Mojave National Preserve

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Science Newsletter

Storm Cloud over Cima Dome – Tracking Vegetation Change after the Fire

Joseph R. McAuliffe[1]

During the summer monsoon season in the American Southwest, I regularly access online satellite images and weather radar maps to track the influx of moisture and development of storms throughout the region. By mid-August 2020, little or no rain had fallen in most of the Sonoran and eastern Mojave Deserts. On August 15, however, satellite imagery showed atmospheric moisture moving into parts of southern California. Switching to radar images, I saw the development of a convective storm cell directly over Cima Dome, offering promise of the first summer rain. Hopeful anticipation turned to dismay when I learned that the storm cloud delivered only lightning, igniting what would become the second largest wildfire in the history of Mojave National Preserve (Preserve, Fig. 1). This event was associated with the same large pulse of atmospheric moisture that initiated thousands of lightning strikes across much of California from August 15-17, igniting wildfires that eventually burned more than 4 million acres

19 Sep. 2013

3 Nov. 2020

Figure 1. Photo station Cima-13, approximately 2 km east of the Cima Dome summit. Even uppermost branches of the tallest Joshua trees were scorched by the fire. Stems of all shrubs have been completely burned; dark smudges of fine charcoal and ash mark the original locations of shrubs. Buckhorn cholla stems remain standing (e.g., lower left corner and right side, mid-ground). Above-ground portions of banana yucca (lower right and center) were scorched but not completely consumed at this site.

In this Issue:

[1] Desert Botanical Garden, Phoenix, Arizona.

across the state during the 2020 fire season.

A lightning strike about 1.75 km northwest of the summit of Cima Dome ignited the Dome Fire in mid-afternoon, August 15. Erratic winds initially drove the fire in all directions. The next day, winds from the west rapidly spread the fire eastward, and by 11:00 that morning, the fire had grown to 16,000 acres (64.75 km^2). The fire's spread was largely stopped by the end of the fourth day through the efforts of an interagency fire management team that included aerial support. Ultimately, 43,273 acres (175.12 km^2) were burned (*1, 2*). The Hackberry Complex Fires in late June 2005, also ignited by lightning, charred 70,736 acres (286 km^2) in the Mid-Hills and New York Mountains, approximately 20-30 km east and southeast of Cima Dome (*3*).

