



Sweeney Granite Mountains Desert Research Center

# Science Newsletter

## The Ecology and Genetics of Crypsis in Desert Clickers (*Ligurotettix coquilletti*)

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*Cht – cht cht cht. Cht cht.  
Cht cht cht cht.*

The insistent rasping of the desert clicker grasshopper (*Ligurotettix coquilletti* McNeill) defines the soundscape of summer in North America's western deserts. Their chatter is inescapable from the Owens Valley of California south to the Vizcaino Desert of Baja California, from Antelope Valley in California east to the Sonoran Sky Islands in Arizona. Even the most parched and desolate creosote flats can host a boisterous cadre of males calling up to 16 hours per day to draw in mates and forestall rivals (1).

It is therefore no surprise that desert clickers caught my attention when, as a new graduate student, I strode into the Sonoran Desert near Tucson, AZ. The clickers were everywhere to be heard but nowhere to be seen. My first day in the field I spent twenty minutes circling a single creosote bush trying to home in on the source of the clicking. I moved like a mantis rocking with the breeze,

### In this Issue:

- Page 1. *The Ecology and Genetics of Crypsis in Desert Clickers (Ligurotettix coquilletti)*
- Page 6. *Arbuscular Mycorrhizal Fungi Tolerate the Dome Fire*
- Page 10. *A Microclimatic Facilitation by Shrub Canopy: a Test of Ephedra californica and Larrea tridentata*
- Page 15. *Monitoring Vegetation Recovery after the Dome Fire*

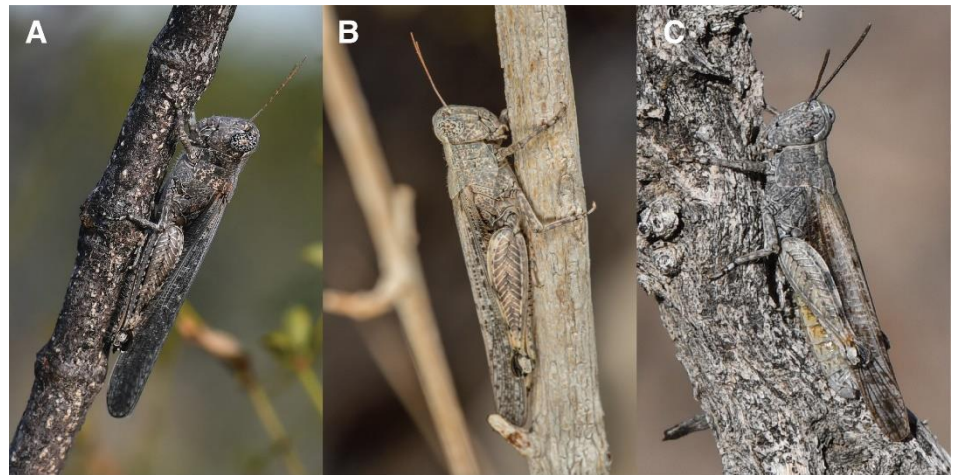


Figure 1. Variation in desert clicker coloration on different host plants. A. On creosote bush (*Larrea tridentata*) near Tucson, AZ (photo by ©Dave Beaudette). B. On creosote bush in Anza-Borrego Desert State Park, CA (photo by ©Alice Abela). C. On greasewood (*Sarcobatus*) near Mina, NV (photo by Tim O'Connor). All individuals are of the uniform morph.

insinuating myself among the branches here, there, then around the other side. Each time I was dismayed to find that the sound seemed to come from the spot I had just left. Not until the stridulation was as close as my own nose did I finally find the grasshopper two inches away. Wedged deeply in the desert foliage, I also found a begrudging respect for the species' ability to conceal itself (crypsis). Through this hunt and the thousands that followed, I observed how multiple dimensions of crypsis together make desert clickers so elusive.

The first dimension of crypsis is behavioral. Both sexes spend the majority of their lives within the branches of their host plant, which offers abundant hiding places. Males call from branches whose girth is slightly larger than their own. From this perch they can be seen and heard by

females, but also swiftly pivot out of sight, surveil an approaching predator (or biologist), and remain quiet until the coast is clear. Females are more furtive still – they do not sing and move very little except when courting with a male. I typically encountered females only in courtship or by accident.

The second dimension of desert clicker crypsis is camouflage. Across the species' range, the color and mottling of both sexes matches their local host plants remarkably well (Fig. 1). In most populations, desert clickers are typically found on creosote bush (*Larrea tridentata*), though saltbrush (*Atriplex* spp.) and greasewood (*Sarcobatus vermiculatus*) are primary host plants in the Great Basin. This close correspondence suggests the hypothesis that desert clickers can escape predation by resembling plant stems. Desert clickers are prey for *Uta*

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and *Cnemidophorus* lizards, robber flies, mantids, katydids, and spiders; cactus wrens are also likely predators (M. Greenfield, personal communication). In addition to the continuous color variation among populations, there is also discrete pattern polymorphism within populations (2–4). A **uniform** morph (with relatively homogeneous color) and a **banded** morph (with boldly contrasting patches) coexist at frequencies that vary across the species’ range (Fig. 2).

The significance of pattern polymorphism is less obvious than color variation. One possibility is that uniform morphs resemble stems of homogeneous color while the bold markings of banded morphs mimic stems with dark resinous spots (found in some creosote bush populations) or dappled shadow. An alternative is that banded morphs provide crypsis in a different context. While males rarely leave their host plant, females descend to the desert floor for several hours in the early morning (1). There, females are immobilized for up to 45 minutes as they deposit egg pods into the soil (5) and are particularly vulnerable to crepuscular predators. The banded morph might provide females camouflage by matching the heterogeneous desert substrate (Fig. 3) or by creating false body lines (“disruptive patterning”) that disguise the grasshopper’s contours (6).

It seemed clear that uniform and banded morphs are two distinctly different targets for visual predators. How and why both morphs coexist was a question I decided to pursue further. Coloration has intrigued evolutionary biologists since the field’s inception (7, 8), and I was no exception. There are several reasons for this. The first is somewhat trivial: color is easily observed and measured, making it a tractable study subject.

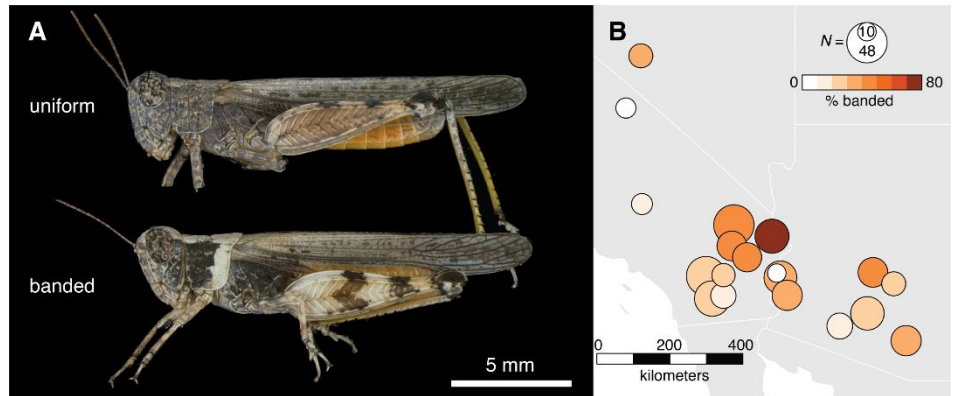


Figure 2. A. Exemplars of two desert clicker morphs from Ocotillo Wells, CA. B. Morph frequency variation across 19 focal sites. Modified from O’Connor et al., 2021 (12).

