrieved from the TRY database (Kattge, 2020). Leaf $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were measured at the University of Wyoming Stable Isotope Facility (<http://www.uwyo.edu/sif/>) where samples were ground with a steel ball mill and analysed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ on a Carlo Erba 1110 Elemental Analyser coupled to a Thermo Delta V IRMS. Isotope ratios were calculated as

$$\delta [^{13}\text{C}, ^{15}\text{N}]_{\text{samples}} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000,$$

where R_{sample} and R_{standard} are the $\delta^{13}\text{C}/^{12}\text{C}$ or $\delta^{15}\text{N}/^{14}\text{N}$ molar abundance ratios of samples, with 36-UWSIF-Glutamic 1 and 39-UWSIF-Glutamic 2 used as reference samples.

2.5 | Data analysis

We tested for temporal changes in community-level attributes of total perennial plant cover, species richness (alpha diversity) and Shannon diversity by building linear mixed-effect models with fixed effects of elevation, year, their interaction and habitat. We used transect ID as a random effect to account for the non-independence of our observational units (transects). We expressed coefficients of determination as both marginal and conditional R^2 , where the former is the variation explained by fixed effects, and the latter the variation explained by both fixed and random effects. Models were conducted using the LME4 package (Bates et al., n.d.), and tests of significance were assessed with the package LMERTEST (Kuznetsova et al., 2017) using Satterthwaite's method.

We assessed changes in individual species' elevational distributions over time based on changes in leading edge range limits, rear edge range

limits and average elevation for each species (Figure 3a). Leading edge and rear edge limits were defined as the highest and lowest transects of occurrence across the elevation gradient. We also calculated the average abundance-weighted elevation for each species per survey year because range shift detection can potentially be misleading for species' upper and lower boundaries compared to changes in mean elevation (Shoo et al., 2006). To capture the complex changes in abundance across each species' entire range, we calculated probability density functions for each species spanning the entire gradient separately for each survey year using the *density* function with Gaussian kernel smoothing and weighing by species' cover values at each elevation (Rumpf et al., 2018). We used density estimation rather than comparing changes in abundance at each transect over time due to substantial range limit and abundance fluctuations between both survey intervals. Abundance was therefore defined as the integral of density functions. We then used the sum of modified density functions to calculate absolute changes in abundance across survey years, as well as changes in elevation optima defined as the peak of the density distribution and changes in maximum density to account for abundance changes at optimum range positions. Since abundance changes in individual species can differ substantially among range positions (leading versus rear edge), we assessed abundance changes at the 25% and 75% quantiles of density functions between original and most recent surveys. To account for changes at the median of species' distributions, we additionally evaluated the 50% quantiles. Additionally, we tested whether species' range limits, including average and optimum elevation, were contingent upon their original elevation for each survey

interval. Changes in individual species' range dynamics were assessed using linear mixed-effect models with survey year as a fixed effect and species as a random effect. To assess differences among survey intervals, we used paired t-tests for all the above range attributes.

To understand how functional traits might be related to observed range dynamics, we performed linear regressions using changes in range attributes as response and each individual trait as a predictor. Individual traits were tested for normality using Shapiro–Wilk normality tests, and traits not conforming to normality were log-transformed. In addition to individual traits, we conducted a principal components analysis (PCA) after scaling trait variables, retaining the first two principal components, and obtained scores on these two components for each species to use as predictors. Composite trait predictors from our PCA were only available for 26 species due to missing traits. Individual trait regressions were performed using trait data for 36 species, with some species missing traits either due to their physiology (cactus species were not collected for leaf traits) or due to missing data.

3 | RESULTS

3.1 | Climatic changes

Nearby weather station data showed pronounced changes since 1947, with general increases in nearly all temperature variables (Table S1). Gridded climate data from the lowest, middle and highest

