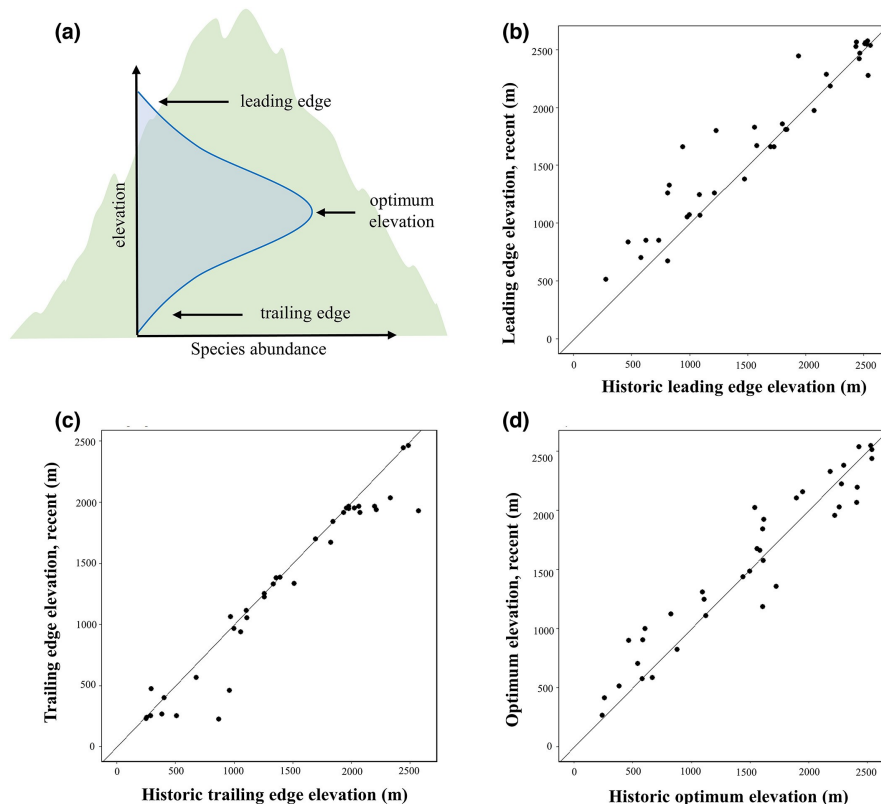


4.4 Vegetation Distribution Shifts

Increasing climate stress in an extreme desert environment is pushing many plant species toward their physiological limits. Along an elevational transect in the Sonoran Desert, vegetation has shifted to higher elevations in response to climate change. Taller and slower-growing species moved upward and declined in abundance, whereas smaller, faster-growing species shifted to lower elevations and increased in abundance.

Figure 4.4.1. Changes in Species Elevational Ranges.



The graphs above compare recent (2019) vs historic (1977) elevational ranges of 36 plant species in the Deep Canyon Transect in the Santa Rosa Mountains of the Sonoran Desert. a) conceptual diagram illustrating species abundance across elevation; b) the leading edge (where the plant species expand into new areas); c) trailing edge (the contracting or retreating edge); and d) the optimal elevation of each species.

Source: Madsen-Hepp et al. (2023)



What does the indicator show?