Secondly, color often mediates the key interactions within species (e.g., attracting a mate) and between them (e.g., evading predators) that determine how well an individual survives and reproduces – that is, its fitness (9). The intuitive link between this trait (“phenotype”) and fitness has long attracted the attention of evolutionary biologists. Coupled with a recent explosion of genetic data (10), animal coloration provides some of the most complete demonstrations of natural selection at the organismal and genetic level. One classic example from North American deserts are rock pocket mice (*Chaetodipus intermedius*), which can be either light tan or deep brown-gray and are adapted to sandy and volcanic substrates, respectively (11).

Finally, desert clickers embody an enduring question in evolutionary biology, namely: why is genetic and phenotypic variation maintained when manifold forces act to homogenize populations (e.g., selection against new and harmful mutations, selection for unconditionally helpful mutations, and random chance)? Color polymorphisms have historically provided valuable insight into this question, demonstrating that stable (“balanced”) polymorphisms can result from evolutionary tradeoffs. For example, if an organism uses two environments and each morph provides a fitness advantage in a different environment,

both may be maintained in the long run. In the desert clicker, such “balancing selection” may be due to tradeoffs between morph performance in different physical environments (e.g., upon stems of different appearance), but also tradeoffs between sexes if males and females are subject to different predation pressure.

I therefore decided to pursue the ecological factors that maintain pattern polymorphism in the desert clicker (12). My collaborators and I leveraged the fact that morph frequencies varied substantially across the species’ range (0-80% banded) to ask whether the appearance of local stems and/or substrate could predict those frequencies. Such phenotype-environment correlations would provide insight into 1) the ecological contexts that favor banded morphs, and 2) the kind of tradeoffs that maintain or generate pattern polymorphism.

To complement our ecological study, we also sequenced the DNA of >500 desert clickers at ~9,000 positions in their genomes (loci) and looked for associations between DNA sequences (genotype) and pattern morph of each grasshopper. This analysis was a bit of a long-shot – our sequence information covered a mere ~0.03% of the grasshopper genome, with one locus every million or so base pairs. With such an incomplete view of desert clicker genetics, the odds of finding a



genotype-phenotype association were slim.

Our group surveyed morph frequencies in 19 desert clicker populations across Arizona, Nevada, and California, including two UC Natural Reserves (Boyd Deep Canyon and Sweeney Granite Mountains; Fig. 2B). At each site we also took standardized photographs of the host plant stems and desert substrate (Fig. 4) for quantitative analysis of these visual environments. Because the primary difference between uniform and banded morphs is the patterning of light and dark (“luminance patterning”) along the body, we reasoned that luminance patterning would also be a useful way to characterize likely predation environments (stems and substrate). We therefore summarized the magnitude of luminance patterning across a range of spatial scales (Fig. 5)(13). For example, the fine-scale contrast between light and dark sand grains creates high “pattern energy” at fine scales, while contrasting colors of granite creates pattern energy at larger scales, and contrasting pebbles create pattern energy at still larger scales. With these summaries, we then tested whether luminance patterning in stems and substrate predicted the desert clicker morph frequencies.

Our results surprised us and held some interesting lessons about desert clicker ecology. Although both sexes spend the majority of their life within plants and uniform morph coloration clearly matches local stems, morph frequencies were uncorrelated to variation in stem appearance. Instead, substrate appearance predicted more than 75% of the variation in morph frequency among sites. Banded morphs were more common where substrate had higher overall contrast, and specifically in environments where the luminance patterning closely resembled that of the grasshoppers.



Figure 3. Banded female desert clicker in the heterogeneous desert substrate near Franconia, AZ (photo by © Dave Beaudette).

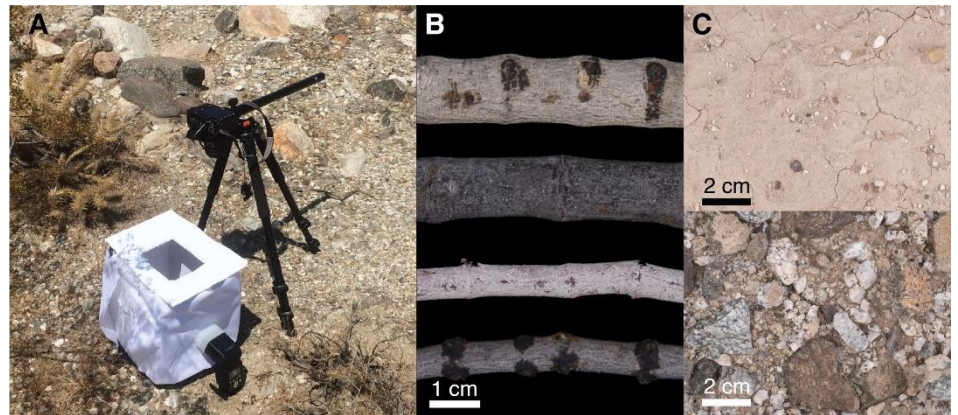


Figure 4. Standardized photographs of putative predation environments for testing correlations between the visual environment and morph frequencies. B. Stems of creosote bush demonstrating a range of color and luminance patterning. C. Desert soils ranging from silt (top) to granitic gravel (bottom). Modified, in part, from O'Connor et al., 2021 (12).

The great naturalist J.A.G. Rehn noted that desert clickers are “...as truly bush-loving as any [grasshopper] of my acquaintance...” (3), but host plants are not the predation environment that matters for pattern polymorphism. Rather, it suggests that predation on ovipositing females in the narrow timeframe that they visit the ground largely determines the phenotypes for both sexes. Does this mean that predation on stem-dwelling clickers – especially calling males – is unimportant? Not at all. While our results are compatible with several models, one possibility is that a tug-of-war between natural selection that

occurs in plants (mostly on calling males) and on the ground (mostly on females) results in a balanced pattern polymorphism. Such sex-specific habitat use is known to favor opposing color morphs in other species, including pygmy grasshoppers (14) and several reptiles (15, 16).

I hypothesized that stem-foraging predators overlook uniform morphs that resemble plant stems but more readily detect banded morphs, giving uniform morphs a fitness advantage. Because morph frequencies showed no association with the appearance of plant stems, I speculated that the

strength of the uniform morph's advantage is similar across sites. By contrast, ground-dwelling predators are more likely to discover banded morphs when they stand out against a homogeneous substrate (e.g., silt) and uniform morphs in more visually complex environments. How strongly predators "pull" females toward each morph depends on the local environment, and the balance between ground and stem predation defines the local morph frequencies.

Our genetic analysis of pattern polymorphism yielded complementary insights. Despite our limited genetic data, we found a single locus strongly (but imperfectly) associated with desert clicker pattern morph. This suggests we fortuitously sequenced a region of DNA close to the causative locus, and the genetic variants we observed tend to be co-inherited with the variants that determine coloration. Because balancing selection can leave characteristic footprints in the genetic variation of loci under selection (i.e., the locus determining pattern morph) as well as nearby regions, we next asked whether the morph-associated locus bore such an imprint. Consistent with our ecological model of balancing selection, this locus did have signs of balancing selection. Specifically, the relative frequencies of mutations in the locus were unlikely to result from directional selection (favoring one genotype) or the absence of natural selection ("neutral" evolution) but were expected under balancing selection.