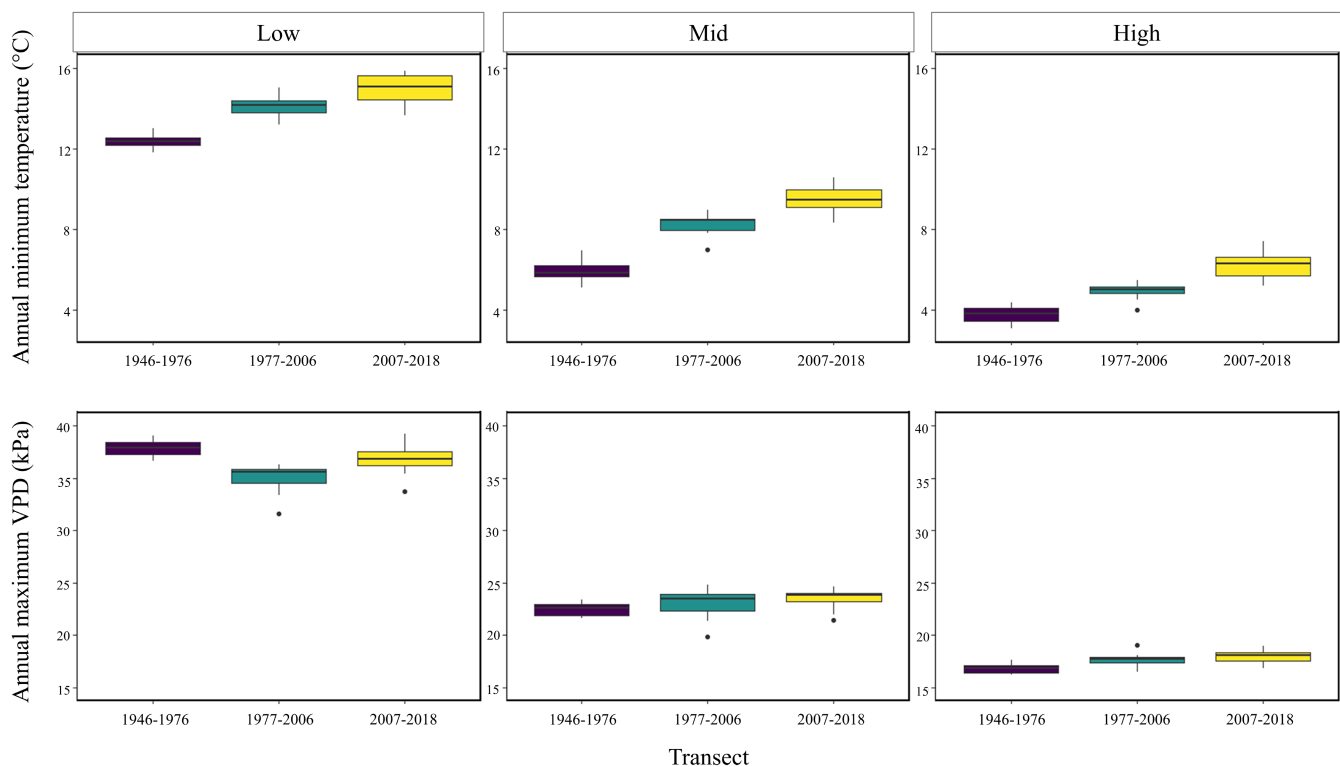


FIGURE 2 Annual minimum temperature and annual maximum vapour pressure deficit (VPD) in the years preceding each survey (Survey 1 in 1977: 1946–1976; Survey 2 in 2007/8: 1977–2006; Survey 3 in 2019: 2007–2018) from the lowermost (low), middle (mid) and highest (high) elevation transects across the sampled gradient.

elevation transects showed substantial warming trends, with annual minimum temperature increasing by 2.77°C at the lowest, 3.84°C at the middle and 2.3°C at the highest elevation between the years preceding the first and most recent surveys (Figure 2; Table S2). Notably, there were heterogeneous changes among different elevations, where rate and magnitude of warming was generally highest at the middle elevation, while the lowest elevation exhibited increases in precipitation (54 mm) and decreases in VPD (−2.17 kPa) and maximum temperature (−2.17°C) between the first and second surveys (between the third and fourth quarters of the 20th century). Long-term climate data dating to 1961 from the Boyd Deep Canyon centre station (Table S1) showed a trend towards increased interannual precipitation variability (measured as the coefficient of variation, $F = 2.84$, $p = 0.091$), and no overall significant changes in mean annual or seasonal (winter and summer) precipitation (MAP: $F = 0.02$, $p = 0.884$; winter precipitation: $F = 0.01$, $p = 0.93$; summer: $F = 0.44$, $p = 0.506$). However, there was a significant increase in average minimum temperature (0.98°C; $F = 10.5$, $p = 0.001$) and average maximum temperature (3.61°C; $F = 108.8$, $p < 0.001$) over the same time period (see Supporting Information for details).

3.2 | Range dynamics

We found evidence for both species range edge shifts and population abundance changes, and that these changes were predicted by interspecific differences in functional traits. First, we found substantial changes in leading edge distributions, with an