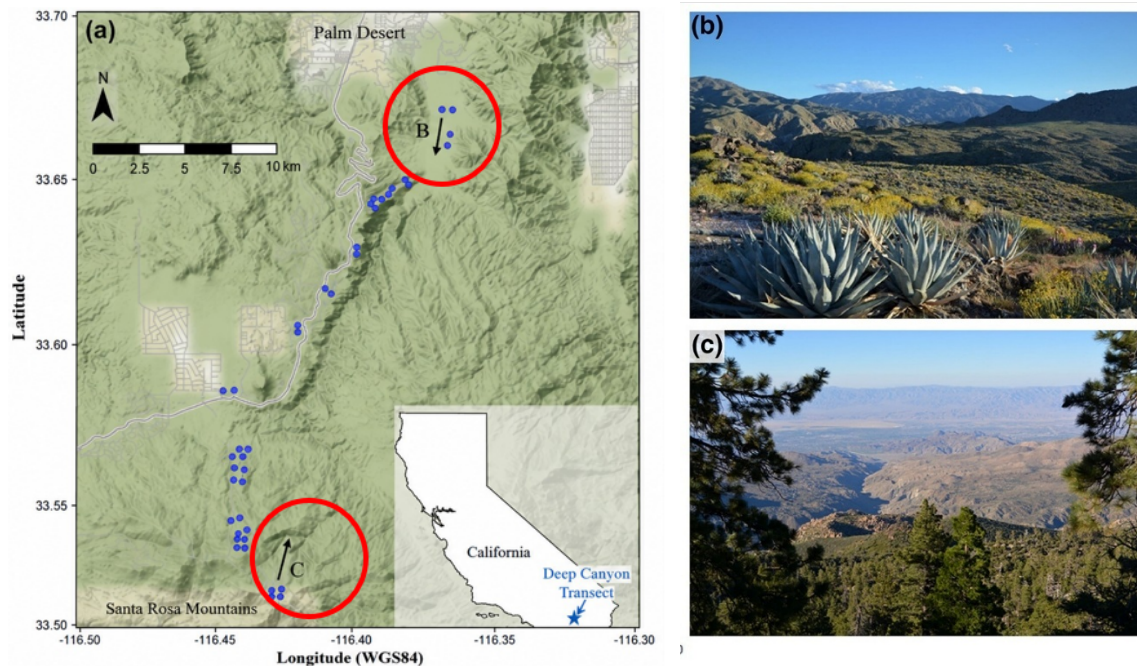
Vegetation in a steep elevation gradient in the Sonoran Desert underwent substantial range shifts ([Figure 4.4.1](#)) as well as pronounced changes in patterns of species abundance from 1977 to 2019. Range shifts occurred at both the leading edge (advancing or colonizing front where the species is expanding into new, previously unoccupied areas) and the trailing edge (retreating or contracting edge). At about 29 meters per decade, the overall upward range shifts are on par with the higher end of global rates for plant movement in response to climate warming — on average, plants in temperate regions have shown range shift rates between 5 and 30 meters a decade (Madsen-Hepp et al., 2023)

The vegetation shifts were observed in the Deep Canyon Transect, part of the Boyd Deep Canyon Desert Research Center in the Sonoran Desert of southern California, a steep elevational gradient gaining 2438 meters (m) over 16 kilometers (km) ([Figure 4.4.2](#)). The gradient encompasses nine distinct plant communities, represented by over 600 species documented in the original 1977 survey (Zabriskie, 1979). In 2008, Kelly and Goulden documented extensive range shifts in the 10 most widely distributed species, attributed to climate change (Kelly and Goulden, 2008).

Some lower-elevation trees declined in abundance and shifted upwards, while other species moved down into hotter and drier parts of the desert. Taller species exhibiting more conservative traits (i.e., traits that favor slow growth and conserved use of resources) shifted upward in their leading-edge range limit as well as their average elevation, and trailing edge range limit. Substantial downward shifts occurred among shorter species with more acquisitive traits (i.e., traits that promote faster growth), including white bursage (*Ambrosia dumosa*), brittlebush (*Encelia farinose*), big galleta (*Hilaria rigida*), and muttongrass (*Poa fendleriana*), which increased in abundance at their trailing edge and increased their total range size.



Figure 4.4.2. Study Location in Sonoran Desert.



The following figures show (a) elevational distribution of sub-transects where each paired dot represents east and west boundaries of a 400 m sub-transect. The inset map depicts the general location of the Deep Canyon Transect. (b) View from sub-transect 1 looking to sub-transect 20, in [Figure 4.4.2\(a\)](#) this is marked with a 'B' (circled in red) and an arrow depicting direction of view. (c) View from sub-transect 20 looking to sub-transect 1, in [Figure 4.4.2\(a\)](#) this is marked with a 'C' (circled in red) and an arrow depicting direction of view.

Source: Madsen-Hepp et al. (2023)

The Sonoran Desert became more barren, as taller trees and plants shift to higher elevations and declined in numbers, while smaller brush-like plants filled in the gaps. Specifically, stress-tolerant species like California Juniper and Pinyon pine declined or shifted upwards and did not appear to be thriving at their new ranges. Plant species with shallower root systems, such as brittlebush, burrow bush, and ocotillo, moved downward. These shorter plants rely less on deep soil water (increasingly scarce in the region). In addition, they grow faster and invest fewer resources in their leaves, and are drought-deciduous (i.e., their leaves drop during drought). Plants that retain their leaves all year tend to have thicker leaves with a higher carbon content. They are at a disadvantage compared to plants that are more easily able to shed leaves: when plants



drop leaves, the atmosphere can no longer pull water from them, which eases the demand on the roots to make up for the lost water.

Why is this indicator important?