Our second result was also unexpected. Banded and uniform morphs differed in the presence / absence of a genomic region (several million base pairs in size). All banded individuals carried this region, suggesting that its presence might cause the banded phenotype. More surprising still, the genetic dominance of this locus has switched relatively recently. While two copies of the region

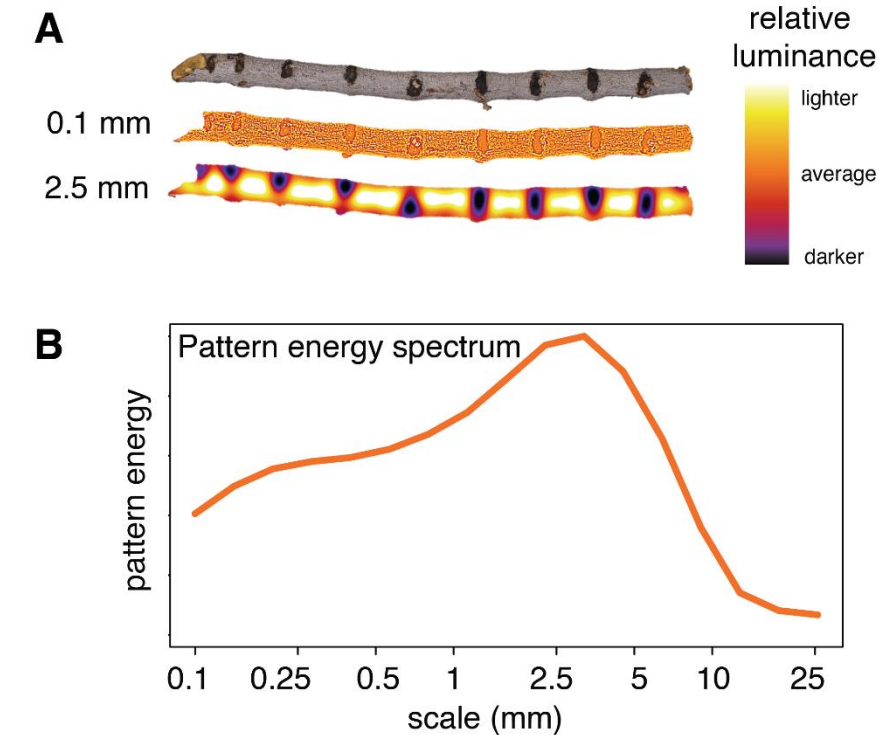


Figure 5. Quantifying the appearance of environments where desert clickers may be preyed upon. A. Visualizing the pattern energy of a creosote bush stem at different spatial scales. Top: original image. Middle: luminance patterning at a small spatial scale (0.1 mm). Orange pixels indicate regions of average brightness compared to other pixels in a 0.1 mm radius. Other colors highlight regions that are lighter or darker than average, respectively. This analysis highlights the fine texture in the creosote bush bark. Bottom: Applying the same approach to a larger spatial scale, this time 2.5 mm. Resin stains in the stem image create a regular pattern of strongly contrasting patches. B. Pattern energy calculations at multiple spatial scales can be combined with a pattern energy spectrum. These spectra can then be used to compare images or used in statistical models that predict the frequency of desert clicker morphs as a function of their environments.

are required for a banded phenotype in the eastern part of the desert clicker range, just one is necessary in the west. Although the evolutionary transition between genetic dominance regimes has been well studied from a theoretical perspective, there are scant examples from wild populations (17).

Both the ecological and evolutionary findings provide tantalizing leads to pursue in the future. On the ecological side, it would be fascinating to directly test whether predation rates for each morph differ between males and females (for example, with mark-recapture studies or longitudinal surveys across a season). Manipulative experiments (e.g., painting grasshoppers to swap their phenotype) could provide an interesting complement to these observational

studies.

On the evolutionary side, a deeper dive into the genetic details of pattern polymorphism would round out the desert clicker story. Can we shed light on how the genetic program for pattern development was changed in order to reverse the ancestral dominance relationships? Is the underlying genetic mutation new in western desert clicker populations? Or might it have been introduced by hybridization with another species? In a separate project, I have identified a novel *Ligurotettix* species from Baja California that has historically hybridized with the desert clicker. DNA inherited from other species is now widely recognized as an important source of genetic and phenotypic variation that can be favored during the process of

adaptation (18). For now, this remains speculative in desert clickers.

What is certain is that the desert clicker provides a rich system for further inquiry. It is worth noting that much of the foundational work on the species' ecology was performed within the UC Natural Reserve System in the 1980's and 90's. Liz Bernays, Reg Chapman, Michael Greenfield, Katherine Muller, Todd Shelly, and Guang-Yu Wang (among others) detailed the territoriality, host plant use, phenology, and ethology of the species at Boyd Deep Canyon Desert Research Center. Future work on these topics might benefit from a comparative approach between Sweeney Granite Mountains Desert Research Center and other UC Reserves.

#### Acknowledgements

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# Arbuscular Mycorrhizal Fungi Tolerate the Dome Fire

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The 2020 Dome Fire was an uncharacteristically large fire for the Mojave Desert, covering 43,273 acres of eastern Joshua tree (*Yucca jaegeriana*) forest. It is surpassed in size only by two recent fires: the 2005 Hackberry Complex Fires in the nearby Mid Hills, which burned 70,736 acres, and the 2023 York Fire only 25 kilometers to the east at 93,078 acres. There have been a number of studies assessing the impact of fires on vegetation in different areas of the Mojave, such as in Joshua Tree NP (1) and also in Mojave National Preserve (2); however, little is known about long-term impacts of fires on desert soil microbes. When there is enough dry vegetation to sustain a desert wildfire, fire will spread quickly through the grass, but won't linger in one place long enough to transfer heat belowground. While high soil moisture can slow the penetration of heat below ground (3), a lack of moisture can reduce the residency time of heat because the sandy soil has a naturally low specific heat capacity (4). The depth of heat penetration may also be important to consider since subsurface soil temperatures are typically not impacted below 5cm during similarly low-intensity prescribed fires (5).

An important group of microbes found in desert soils are the arbuscular mycorrhizal fungi (AMF). AMF have been associating with plant roots (Fig. 1) in order to exchange nutrients for plant-fixed carbon for over 460 million years (6). AMF broadly associate with most desert plants, and in fact can form mycorrhizal associations with 80% of

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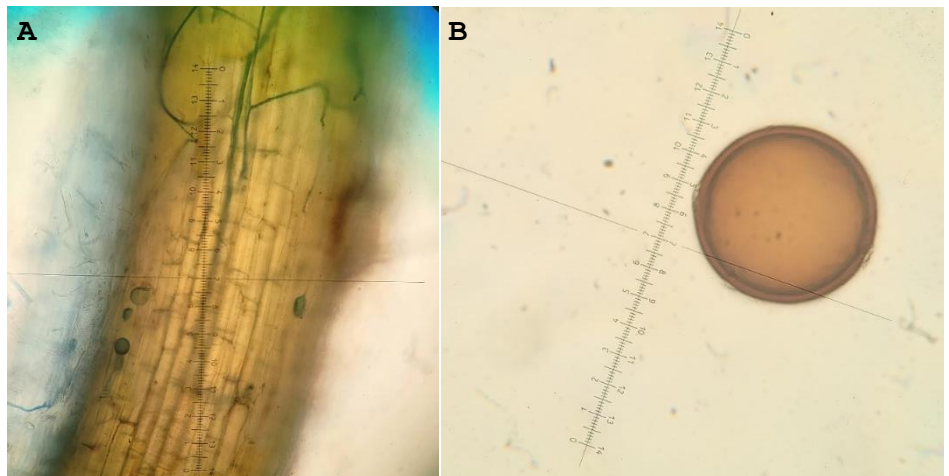


Figure 1. (A) Arbuscular mycorrhizal fungi (AMF) hyphae and vesicles stained with Trypan Blue to confirm their presence within an eastern Joshua tree root. Hyphae are approximately 5-10  $\mu\text{m}$  thick while vesicles range from 20-30  $\mu\text{m}$ . Photo taken at 200x magnification, each dash on the scale representing 5.1  $\mu\text{m}$ . (B) An AMF spore spanning over 50 $\mu\text{m}$  wide. Photo taken at 1000x magnification, each dash on the scale representing 1  $\mu\text{m}$ . Photos by A. Joukhajian.

vascular land plants (7). AMF form hyphae, which are fine filaments that can transport water and nutrients directly to plant roots, an especially important trait to aid plant survival in deserts (8).