average elevation increase of 116.1 meters from 1977 to 2019 (1977 mean: 1612 ± 34.6 (SE) m; 2019 mean: 1728.1 ± 34.6 (SE) m, $t = 3.44$, $p = 0.001$, Figure 3b) and substantial changes in rear edge range limits with an average downward shift of 84.9 m (1977 mean: 1389.4 ± 28.12 (SE) m; 2019 mean: 1304.49 ± 28.12 (SE) m, $t = 3.01$, $p = 0.004$, Figure 3c). Species with higher $\delta^{13}\text{C}$, indicating higher intrinsic WUE, showed greater upward shifts ($F = 5.08$, $p = 0.034$, Figure 4a; Table 1) and species exhibiting higher SLA ($F = 11.55$, $p = 0.002$) and shorter species ($F = 6.66$, $p = 0.016$) shifted downward in their lower edge elevation range (Table 1). Moreover, principal component axis 1 (PC1 accounting for 37.8% of total trait variation and associated with seed mass (0.49), SLA (−0.40), $\delta^{13}\text{C}$ (0.38) and height (0.37) (Figure 4b)) showed a positive relationship with lower elevation margin changes ($F = 8.25$, $p = 0.008$), where species with lower PC1 scores showed downward shifts (Figure 4d; Table 1). In addition, total elevational range size increased across sampling years ($t = 4.28$, $p < 0.0001$), owing to a large increase in average range size from 1977–2008 (1977 mean: 222.62 ± 50.9 (SE) m; 2008 mean: 485.46 ± 50.9 (SE) m, $t = 5.15$, $p < 0.0001$) where shorter statured species increased their range span while taller species exhibited range contractions ($F = 6.95$, $p = 0.01$; Table 1). However, like maximum elevation limits, there was a reversal where average range size contracted from 2008 to 2019 by an average of 61.8 m (2008 mean: 485.46 ± 25.4 (SE) m; 2019 mean: 423.65 ± 25.4 (SE) m, $t = -2.43$, $p = 0.020$). Range contractions during the most recent survey interval were positively associated with LDMC, where lower LDMC species showed greater range contractions ($F = 4.94$, $p = 0.034$; Table 1). Changes

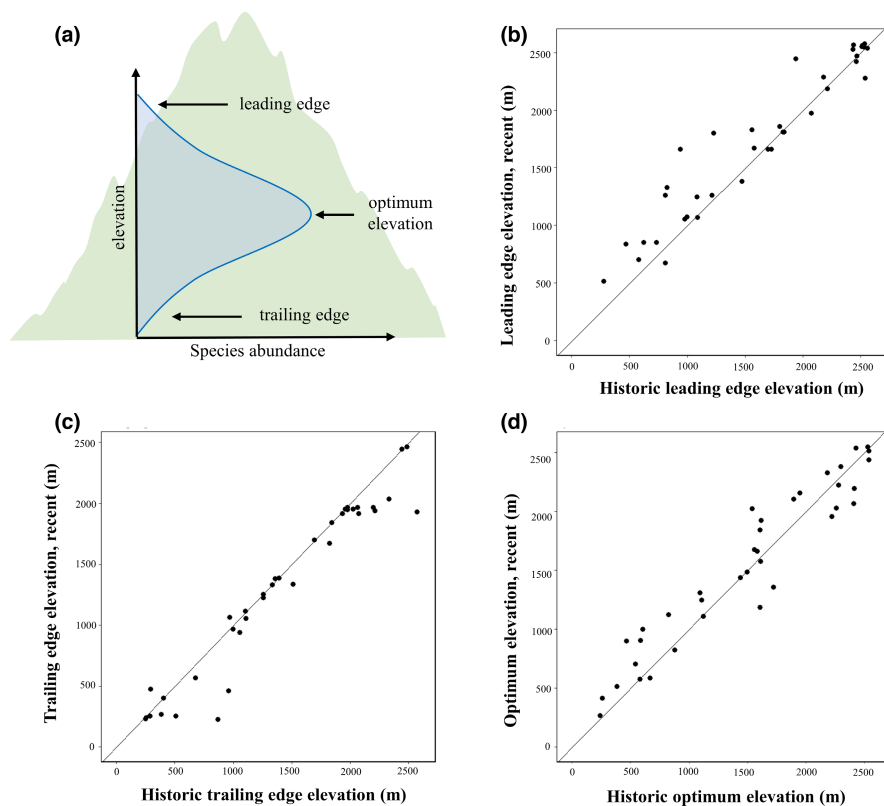


FIGURE 3 (a) Schematic describing elevational range attributes; (b) changes over time in species' leading edge; (c) trailing edge; and (d) optimum elevational distributions. $N = 37$ species. Each data point represents a single species. Diagonal (1:1) line represents no elevational change. Points above the line indicate X and points below the line indicate Y.