Global climate change is rapidly altering terrestrial biodiversity (Díaz et al., 2019). While many studies have shown how hotter and drier temperatures are redistributing plant species in alpine regions and mountain ranges, observations from the Deep Canyon transect show that even hardy desert vegetation – long thought to be tolerant to stressors like drought and heat – are vulnerable to the impacts of climate change. The high incidence of range-shifting species in Deep Canyon may result in novel biotic interactions, including both the gain in antagonistic interactions (novel competitors, pathogens and herbivores) and 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, 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 will likely 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, normalized difference vegetation index (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), observations in Deep Canyon provide critical insight into the distributions of dryland plant species in California under rapidly changing conditions and how trait-mediated changes might impact future ecosystem functioning.



The climate and vegetation gradient of Deep Canyon's slopes is analogous to the south-to-north gradient of California. Deep Canyon's climate ranges from hot desert at the mountain base, stretching upward through warm chaparral, and finally into mild conifer forests at the mountain peak. This pattern is similar to the transition along the state of California, from the southern deserts northward through chaparral-covered foothills and mountains, and into the mild evergreen forests of northern California. Understanding the effects of local climate change on Deep Canyon's vegetation gradient can provide insight into how California's vegetation may respond to a warmer or drier climate.

What factors influence this indicator?

Dryland ecosystems such as Deep Canyon 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). Taller species with more conservative traits which typically rely on deeper water sources show upward shifts and decline at their lower and median elevations (Goulden and Bales, 2019).

Nearby weather station data showed pronounced changes since 1947, with general increases in nearly all temperature variables. Gridded climate data from the lowest, middle and highest elevation transects showed substantial warming trends, with annual minimum temperature increasing by 2.77 Celsius (°C) (4.99 degrees Fahrenheit (°F)) at the lowest, 3.84°C (6.91°F) at the middle and 2.3°C (4.14°F) at the highest elevation between the years preceding the first and most recent surveys.

Notably, climatic changes varied among elevations, where rate and magnitude of warming was generally highest at the middle elevation, while the lowest elevation exhibited increases in precipitation (54 millimeter (mm)) and decreases in vapor pressure deficit (VPD, a measure of air dryness, defined as the difference between the amount of moisture in the air and the maximum moisture the air could hold) and maximum temperature between the first and second surveys.



Long-term climate data dating to 1961 from the Boyd Deep Canyon center station showed increased interannual precipitation variability over time, and no overall significant changes in mean annual or seasonal (winter and summer) precipitation. However, there was a significant increase in average minimum temperature (0.98°C (1.76°F)) and average maximum temperature (3.61°C (6.5°F)) over the same time period. Substantial increases in winter minimum temperatures were more pronounced at lower and mid elevations.

These results support recent work highlighting elevational differences in warming rates (Pepin et al., 2015), and findings of elevational differences in climate help 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, smaller and faster-growing species exhibited downward shift in leading-edge margins between the second and most recent survey, a period characterized by anomalously warm regional drought which caused extensive mortality (Dong et al., 2019; Goulden and Bales, 2019). These conditions likely affected newly establishing juveniles of species that had previously shown upward leading-edge shifts. In contrast to more temperate mountain ecosystems (Pepin et al., 2015), these elevation-dependent range shifts likely reflect more rapid warming at lower elevations in this dryland system, 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 appear to be promoting the replacement of stress-tolerant species, such as California juniper and pinyon pine, alongside increases in more resource-acquisitive species that possess drought avoidant traits, including brittlebush, burrow bush, and ocotillo (Berdugo et al., 2020).



The observed change in plant distribution in Deep Canyon may be attributed in part to a severe drought from 1999 to 2002. This drought caused marked vegetation mortality throughout Southern California, directly through drought stress and indirectly through insect attack, and many recently dead plants were observed during the survey.

However, recent mortality alone could not explain the elevation shifts. Many plants that had died before the 1999–2002 drought were also noted, as well as an increase in cover in the upper half of the species' ranges. These trends indicate that warming and/or drying of climate has been stressing the lower elevation plants and providing more favorable conditions for plants at higher elevations over the 30-year period. These changes are consistent with predictions of the effects of climate warming and drought on mountain ecosystems.