AMF appear to be highly tolerant of fires (9). AMF can persist at soil temperatures up to 94°C (10) and can grow from root propagules even after a plant has burned, allowing them to reinfect the first re-sprouting plants after the fire. Yet, fire can reduce the abundance of mature plants capable of supplying derived sugars or kill AMF inhabiting a shallow depth in the soil. Even low-severity fires in sand can exceed 100°C at the surface, but temperatures drop by half at only 2cm depth (11). While direct killing of subsurface microbes from the heat of fast-moving desert fires is limited, there is likely a link between the drastic changes aboveground and the below ground AMF community, because AMF

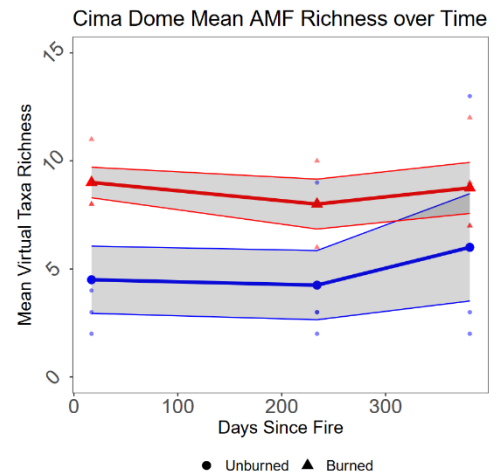
are obligate symbionts that will not survive for long without their plant host. In the Mojave Desert, annual plants have lower mycorrhizal colonization rates than perennial plants (12), and their early sprouting in post-fire landscapes could alter long-term trajectories of AMF communities (13). AM fungal associations are not usually exclusive with any one particular plant host, but early successional plants could alter the soil pH, compounding the typical post-fire pH increase (4), causing a shift towards species of AMF adapted to the new pH (14). As generalists, AMF associate with many of the abundant plant taxa in the Mojave Desert (12), allowing them to thrive with invasive grasses, shrubs, and woodier plants like the eastern Joshua trees. Their spores are limited in their longevity based on predation rates and spore size, with larger spore-forming AMF species being more capable of waiting for a plant host, but also being more appetizing for soil

microfauna (15). Large spore size has further drawbacks, as wind is much more likely to disperse smaller AMF propagules (16). Cima Dome is a large granitic outcrop where the Dome Fire occurred, placing the burn scar at a higher elevation than the unburned areas around it which could restrict movement of wind-dispersed AMF. Therefore, despite AMF showing some evidence of fire resilience, the Dome Fire could have led to a reduction of AMF species in the soil. Here, we used a DNA-based approach to test whether AMF species richness and composition were impacted by the Dome Fire. We predicted that despite their resiliency, there would be fewer AMF species in burned soils, due to the large size of the fire and high mortality rates on the aboveground vegetation. Furthermore, we predicted this decrease in AMF richness to persist up to 1 year post-fire, since the early successional annual plants often have lower rates of AMF colonization than perennial plants (12).

To investigate the effect of the Dome Fire on AMF species richness, we sequenced barcode regions of DNA extracted from soils in burned and unburned samples collected at 2 weeks, 8 months, and 1-year post-fire. We sampled four plots in the burn scar along Cima Road and four plots just outside the burn scar on Morning Star Mine Road. We collected ~500g of soil using bulb planters to reach 10cm below the surface, then homogenized and sieved the soil through 2mm mesh before freezing 10g of soil for DNA extractions. We used Qiagen DNEasy Powersoil Pro kits to extract DNA from a quarter gram of soil and then amplified the DNA using the PCR primer pair WANDA-AML2 (17, 18) targeting the 18S SSU rRNA region. This allowed us to identify AMF species from the MaarjAM database (19), which uses “virtual taxon” numbers instead of species names to account for genetic diversity of undescribed AMF. We used

a second round of PCR to anneal DIP barcodes to the sequences to enable multiplexing of all samples in a single library that we sequenced using Illumina MiSeq at the UCR Genomics Core. We used a generalized linear mixed-effects model to examine the statistical significance of the burn treatment, after accounting for random effects from repeated samplings from the same plot and elevation (with a gamma distribution for taxa richness) using the following formula: Generalized Linear Mixed-Effects Model = Species Richness ~ Treatment\*Timepoint + (1|Plot) + (1|Elevation), family = Gamma.

After sample processing and sequencing, we had sequences for 23 samples, with 7-8 samples from each of the 3 time points. We filtered out the reads of DNA fragments that didn't match an AMF virtual taxon in the MaarjAM database, leaving 90,871 total reads with a median of 3,246 reads per sample. With these reads, we were able to detect 31 virtual taxa (VTs) from 4 AMF families representing 1 *Paraglomus*, 4 *Diversispora*, 4 *Claroideoglomus*, and 22 *Glomus* virtual taxa. This bias towards *Glomus* is typical of AMF communities, as they are the most abundant genus in the subphylum containing AMF, Glomeromycotina. Surprisingly, the mean richness of AMF virtual taxa was consistently higher in the burned plots across all timepoints ( $z = -2.113$ ,  $p = 0.0346$ , Fig. 2), although none of the pairwise comparisons between the mean richness of burned and unburned samples were significantly different at any of the timepoints. Burned plots also contained more unique AMF taxa than unburned plots (Fig. 3). Due to the inherent elevation gradient descending from Cima Dome, it is difficult to disentangle the effects of the burn treatment from elevation, as the plots within the burn scar are situated approximately 200m higher than the unburned plots on a large granitic

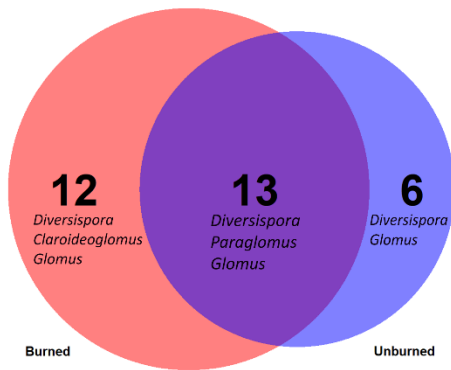


**Figure 2. Comparison of AMF virtual taxa richness at burned and unburned plots around the Cima Dome at 3 timepoints (2 weeks, 8 months, and 1 year post-fire).** The bold line passes through the mean richness from soil in burned (red) and unburned (blue) plots. Large points indicate the mean richness at each timepoint, smaller points indicate individual sample richness values, and the thinner lines represent the top and bottom boundaries for the standard error of the mean, with gray shading filling the space above and below the mean line per treatment.

outcrop. To account for this, we used plot and elevation as random effects in our linear model since there were slight elevation differences between plots within the burned and unburned groups. Our model showed significant effects of the fire and a significant difference between richness at two weeks and at 1 year. It is unclear whether the Cima Dome burn scar had more species of AMF present prior to the fire, or if other factors allowed a greater amount of AMF species to disperse to the region. Nevertheless, the lack of decreased AMF species within the burn even at the 1-year post-fire mark may suggest long-term resiliency of AMF in the face of slow plant recovery (Fig. 4). While DNA presence alone doesn't confirm a thriving below ground community, the likelihood of leftover relic DNA from dead cells impacting measurements is low in soil (20), especially after a year.