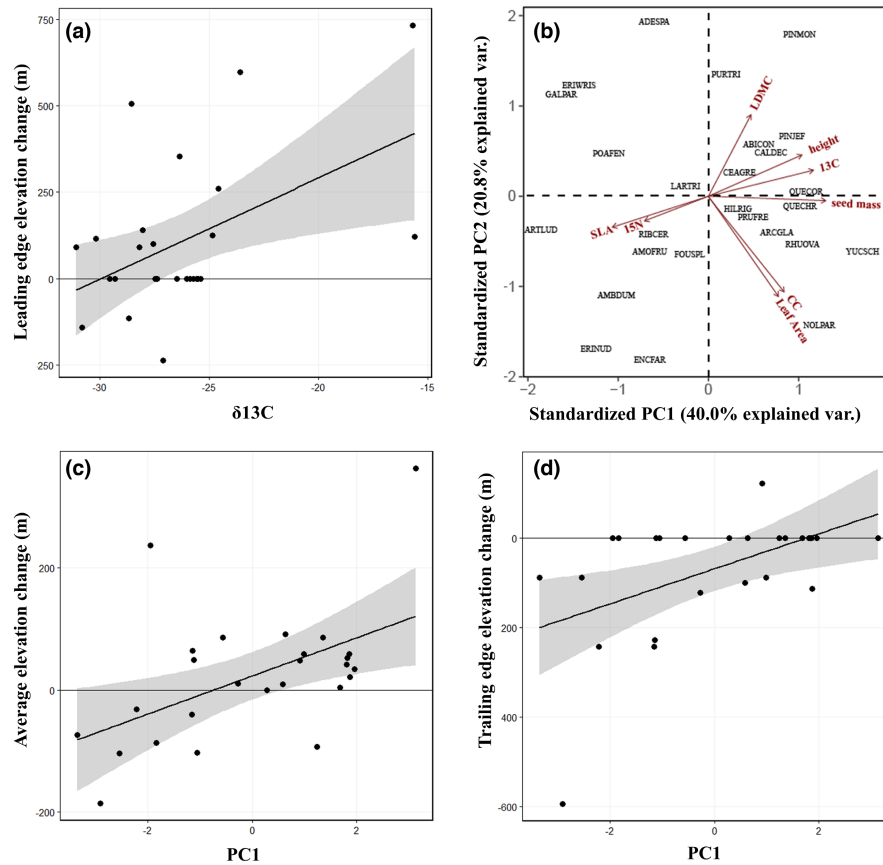


FIGURE 4 Functional traits predict range dynamics in response to 42 years of climatic change. A single trait, ^{13}C , explained changes in leading edge elevational changes (a), while multidimensional traits associated with PC axis 1 (b) explained changes in average (abundance weighted) elevation (c) and trailing edge range limits (d). Lines and their shades represent significant linear regression models (Table 1) with shading depicting 95% confidence intervals. Species' codes: *Abies concolor* = ABICON, *Adenostoma sparsifolium* = ADESPA, *Ambrosia dumosa* = AMBDUM, *Amorpha fruticosa* = AMOFRU, *Arctostaphylos glauca* = ARCGLA, *Arctostaphylos patula* = ARCPAT, *Arctostaphylos pringlei* = ARCPRI, *Artemisia ludoviciana* = ARTLUD, *Bernardia incana* = BERINC, *Calocedrus decurrens* = CALDEC, *Ceanothus greggii* = CEAGRE, *Encelia farinosa* = ENCFAR, *Eriogonum nudum* var. *pauciflorum* = ERINUD, *Eriogonum wrightii* var. *subscaposum* = ERIWRIS, *Fouquieria splendens* = FOUSPL, *Galium parishii* = GALPAR, *Hilaria rigida* = HILRIG, *Larrea tridentata* = LARTRI, *Lupinus formosus* = LUPFOR, *Nolina parryi* = NOLPAR, *Pinus jeffreyi* = PINJEF, *Pinus monophylla* = PINMON, *Poa fendleriana* = POAFEN, *Prunus fremontii* = PRUFRE, *Psoralea schottii* = PSOSCH, *Purshia tridentata* = PURTRI, *Quercus chrysolepis* = QUECHR, *Quercus cornelius-mulleri* = QUECOR, *Rhus ovata* = RHUOVA, *Ribes cereum* = RIB CER, *Symphoricarpos rotundifolius* var. *parishii* = SYMPAR, *Yucca schidigera* = YUCSCH.

in overall range size were correlated with rear edge elevation changes ($F = 23.3$, $p < 0.001$), where species that shifted downward in their rear edge showed the greatest increases in range size while species shifting upward showed range contractions.

In addition to distributional changes, we found that interspecific differences in functional traits predicted patterns of population abundance change. There was an upward shift in species' optimum elevation as defined by the peak of density distributions (1977 mean: 1491.8 ± 69.8 (SE) m; 2019 mean: 1547 ± 64.1 (SE) m, $t = -2.8$, $p = 0.006$; Figure 3d) where species possessing lower chlorophyll content shifted their optima downward, and vice versa ($F = 4.91$, $p = 0.035$; Table 1). Due to divergent responses among species correlated with directional changes in range margins, average abundance-weighted elevation showed no overall change from 1977 to 2019 (1977 mean: 1504.49 ± 17.8 (SE) m; 2019 mean: 1521.04 ± 17.8 (SE) m, $t = 1.05$, $p = 0.297$). However, the divergent responses were captured by differences in functional traits, where