Several considerations in the 2008 survey (Kelly and Goulden, 2008) provide evidence that the observed vegetation redistribution is attributable to climate change:

- Vegetation shifts were uniform across elevation, implying that the ultimate causal factor was uniformly distributed. Recent climatic trends in Southern California do not appear to vary strongly with elevation.
- The vegetation shifts are consistent with the expected bioclimatic effects of most of the observed climatic shifts. Increased temperature, longer frost-free period, increased elevation of the snow line, and occurrence of severe drought should increase plant stress in some years. This increased stress would be expected to decrease a species' ability to survive in the drier, warmer, lower parts of its range and increase its ability to survive in the wetter, cooler, upper parts of its range.
- The change from a symmetrical vegetation distribution to an upwardly skewed distribution, when averaged across species and elevation, can be interpreted as evidence of the impact of climate change on vegetation distributions.
- The vegetation shifts resulted in part from mortality during the 1987–1990 and 1999–2002 droughts. The connection between mortality and drought is consistent with a fingerprint of climate change.

Two alternative explanations for the vegetation redistribution, changes in fire frequency or air pollution, merit consideration. The wildfire regime in Southern California has



changed over the last century, resulting in plant demographic shifts, especially in montane forest. However, the fire regime in Deep Canyon is similar to its historical norm, and fire effects would not produce uniform changes across the elevation gradient. Schwilk and Keeley (2012) claim that the upslope redistribution of one species in Deep Canyon, *Ceanothus greggii*, was due to elevational differences in historic fires and not by climate warming. However, observations of postfire recovery of *C. greggii* outlined in Zammit and Zedler (1993) support the conclusion that an influence stronger than fire history is redistributing Deep Canyon's dominant species upwards. Air pollution as an explanation is similarly problematic: ozone-related mortality is concentrated at higher elevations and would not produce the uniform changes observed across the elevation gradient.

The observed local changes could reflect regional urban heat island effects or long-term climate fluctuations, such as the Pacific Decadal Oscillation. Nonetheless, the documented climate changes are similar to those predicted or attributed to anthropogenic climate change. Findings from the resurveys in the Deep Canyon transect suggest that surprisingly rapid shifts in the distribution of plants can be expected with climate change, at least in areas where seed dispersal is not a major constraint, and that global climate change may already be influencing the distribution of vegetation.

Additionally, the exact mechanisms of the plant mortality remain unknown. How trees die in response to drought is an active area of scientific investigation (Breshears et al., 2009; van Mantgem et al., 2009; Waring, 1987). However, drought and warming have caused forest mortality worldwide, and no alternative explanation currently better accounts for the vegetation shifts were observed.

Technical considerations

Data characteristics

The original survey in the Deep Canyon Transect (Zabriskie, 1979) consisted of 22 linear transects along the elevation gradient, equally spaced at 122-meter intervals beginning at 24 meters elevation and following 400-m isocontours. Due to urban development in the Coachella Valley, the lowermost transect was lost beneath an



irrigated golf course subdivision, and therefore surveys in 2019 only resurveyed 21 of the original transects. All transects at peak biomass were surveyed across the elevational gradient, from March 2019 at the lowest elevation, to August 2019 at the highest elevation. At each 400-m transect, all perennial plant species were identified, and their abundance was estimated as the amount of foliage intercepted by the tape to the nearest centimeter. Permits were obtained for sampling on the Boyd Deep Canyon reserve, and no permits were needed at other locations.

Climate data was analyzed from local weather stations within 75 km of the study site, representing the elevation range within the transect, and containing nearly continuous records since 1947. Also analyzed were 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.

To analyze climatic trends across the elevation gradient, changes in 800-m resolution gridded climate data (PRISM, 2022) were analyzed 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 this data, we evaluated trends in annual minimum, maximum and mean temperature, along with annual precipitation and VPD. Climatic changes across survey intervals were compared between each survey period using t-tests.

Strengths and limitations of the data

A common challenge in revisiting historic studies is finding the exact location of the original sites. Discussion with Zabriskie, original maps, careful and consistent site location criteria, and a relatively small geographic area, provide confidence in the investigators' accuracy in relocating the original survey sites. Location inaccuracy is the largest source of uncertainty in the data. The vegetation coverage methodology was identical to Zabriskie's and could result in biases of less than a few percent per transect. Year-to-year fluctuations could be a problem in extrapolating one survey to a 42-year



trend. A major strength of this survey is that the species evaluated in this survey are generally long-lived, thus the vegetation changes observed are the result of long-term trends and not short-term variability. Species in the survey such as yucca, white fir, creosote, and California lilac have lifespans of decades to centuries, and thus high mortality rates within 42 years are considered significant changes. Finally, weather station data does not come from within the survey site; the climate data comes from nearby stations around the Southern California desert mountains.

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