Overall, the results show that both AMF richness and diversity were greater in our burned plots, despite the fire consuming a vast majority of the vegetation around the plots. Although





**Figure 3.** A Venn diagram of virtual taxa detected across all timepoints in burned (red) and unburned (blue) plots. Numbers indicate the amount of unique virtual taxa in each group, with names indicating AMF genera represented in those virtual taxa.

not consistent with our hypothesis, increased AMF richness has been seen in other low-intensity burns such as prescribed fires (21). This suggests that post-fire vegetation recovery on Cima Dome is likely not hindered by lack of AMF partners, and that the AMF community likewise may be able to maintain its diversity without its former plant community. One potential reason for increased AMF richness in burned plots could be the ability to place plots on top of the remains of shrubs, which would have acted as resource islands for AMF (22). A bias towards accessibility around shrubs in the unburned habitat could sway analysis towards the AMF-poor interstitial space (23) in between plants, but a comparison of our unburned plots showed that increased vegetation coverage within the plot actually correlated with reduced AMF taxa richness. However, further research might detect other changes beyond this assessment of AMF diversity. Considering that the AMF taxa detected in the roots of western Joshua trees appeared to show elevation preferences (24), there is further opportunity to show whether that same structuring is present across Cima Dome, which has a similar elevation gradient compared to that previously sampled in Joshua Tree National Park (24). The plots we established around Cima Dome include several projects



**Figure 4.** (A) As shown in this burned plot on Cima Dome, minimal plant growth occurred by 8-months post-fire, April 15 2021. The light pink patches on the burned stems of Joshua trees in the photo are remnants of the fungal fruiting bodies of *Neurospora*. (B) Even 1-year post fire, the slow recovery of plant life is obvious across Cima Dome, September 9 2021. Photos by A. Joukhajian.

monitoring both AMF associating with the eastern Joshua tree and the response from soil microbial communities to fire, but these preliminary findings open doors to new

questions. Future investigations into Mojave AMF could test if AMF spore or virtual taxon abundances vary at different soil depths, to better understand what factors play into their



survival in a burn like the Dome Fire, or the more recent York Fire. Additionally, more detailed sampling along an elevational transect may reveal elevation-based stratification of AMF taxa around Cima Dome. Finally, incorporating infectivity assays, root colonization assays or microscopic spore counts could confirm the resilience of these microbes and their continued associations with plants after different fires in Mojave National Preserve.

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# A Microclimatic Facilitation by Shrub Canopy: a Test of *Ephedra californica* and *Larrea tridentata*

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Foundation species are key components of environmental heterogeneity. Environmental heterogeneity, defined as non-uniformities in physical and ecological landscape characteristics (1), can be divided into many subcomponents including climatic heterogeneity (2). Climate can introduce heterogeneity horizontally by determining the type of vegetation that grows in an area, but also vertically because plant structures can physically impact canopy microclimate (3, 4). In drylands, where increased mean temperatures, variability in precipitation and temperature, as well as extended drought periods are increasing, foundation plants offer resiliency and microclimatic heterogeneity (5). 'Microclimate' is the climate experienced in the lower 2m of the atmosphere and the upper 0.5-1m of the soil and is dependent on local topography, soil type, and vegetation (6). The impacts of plants in buffering climate have been primarily tested through landscape-level analyses, such as NDVI (Normalized Difference Vegetation Index) or vegetation land cover (7); however, the structure of foundation species offers important ecological functions that are crucial for offering climatic refuge at finer scales (8).

Like plant canopies in other systems, shrub canopies are able to, directly and indirectly, buffer climatic regimes. Plant canopies provide mediation from harsh climates by increasing environmental heterogeneity and cover (9). Both incoming sunlight and air movement

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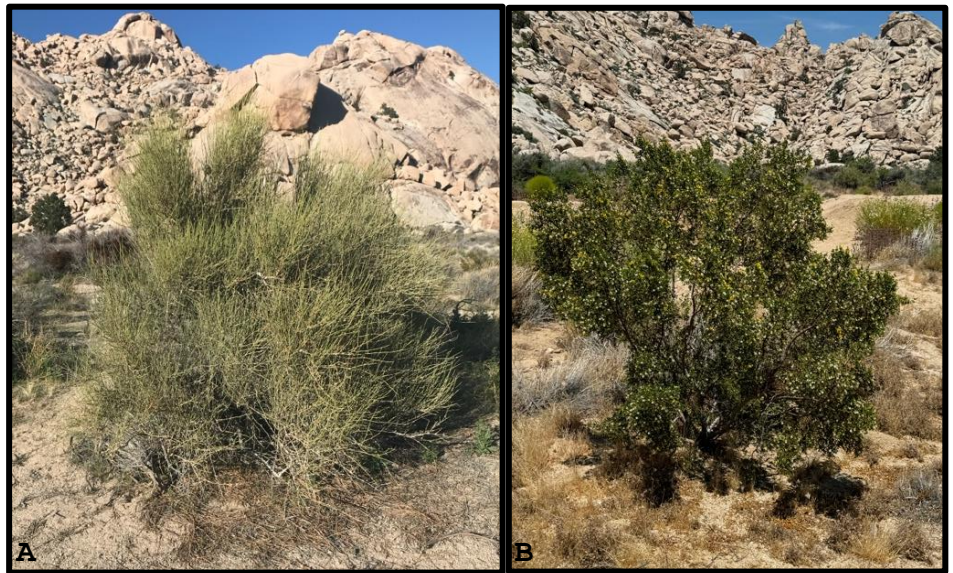


Figure 1. A) *Ephedra californica* (Mormon tea) and B) *Larrea tridentata* (creosote bush) are both common shrubs found throughout the arid lands of southwestern US. Photos by T. La Doux.

can be affected by the canopy structure, which in turn will alter the temperature and precipitation regimes experienced by associated plants or animals (4). Shrub volume is directly associated with microclimatic conditions, with larger shrubs showing a greater microclimatic heterogeneity in their understory (10). Many dryland organisms are vulnerable to small, fine-scale oscillations in addition to large-scale changes (11, 12), which can further push species past the point of no return. Foundation shrubs, including *Ephedra californica* and *Larrea tridentata*, can help facilitate some of these less stress-tolerant species (13) through climatic amelioration.

*Ephedra californica* (Mormon tea) is a foundation shrub native to the southwestern regions of California (Fig. 1A) (14). *Larrea tridentata* (creosote bush) is a dominant or co-dominant flowering shrub that is often found in

sandy soils, desert pavements, and the well-developed cryptogam layer of the Mojave Desert (Fig. 1B) (14, 15). In this study, we examined microclimatic parameters, including near-surface air temperature (NSAT), near-surface relative humidity (NSRH), and surface ground temperature (SGT) using a handheld device across seven sites in California to test the hypothesis that foundation shrub canopies provide microclimatic amelioration across a regional aridity gradient in dryland ecosystems. To test this hypothesis, we predicted: 1) Shrub volume is directly associated with cooler, and more humid microsites, with larger shrubs exhibiting lower temperatures and retaining more humidity, 2) *E. californica* is a denser, bigger shrub at our study sites and hence has superior microclimatic amelioration effects compared to *L. tridentata*, and 3) microclimatic measures of shrubs will vary between sites with more arid sites



exhibiting higher temperatures and lower humidity. Shrubs and vegetation can provide key microclimatic heterogeneity, thus acting as climatic shelters that are crucial to the persistence of many dryland species given the current paradigm of climate change.

We surveyed a total of eight sites across arid and semi-arid deserts during the winter of 2023 (Table 1) to form an aridity gradient. The sites were located in southwestern California, United States, and divided into three main geographical areas: Cuyama Valley, Carrizo Plain National Monument, and Mojave Desert. The surveys took place between February 13 and 23, 2023. We surveyed a total of three sites in Cuyama Valley, three sites in the Carrizo Plain, and two sites in the Mojave Desert. Site-level mean annual temperature (MAP) and mean annual precipitation (MAP) were obtained from [WorldClim](#) at a 1km resolution. We calculated DeMartonne's aridity values using the following formula:  $\text{aridity} = P/(T + 10)$  where  $P$  = annual precipitation and  $T$  = mean annual temperature (16).