species showing an upward shift in abundance-weighted elevation had lower SLA ($F = 7.55$, $p = 0.010$) and higher $\delta^{13}\text{C}$ ($F = 7.25$, $p = 0.012$; Table 1) and had higher PC1 scores ($F = 8.39$, $p = 0.008$; Figure 4c). While average leading-edge abundance (75% quantiles of density functions) among species showed no change overall ($F = -0.83$, $p = 0.411$; Figure S3), average abundance at median elevation (50% quantiles of density distributions) decreased ($t = -2.98$, $p = 0.038$), and trailing-edge abundance (25% quantiles of density functions) decreased ($t = -2.22$, $p = 0.029$; Figure S4). Importantly, species with higher LDMC ($F = 4.3$, $p = 0.046$), lower SLA ($F = 6.09$, $p = 0.019$), higher seed mass ($F = 6.86$, $p = 0.014$), higher $\delta^{13}\text{C}$ ($F = 7.2$, $p = 0.011$) and taller stature ($F = 4.12$, $p = 0.052$) tended to decrease in median elevation abundance across the survey period (Table 1). Consequently, PC1 was the strongest predictor of median elevation abundance change, where species scoring higher declined the most ($F = 9.46$, $p = 0.005$). However, PC1 was a weaker predictor of abundance changes in rear edge abundance, where species

TABLE 1 Plant functional traits describing long-term changes in distributional range attributes across multiple survey periods between 1977 and 2019.

Range attribute	Trait	Change 1977–2008			Change 2008–2019			Change 1977–2019		
		Coefficient	R2	p-value	Coefficient	R2	p-value	Coefficient	R2	p-value
Average elevation	Chlorophyll content	34.08	0.164	0.014						
	Leaf area	27.11	0.133	0.025						
	Specific leaf area	-0.88	0.118	0.033				-1.14	0.179	0.01
	13C							102.73	0.168	0.012
	PC1							31.13	0.228	0.008
Optimum elevation	Chlorophyll content						62.9	0.115	0.025	
	13C	27	0.147	0.018				187.94	0.16	0.013
Rear edge range limit	Chlorophyll content	48.4	0.108	0.04	-37.69	0.106	0.042			
	Specific leaf area	-1.94	0.233	0.004				-1.83	0.308	0.001
	Height	70.52	0.29	0.001				45.5	0.162	0.016
	seed mass	31.44	0.172	0.012						
	13C	167.86	0.196	0.007						
Total range size	PC1							39.08	0.26	0.008
	LDMC				589.7	0.116	0.034			
Height	Height	-90.41	0.17	0.014						
	LDMC	-1.13	0.178	0.018						
Leading edge abundance (75% quantile)	13C	-0.03	0.15	0.029						
	seed mass	-0.05	0.27	0.004						
	PC1							-0.07	0.114	0.051
Rear edge abundance (25% quantile)	LDMC	-1.27	0.144	0.02				-1.19	0.1	0.046
	seed mass	-0.05	0.113	0.037				-0.06	0.163	0.014
Median abundance (50% quantile)	SLA							0	0.145	0.02
	13C	-0.04	0.126	0.026				-0.04	0.167	0.012
	PC1							-0.1	0.253	0.005
Optimum abundance (peak of density distribution)	Leaf area	-0.11	0.297	0.001						
	13C							0.21	0.12	0.03
Absolute abundance (sum of density distribution)	13C									
	Proportional change in abundance	0.09	0.105	0.039				0.09	0.142	0.019

Abbreviations: LDMC, leaf dry matter content; SLA, specific leaf.

scoring lower (smaller seed mass, shorter stature and lower LDMC) showed increases ($F = 4.22$, $p = 0.051$) and no other trait being predictive. Lastly, species showing declines in abundance at the leading edge were associated with higher $\delta^{13}\text{C}$ ($F = 5.07$, $p = 0.029$), larger seeds ($F = 13.5$, $p = 0.004$) and greater LDMC ($F = 7.04$, $p = 0.018$; Table 1).

Finally, changes in leading and rear edge abundance were positively related ($F = 4.51$, $p = 0.041$), where species increasing at one range margin tended to increase at the other, and likewise, species that declined at one margin declined in the other. Species that increased their overall range size likewise showed significant increases in their proportional abundance ($F = 6.43$, $p = 0.016$). Similarly, species shifting upward at their leading-edge range margins showed a decreasing trend in abundance at their median ($F = 4.82$, $p = 0.035$) and rear edge ($F = 3.07$, $p = 0.089$). Species occupying a lower historic average elevation showed more pronounced upward shifts in their leading edge, and vice versa, from 1977 to 2008 ($F = 4.215$, $p = 0.047$). Similarly, historic leading-edge elevation was predictive of leading-edge range shifts, where species with historically lower elevation margins showed more pronounced upward leading-edge shifts ($F = 9.81$, $p = 0.003$). A similar pattern was found for optimum elevation, where species with historically lower elevation optima showed greater upward shifts in their optimum elevation ($F = 7.64$, $p = 0.009$). However, while these range redistributions were correlated with historic elevation, only one trait—chlorophyll content—showed systematic variation with historic range attributes, where species occupying lower elevations tended to have higher chlorophyll content and vice versa (Table S6). Species that were historically more abundant showed stronger decreases in total abundance, and vice versa, from 1977 to 2008 ($F = 8.47$, $p = 0.006$). Changes in total perennial plant cover remained relatively stable across the survey period, but habitat-specific changes reflected changes in species abundance patterns, where cover increased at the lowest elevation transects and decreased at the highest elevations (Figure S1; Table S3).