We selected 30 pairs of shrub-open microsites at each study site. Open sites were the empty, interstitial spaces of bare soil adjacent to the measured shrubs at all sites except Tecopa, where the open measurements were taken in a completely shrub-free zone adjacent to the Tecopa 'shrub' sites. *Ephedra californica* was the dominant shrub across all sites except Tecopa where *L. tridentata* was dominant, though *Ephedra* was also present. The length (at longest axis), width (perpendicular to length), and height to tallest vegetation branch that had green tissue were measured for every shrub. We used the equation for the volume of a hemisphere  $v = 2/3 abc$  to calculate shrub volume and the equation for the area of an ellipse  $area = \pi ab$  to calculate the shrub area

(17). We used the Mengshen Digital Temperature and Humidity Meter (18) to record near-surface air temperature (NSAT, °C) and near-surface relative humidity (NSRH, %) at the north side of the shrub within the canopy dripline. We recorded the same parameters in the adjacent open, interstitial space. Furthermore, we used the Etekcity Laser Thermometer Gun (19) to record surface ground temperature (SGT, °C) both underneath the shrub canopy and in the open.

All statistical analyses were done using the software R version 4.3.1 (20). Data and codes are publicly available on Zenodo (3). Data distribution was examined using Q-Q plots, and homoscedasticity and normality were tested (21). To explore whether microclimatic measures show the same directionality, or trends are independent of the others, the relationship between NSAT and NSRH, NSAT and SGT, and SGT and NSRH was examined using Pearson's correlation for parametric, related pairs measurements (22). The relationship between shrub area and volume was examined using Pearson's correlation, as well. We used Welch's t-test to compare shrub volume between the two shrub species (23). We fit generalized linear models (GLM) to test for differences in shrub species. To test for differences in shrub volume and its effects on NSAT, NSRH, and SGT, we used GLMs as well. Site was used as a covariate in models. We further analyzed our data for site-level difference by filtering for *E. californica* only. GLM dispersion parameters with AIC scores were used to compare and select the appropriate family to fit to models (24). Post-hoc tests were done using the function *emmeans* from the *emmeans* R package (25).

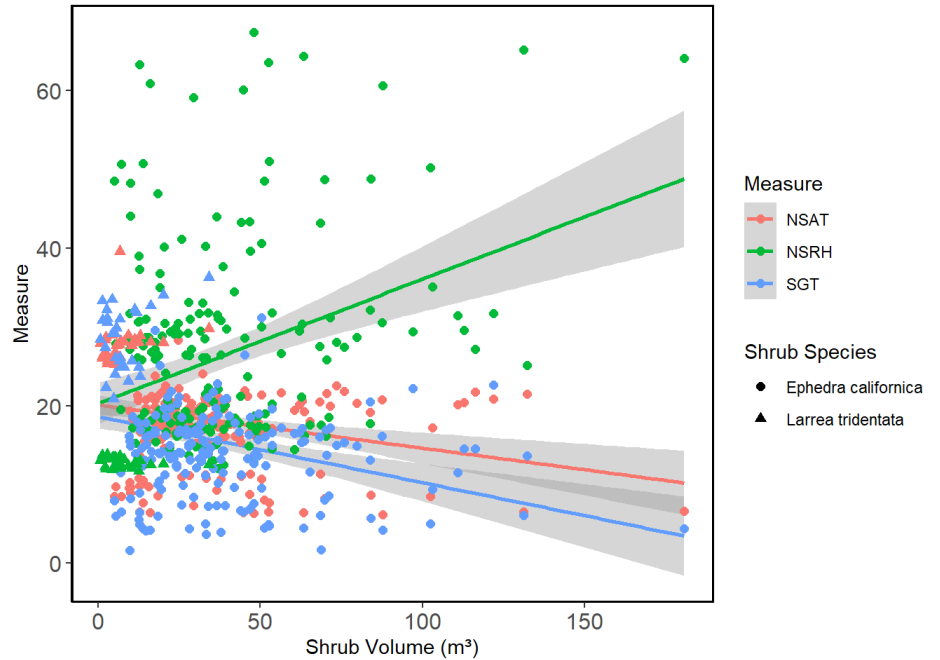
A total of 210 shrub-open microsites were surveyed. Average shrub volume and shrub area for *E. californica* were  $39.64 \pm 27.80 \text{ m}^3$  (mean and standard

deviation) and  $37.16 \pm 22.06 \text{ m}^2$ , respectively. Average shrub volume and area for *L. tridentata* were  $7.56 \pm 6.88 \text{ m}^3$  and  $10.12 \pm 5.64 \text{ m}^2$ , respectively. Certainly, the average shrub volume of *E. californica* was significantly greater than *L. tridentata* (Welch's t-test, t-value = 23.032, df = 558.46,  $p < 0.001$ ). Shrub area significantly, and positively increased with shrub volume (Pearson's product-moment correlation = 0.918,  $p < 0.001$ ); thus, we used shrub volume as a proxy for size in all our models. For *E. californica*, we found variation in shrub volume between the study sites (post-hoc  $p < 0.001$ ). There was a significantly positive relationship between NSAT and SGT (Pearson's product-moment correlation = 0.803,  $p < 0.001$ ), whereas there was a significantly negative relationship between NSAT and NSRH (Pearson's product-moment correlation = -0.713,  $p < 0.001$ ). There was also a significantly negative relationship between SGT and NSRH (Pearson's product-moment correlation = -0.595,  $p < 0.001$ ). Shrub volume had a strong effect on all three microclimatic parameters (NSAT, NSRH, and SGT), and there were site-level differences that influenced these parameters, as well (Table 2, Fig. 2). Generalized linear models (GLMs) showed significant differences between the shrub and open microsites for SGT, NSRH and NSAT (GLM estimate =  $-4.982 \pm 0.553$ ,  $p < 0.001$ ). More specifically, when compared to the open microsites, surface ground temperature (SGT) and near-surface air temperature (NSAT) were significantly cooler under the shrubs, while humidity was greater. The coolest NSAT was recorded in Cuyama\_3 (Estimated Marginalized Mean (EMM)  $8.42 \pm 0.392 \text{ }^\circ\text{C}$ ) and the hottest was in Tecopa (EMM  $21.90 \pm 0.434 \text{ }^\circ\text{C}$ ). The most humid microsite was Cuyama\_3 (EMM  $51.2 \pm 0.854 \%$ ) and the least humid was Tecopa (EMM  $12.30 \pm 0.851 \%$ ). Surface ground temperature was the coolest in Cuyama\_3 ( $6.74 \pm$

0.681 °C) and hottest in Tecopa (28.23 ± 0.723 °C). Lastly, while an increase in aridity was significantly and inversely related to humidity ( $p < 0.001$ ), it did not show a significant relationship with surface ground temperature or near-surface air temperature.

Abiotic amelioration via foundation shrubs is a key component of many dryland ecosystems. We examined the microclimate of two foundation shrub species, *E. californica* and *L. tridentata*, in order to test for the relative importance of microclimate and shrub volume. These were tested across a regional aridity gradient in the drylands of California. We hypothesized that shrub canopies provide microclimatic amelioration and this was observed in our study. Shrub volume was an important factor in explaining microclimatic differences in near-surface air temperature (NSAT) and surface ground temperature (SGT). Both parameters decreased with greater shrub volume regardless of the shrub species. Furthermore, with the increase in shrub volume, the understory environment became more humid. On average, the *E. californica* shrubs in this study had a greater volume than the *L. tridentata* individuals. Furthermore, the role of *E. californica* as a benefactor species in microclimatic heterogeneity is also site-dependent across the aridity stress spectrum. Despite our prediction that increase in aridity decreases humidity and temperature, we only found robust support for the humidity parameter in our study.

More than 30% of the total land area in California is defined as a desert ecoregion (26). Shrubs create heterogeneity in these regions by creating variation in physical structure and thus provide a generalized facilitation function of ameliorating microclimate (15). Shrub canopies create microclimatic benefits, such as increasing shade, reducing summer



**Figure 2.** Relationships between shrub volume ( $m^3$ ) and microclimatic measures are shown. Shaped points are color coded according to the key measures; smoothed means are fitted using the linear method. For both shrubs, a positive relationship between volume and near-surface relative humidity (NSRH, %) was observed, as well as a negative relationship between volume and both near-surface air temperature (NSAT, °C) and surface ground temperature (SGT, °C).

**Table 1.** List of sites surveyed in California for this study and their respective geographical coordinates. Mean annual temperature (MAT) and mean annual precipitation (MAP) were extracted from WorldClim at a 1km resolution. Aridity was calculated using DeMartonne’s index. Lower values indicate a more arid site.

Site	Geographical Area	Desert	Latitude	Longitude	MAT (°C)	MAP (mm)	Aridity
Cuyama_1	Cuyama Valley	San Joaquin	34.849	-119.483	14	136	5.667
Cuyama_2	Cuyama Valley	San Joaquin	34.854	-119.486	14.1	137	5.685
Cuyama_3	Cuyama Valley	San Joaquin	34.938	-119.481	14.2	139	5.744
Carrizo_3	Carrizo Plain National Monument	San Joaquin	35.163	-119.675	14.5	149	6.081
Carrizo_4	Carrizo Plain National Monument	San Joaquin	35.116	-119.621	14.7	147	5.951
Carrizo_soda_shrub	Carrizo Plain National Monument	San Joaquin	35.119	-119.629	14.7	148	5.992
Tecopa	Mojave	Mojave Desert	35.852	-116.187	20.1	165	5.480
Tecopa_open	Mojave	Mojave Desert	35.855	-116.179	20.1	165	5.480

radiation load, increasing nighttime winter temperature, and increasing soil moisture. Canopy structure can play an important role in the differences observed among these microclimatic

parameters (27). For instance, shrub volume and shrub area of *L. tridentata* were on average smaller than *E. californica* in this study, and as a result, all microsites under *E. californica* had



significantly cooler NSAT and SGT values when compared to *L. tridentata*. Similarly, all *E. californica* sites, except Carrizo\_3, had a higher relative humidity under their canopies compared to *L. tridentata*. This is consistent with the findings of Alday et al. (2014) (10) that found larger shrubs create greater microclimatic heterogeneity under the canopies. Furthermore, the branching structure of *E. californica* is much denser than the sparsely branching *L. tridentata*, which may lead to fairly different microclimates under their canopies. Although we did not directly measure canopy branching in our study, we speculate that differences observed in microclimatic amelioration may also be due to differences in branching structure. Maintaining biodiversity of desert regions is crucial as it translates to the overall biodiversity of the entire region of California. There is a direct relationship between environmental heterogeneity and biodiversity, with species richness increasing with greater environmental heterogeneity (28). Maintaining *E. californica* presence and promoting its persistence in the region through conservation, restoration, and management will result in greater heterogeneity in the region and thus higher regional biodiversity.

Foundation shrubs may not always provide direct amelioration of microclimatic parameters as observed here, but nonetheless they provide climatic heterogeneity and climatic buffering that is essential to the persistence of species at risk of extinction (29). Even the canopy of low-stature, long-lived ancient shrubs can nonetheless provide fine-scale climatic refuges for other species (13, 30, 31). Environmental heterogeneity in vegetation enables small areas in the species niche that can allow species persistence in a shifting climate (32). Thus, climatic heterogeneity via plants can provide a microclimatic refuge where other species can establish,

**Table 2. Shrub volume and geographic site both had strong effects on microclimatic parameters: near-surface air temperature (NSAT), near-surface relative humidity (NSRH), and surface ground temperature (SGT). Key contrast values of microclimatic measurements estimated using generalized linear models are shown. Site was treated as a factor. Significant p-values are in bold.**

	Measure	df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
NSAT	NULL			209	7230.42	
	Shrub Volume	1	498.45	208	6731.97	<b>0.001</b>
	Site	6	5759.93	202	972.03	<b>0.001</b>
NSRH	NULL			209	34598.53	
	Shrub Volume	1	4157.96	208	20440.57	<b>0.001</b>
	Site	6	26711.46	202	3729.11	<b>0.001</b>
SGT	NULL			209	11369.39	
	Shrub Volume	1	1170.46	208	10198.93	<b>0.001</b>
	Site	6	7505.28	202	2693.65	<b>0.001</b>

survive, and behaviorally mitigate climate change effects. Hence, management and restoration efforts need to focus not only on protecting existing shrublands and their foundation species, but also on restoring and managing disturbed shrublands, as these areas are key to the persistence of biodiversity. Supporting foundation shrubs like *E. californica* and *L. tridentata*, which both directly and indirectly influence microclimatic heterogeneity, is crucial to the future well-being of dryland ecosystems under the current climate change paradigms.

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# Monitoring Vegetation Recovery after the Dome Fire

Ryan McRae<sup>1</sup>, Jeanne Taylor<sup>1</sup>, Andrew Kaiser<sup>1</sup>, and Erin Knight<sup>1</sup>

On August 15, 2020, a dry lightning strike ignited a fire on Cima Dome in Mojave National Preserve that would proceed to burn approximately 43,273 acres of primarily Joshua tree woodland. In response to the fire, Preserve staff developed a plan to monitor the recovery of both native and non-native plant species within the burn scar. The data collected will be used by resource managers in Mojave National Preserve to inform future management decisions to protect the ecological health of the Joshua tree vegetation on Cima Dome.

Three to six plot center points were randomly generated within 12 sections divided by roads that cross through the burn area, excluding any unburned islands detected by Burn Area Reflectance Classification (BARC) imagery and private inholdings. In total, 54 monitoring plots were created across in the Dome Fire burn scar (Fig. 1). Each plot center point has three 50-meter line transects running radially from the center point every 120° (Fig. 2). For each transect, the line point intercept method was used to interpret the relative cover of ground substrate types (bare soil, dead woody matter, bedrock, gravel, litter, and biological soil crust), and the percent live plant cover by species in each plot. Points were taken using a pin dropped every 0.5 m along each line transect (99 points per line). Species richness data were gathered at five equidistant 10 m<sup>2</sup> circular plots along each line transect. Within each circular plot, each plant species was identified to the most specific level possible and recorded to