4 | DISCUSSION

While recent work has identified plant functional traits associated with growth and survival under climate warming and drying within species' current distributions (Kühn et al., 2021; Soudzilovskaia et al., 2013), few studies have consistently predicted distributional responses of species across ecosystems. Here, we find strong support for the ability of plant functional traits associated with resource use and acquisition to predict plant distributional responses to long-term climate change (Figure 4), especially when considering the multidimensional nature of species' distributions. Concordant with global average rates across other biomes (i.e. 5–30m/decade, Kelly & Goulden, 2008; Lenoir et al., 2008), we found a 29m/decade average upslope shifts for species' leading edge and that taller species exhibiting more conservative traits (lower SLA, greater $\delta^{13}\text{C}$, larger seed mass) shifted upward in their leading-edge range limit as well

as their average elevation, and trailing edge range limit. However, we also found substantial downward shifts where shorter species with more acquisitive traits (higher SLA, lower $\delta^{13}\text{C}$, smaller seed mass) shifted downward, increased in abundance at their trailing edge and increased their total range size, adding to accumulating long-term studies showing downward shifts in elevation or latitude (Abella et al., 2019; Fei et al., 2017; Kopp & Cleland, 2014). Critically, our results suggest that these divergent responses among species in distributional shifts can be understood by examining the variation in coordinated functional traits among species.

Dryland ecosystems are experiencing anthropogenic-driven elevated temperatures and increased chronic and extreme drought (Williams et al., 2020) which has and will continue to decrease soil moisture (Bradford et al., 2020), disproportionately impacting species reliant on deeper soil water (Schlaepfer et al., 2017). Our results are consistent with recent work showing that this is already happening in southern California (Goulden & Bales, 2019), as taller species with more conservative traits which typically rely on deeper water sources show upward shifts and decline at their lower and median elevations. Specifically, our results show that across the entire survey period (1977–2019) species possessing traits scoring higher on PC1 (taller height, lower SLA, greater $\delta^{13}\text{C}$ and larger seed mass) shifted upward in their leading-edge range limit, average elevation and rear edge range limit, while declining in trailing edge abundance and range median abundance. If extreme drought is an important driver of the observed range redistributions, these results are contrary to what would be expected for seed mass and $\delta^{13}\text{C}$, since seed mass plays a critical role in enhancing seedling survival under drought stress (Moles & Westoby, 2004), and higher $\delta^{13}\text{C}$ values are associated with greater iWUE (Farquhar et al., 1989). However, taller plants have wider water-conducting conduits, which make taller species more susceptible to embolisms, and therefore increase their vulnerability to drought (Olson et al., 2018). Thus, the observed declines in rear edge and centre abundance are potentially due to drought-induced embolism, while the same species have increased in abundance at their leading edge owing to their larger seed mass and higher iWUE conferring increased survival of juveniles.

Interestingly, we found that species in this system are highly responsive to recent climatic changes, which adds to the growing body of literature showing high sensitivity of dryland ecosystems to climate change (Burrell et al., 2020; Schlaepfer et al., 2017; Shriver et al., 2022). Both local weather station data and gridded climate data showed long-term patterns consistent with warming temperatures, where substantial increases in winter minimum temperatures showed the most dramatic increases, which were more pronounced at lower and mid elevations. These results support recent work highlighting elevational differences in warming rates (Pepin et al., 2015), and our findings of elevational differences in climate helps explain some of the heterogeneity of range redistributions. For instance, the downward shift in lower elevation range margins occurred following a period of cooler and wetter conditions at the lowest elevation, while the upward shifts in leading edge margins occurred over the same interval, where the middle and highest elevations showed

pronounced increases in temperature and VPD. Additionally, we found a downward shift in leading edge margins between the second and most recent survey, which was characterized by anomalously warm regional drought which caused extensive mortality (Dong et al., 2019; Goulden & Bales, 2019), and which likely caused mortality in newly establishing juveniles of species that had previously shown upward leading-edge shifts. Furthermore, we found that lower-elevation species tended to exhibit more substantial upward range shifts, consistent with recent long-term trends from other mountainous ecosystems (Mamantov et al., 2021; Rumpf et al., 2018). While prevailing explanations include trait covariation with elevation and higher-elevation species having a broader thermal tolerance being adapted to greater diurnal and seasonal temperature fluctuations, only one trait—chlorophyll content—varied with elevation, and was not predictive of any range attribute changes, while our elevation gradient shows an opposite pattern of lower elevations experiencing greater temperature fluctuations than higher elevations. Thus, in contrast to more temperate mountain ecosystems (Pepin et al., 2015), our findings of elevation-dependent range shifts likely reflect that our dryland system is experiencing more rapid warming at lower elevations, consistent with recent work highlighting the potential for differences in climate exposure to drive geographical variation in species' responses (Kling et al., 2020; Oldfather et al., 2019). Despite this heterogeneity in climate change exposure, species showed responses consistent with increasing aridification, where more variable precipitation and hotter drought periods across southern California have promoted the replacement of stress-tolerant species with more resource-acquisitive species that possess drought avoidant traits (Berdugo et al., 2020).