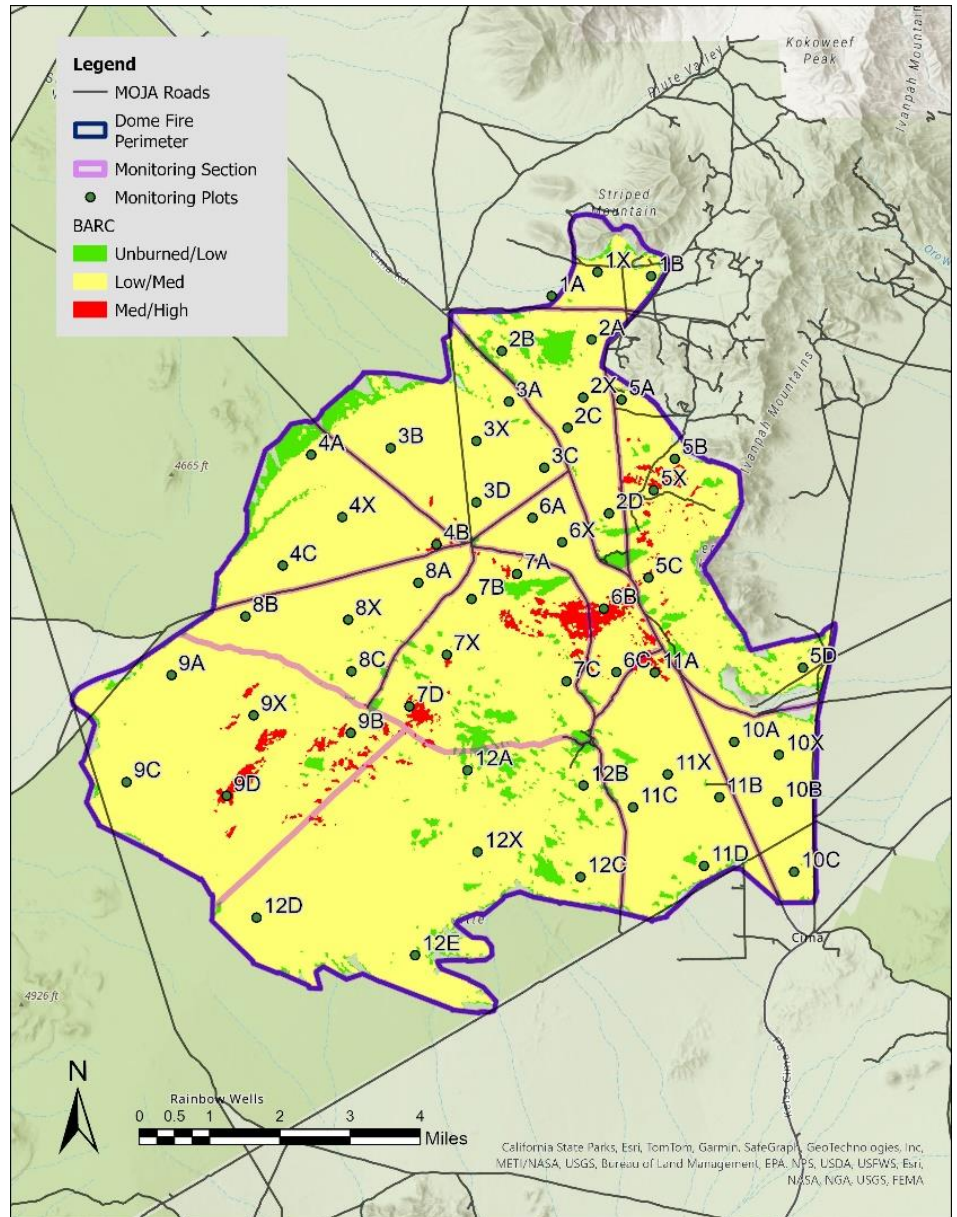


Figure 1. Monitoring plot locations across Dome Fire burn area.

obtain a count of unique species. Each year, a sample of 12-18 plots was monitored.

Due to staffing limitations, only 7 of the 54 plots (1X, 3D, 4B, 5D, 9B, 11B, 12D) were visited each year from 2021

to 2023. In order to present preliminary results, data from these plots were used to generate absolute cover values for vegetation. The plant species recorded in each plot were categorized into the following groups: native perennial grasses, native perennial

<sup>1</sup> Mojave National Preserve

shrubs, native annual forbs/grasses, non-native annual forbs, and non-native annual grasses. No non-native perennial species were found in these plots. Native annual grasses were only represented by one species (*Festuca octoflora*). In spring 2021, no group of plants showed an absolute cover greater than 1% due to low rainfall in the winter of 2020 and spring of 2021 (Fig. 3). Beginning in spring 2022, the absolute cover of all vegetation groups increased. Native annual absolute cover increased the greatest amount from 0.10% to 4.23% in spring 2022, and native shrub cover increased the least, from 0.72% to 1.11%. Nearly all shrubs present in the spring 2021 plots were mature Joshua trees (*Yucca jaegeriana*) and banana yucca (*Yucca baccata*) that had survived the fire. In spring 2023 percent cover for all groups increased again, with native annual plant cover growing the most, from 4.23% to 10.29%.

Annual monitoring by Preserve staff will continue through spring 2025, but after this the frequency of monitoring will be re-assessed. At minimum, the Preserve hopes to revisit these plots every 10 years. This data will provide important long-term post-fire vegetation recovery trends for future management.

Additional considerations for future monitoring efforts may include adding a brush belt (a rectangular area extending from each side of a transect line) to more effectively monitor Joshua tree recruitment and survival.

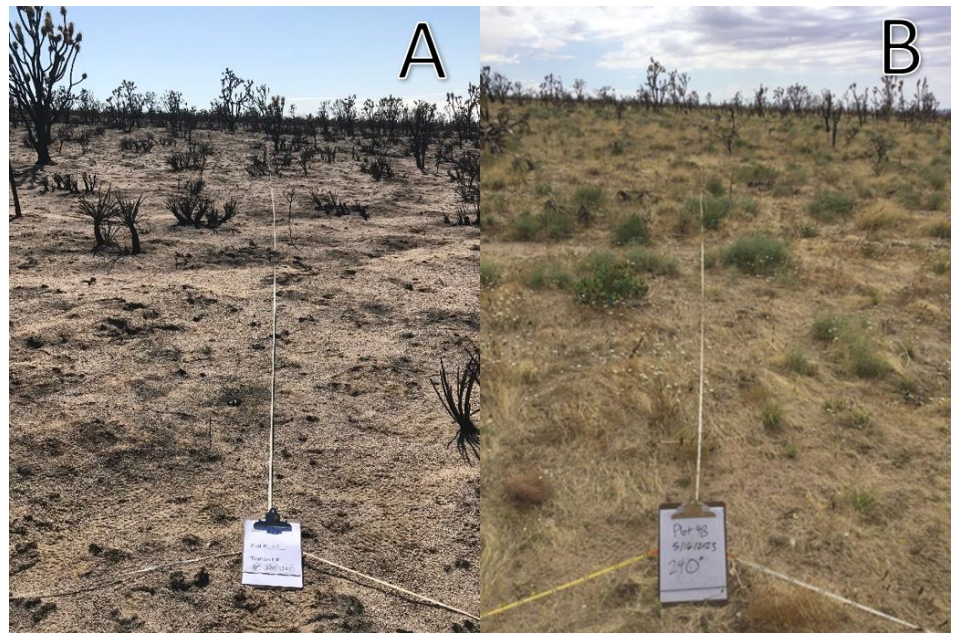


Figure 2. Each plot has three line transects radiating from a center point (clipboard). These photos are looking south along Transect 240° at Plot 4B and show a comparison between March 2021 (A) and May 2023 (B). In 2023, shrubs including paperbag bush (*Scutellaria mexicana*) and grasses such as the native James' galleta (*Hilaria jamesii*) and invasive red brome (*Bromus rubens*) comprise much of the ground cover following two years of sufficient spring precipitation.

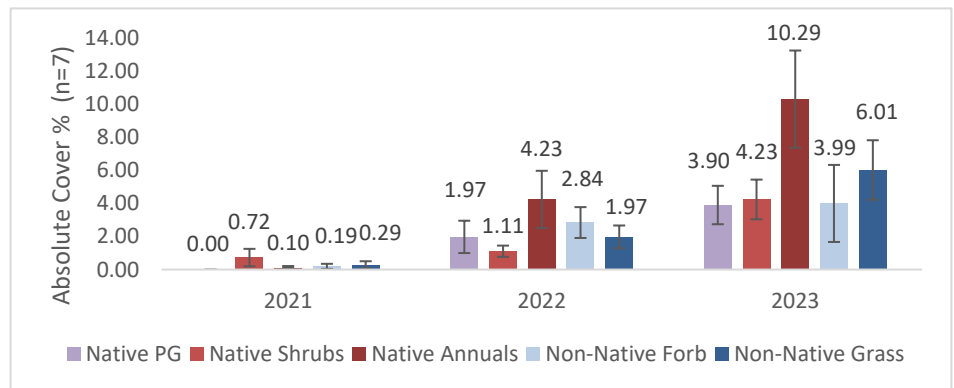


Figure 3. Preliminary results from 2021-2023 showing absolute percent cover of the five vegetation categories used in the study; data were averaged from seven plots.

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