While recent work examining trait-mediated fitness responses to climate change have found that lower SLA and higher $wWUE$ tend to show positive responses to increasing temperatures (Kühn et al., 2021), our long-term results provide contrasting evidence. Intriguingly, while species inhabiting resource-poor environments tend to exhibit more conservative traits than species in resource-rich environments (Reich, 2014), recent studies suggest that there is a reversal in the plant economics spectrum under more arid conditions (Carvajal et al., 2019). Specifically, resource-acquisitive strategies may allow plants to exploit more sporadic and seasonal precipitation, while conservative traits require greater energy expenditure (Mooney & Dunn, 1970). This reversal might also be partially explained by recent work on leaf thermoregulation which has shown that plant species strategize along a spectrum of leaf thermal stability and photosynthetic thermal stability, with more acquisitive species having larger thermal photosynthesis range (Michaletz et al., 2016). Furthermore, plants on the leaf economic spectrum exhibit contrasting extent of decoupling of leaf temperature from ambient air temperature during carbon assimilation, where species with shorter stature and lower WUE_i (lower $\delta^{13}C$) show greater temperature decoupling, allowing them to have cooler leaves while inhabiting low-elevation arid sites (Liancourt et al., 2020). Ultimately, since most long-term vegetation monitoring has occurred in temperate ecosystems, our results likely reflect the differences in trait

selection between arid and temperate biomes. However, our results have important implications more generally, as species with drought-adapted, conservative traits are experiencing extensive mortality worldwide at their driest range margins in response to climate stress exceeding their physiological limits (Anderegg, Trugman, et al., 2019), and such drought-induced mortality is leading to widespread ecosystem-type conversion (Batllori et al., 2020).

Finally, recent work has questioned the reliability of 'snapshot resampling' when inferring climate change impacts, owing largely to the potential for interannual variation to obscure long-term trends (McCain et al., 2016; Stuble et al., 2021). Interannual fluctuations in population abundance, as well as a high frequency of local extinctions and recolonization events could both lead to inaccurate detection through over- or underestimation of range dynamics through time (McCain et al., 2016). However, several aspects of our study make our results robust. First, the plants in our long-term study are all dryland perennial species, which have notoriously slow population dynamics—the median longevity of several of our species is greater than a century (Cody, 2000). Second, while species' range edges are often characterized by high population variability (Sexton et al., 2009), we assessed multiple dimensions of species' distribution dynamics, which all showed consistent patterns based on the synchronous species' responses strongly correlating with their functional traits. Importantly, long-term vegetation data collected at high spatial resolution and spanning decades provides a unique opportunity for understanding biodiversity response to rapidly changing climatic conditions (Magurran et al., 2010) and can overcome many of the issues associated with 'snapshot resampling'.

In conclusion, our results suggest that idiosyncrasies in range shifts can be understood by pursuing a more comprehensive focus on multiple dimensions of species' ranges and by considering functional traits associated with resource use. We found a clear pattern of species' distributional responses to contemporary climate change being mediated by their functional traits, where species possessing more conservative resource-use traits shifted upwards and declined in abundance, while species with more resource-acquisitive traits shifted downward and increased in abundance. Ultimately, the high incidence of range-shifting species within our study has the potential to result in novel biotic interactions, including both the gain in antagonistic interactions (novel competitors, pathogens and herbivores) as well as the loss of mutualists (soil microbes and pollinators), which could either facilitate or hinder species' distributional changes (Alexander et al., 2015; Hagedorn et al., 2019; Keeler et al., 2021). Moreover, as dryland ecosystems have a disproportionate role in the global carbon budget (Ahlström et al., 2015), the replacement towards more acquisitive leaf traits in response to climate change should alter nutrient cycling and carbon sequestration (Buzzard et al., 2019). The increasing prevalence of acquisitive leaf traits in dryland ecosystems may, furthermore, be associated with the beginning of an 'ecosystem breakdown' threshold of aridification, where the mortality of resource conservative species occurs as they are no longer able to cope with increasingly scarce water and nutrient availability (Berdugo et al., 2020).

Indeed, NDVI patterns across southern California's Sonoran desert region show declining vegetation cover (particularly in the more xeric areas) suggesting that the region may already be crossing this threshold (Hantson et al., 2021). Given the paucity of long-term vegetation data from dryland ecosystems, and that more than 20% of the Earth's terrestrial surface is expected to cross at least one threshold of aridification by 2100 (Berdugo et al., 2020), our results provide critical insight into the distributions of dryland plant species under rapidly changing conditions and how trait-mediated changes might impact future ecosystem functioning.

AUTHOR CONTRIBUTIONS

Tesa R. Madsen-Hepp and Marko J. Spasojevic designed the research; Tesa R. Madsen-Hepp, Shane McFaul and Lisa Schauer collected the data; Tesa R. Madsen-Hepp analysed the data; and Tesa R. Madsen-Hepp wrote the manuscript with editing and input from Marko J. Spasojevic and Janet Franklin.

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CONFLICT OF INTEREST STATEMENT

Marko Spasojevic is an Associate Editor of Functional Ecology but took no part in the peer review and decision-making processes for this paper. The authors otherwise declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3n5tb2rn7> (Madsen-Hepp et al., 2023).

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SUPPORTING INFORMATION

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

Table S1. Climatic variables showing significant ($p < 0.05$) changes across survey intervals from local weather station data. DP01 is the number of days with greater than 0.01 inch/0.254 millimeters of precipitation, DP10 is the number of days with greater than 0.1 inch/2.54 millimeters of precipitation, DT32 is the number of days with maximum temperature less than 32 degrees F/0 degrees C, and DX90 is the number of days exceeding 90 degrees F/32.2 degrees C. *Boyd Deep Canyon climate data records date to 1961, rather than 1947.

Table S2. Changes in climatic variables between survey intervals across the elevation gradient using PRISM data, * indicates significance < 0.05 .

Table S3. Summary of sub-transects included in the study and their vegetation changes over the study period.

Table S4. Functional trait values for all species included in the study. Species codes found in Supplementary Figure S3.

Table S5. Elevational range attributes predicted by original elevation. For each range attribute, original elevation is the original value for the given range attribute at the start of the survey interval.

Table S6. Functional trait predictions of range attributes for each survey year.

Figure S1. Temporal changes in perennial plant species cover across the elevation gradient for all three survey years. The overall model showed no significant changes across years for the entire gradient ($F = 0.36$, $p = 0.55$), but showed marginally significant changes across habitats ($F = 2.91$, $p = 0.06$).

Figure S2. Leading edge range limit changes from 1977–2008 (A), 2008–2019 (B), and 1977–2019 (C) and trailing edge range limit changes from 1977–2008 (D), 2008–2019 (E), and 1977–2019 (F).

Figure S3. Changes in leading edge abundance (top row) for all species from 1977–2008 (A), 2008–2019 (B), and 1977–2019 (C); and changes in leading edge limits (bottom row) from 1977–2008 (D), 2008–2019 (E), and 1977–2019 (F). Species' codes: *Abies concolor* = ABICON, *Adenostoma sparsifolium* = ADESPA, *Agave deserti* = AGADES, *Ambrosia dumosa* = AMBDUM, *Amorpha fruticosa* = AMOFRU, *Arctostaphylos glauca* = ARCGLA, *Arctostaphylos parryana* ssp. *desertica* = ARCPAR, *Arctostaphylos patula* = ARCPAT, *Arctostaphylos pringlei* = ARCPRI, *Artemisia ludoviciana* = ARTLUD, *Bernardia incana* = BERINC, *Calocedrus decurrens* = CALDEC, *Ceanothus greggii* = CEAGRE, *Cylindropuntia ganderi* = CYLGAN, *Encelia farinosa* = ENCFAR, *Ephedra nevadensis* = EPHSPP, *Eriogonum nudum* var. *pauciflorum* = ERINUD, *Eriogonum wrightii* var. *subscaposum* = ERIWRIS, *Fouquieria splendens* = FOUSPL, *Galium parishii* = GALPAR, *Hilaria rigida* = HILRIG, *Larrea tridentata* = LARTRI, *Lupinus formosus* = LUPFOR, *Nolina parryi* = NOLPAR, *Cylindropuntia ramosissima* = OPURAM, *Pinus jeffreyi* = PINJEF, *Pinus monophylla* = PINMON, *Poa fendleriana* = POAFEN, *Prunus fremontii* = PRUFRE, *Psoralea schottii* = PSOSCH, *Purshia tridentata* = PURTRI, *Quercus chrysolepis* = QUECHR, *Quercus cornelius-mulleri* = QUECOR, *Rhus ovata* = RHUOVA, *Ribes cereum* = RIB CER, *Symphoricarpos rotundifolius* var. *parishii* = SYMPAR, *Yucca schidigera* = YUCSCH.

Figure S4. Changes in trailing edge abundance (top row) for all species from 1977–2008 (A), 2008–2019 (B), and 1977–2019 (C); and changes in trailing edge limits (bottom row) from 1977–2008 (D), 2008–2019 (E), and 1977–2019 (F).

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