Drawn to this area because of its striking beauty, I have been studying vegetation on Cima Dome since 1992. The Preserve is unusual because it straddles a zone of climate transition from east to west in the Mojave Desert. Significant warm-season rainfall occurs in the eastern Mojave Desert of California but declines markedly to the west (*4*). Warm-season rainfall fosters the occurrence of distinct types of vegetation in parts of the Preserve, including on Cima Dome, that do not occur in western and northern portions of the Mojave Desert. In particular, native warm-season perennial grasses are a significant component of the understory vegetation within some stands of Joshua trees. These "Mojavean Joshua tree savannas" generally occur above 1200 m in the Preserve, adjacent areas in southernmost Clark County Nevada, and also to the east in Mohave County, Arizona. Ecologically, they represent the western-most outposts of the "desert grasslands" of the American Southwest (*4*). After nearly three decades of exploration and research on Cima Dome, I amassed a substantial collection of site photographs together with associated vegetation data. To date, I have used some of this information to document vegetation changes that occurred after the removal of livestock from most parts of the Preserve 20 years ago. A compelling form of evidence to document vegetation change is repeat photography, consisting of photographs separated in time, but from a fixed camera position showing the same view of the landscape (*5*). After the Dome Fire, I realized that the
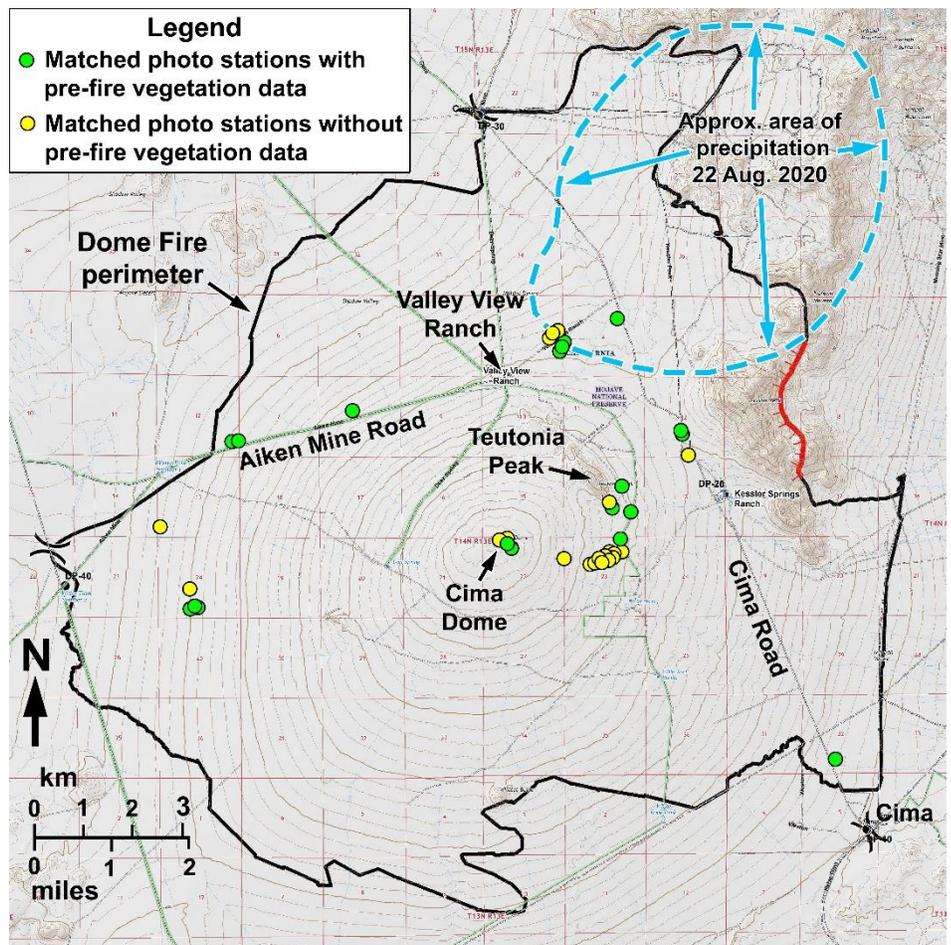

Figure 2. Locations of repeat photography stations within the footprint of Dome Fire. The black portion of the fire perimeter is the contained fire line on 22 August 2020; the short red segment on the east represents an uncontained fire edge on that date. Base map and fire perimeter source: https://inciweb.nwcg.gov/photos/CAMNP/2020-08-18-1212-Dome/pics/2020_08_22-21.01.46.650-CDT.jpeg. The approximate area of precipitation on 22 August is based on field observations by NPS personnel (*11*).

photographs and information that I gathered over the last three decades were a valuable archive of information that could be used to assess future vegetation recovery and change. In the two months following the fire, I poured over those photographic and data records, and assembled a set of 40 locations to revisit for this repeat photography work. During the first week of November 2020, I returned to Cima Dome with a binder filled with images I had recorded and set out to relocate the sites in order to photograph them once again. In this article, I describe that effort: observations on the impacts of the fire, factors that may have contributed to the fire's expansive geographic extent, and finally what to expect in terms of vegetation recovery and changes over time – within the first decade as well as a century from now.

Repeat photography stations. The 40 repeat photography stations are distributed widely across Cima Dome, from a lower elevation of 1320 m to 1750 m at the summit (Fig. 2). I took the initial photographs at various times from 1992 through 2016 and had already taken repeat photographs at some locations before the Dome Fire. Although some plant species, like Joshua trees, occur throughout the entire elevation range of Cima Dome, others, including native perennial grasses, exhibit distinct elevation zonation. For example, big galleta (*Hilaria rigida*) occupies lower elevations below 1400 m; black grama (*Bouteloua eriopoda*) and galleta (*Hilaria jamesii*) are predominant in intermediate elevations, and blue grama (*Bouteluoa gracilis*) occurs only in the uppermost elevations. I selected the stations for repeat photography partly to reflect vegetation variation with elevation as well as soil conditions. I also included sites with distinct vegetation

composition, for example, those dominated by blackbrush (*Coleogyne ramosissima*), in order to provide a broad representation of the diversity in composition of pre-fire vegetation. At various times in the past (preceding the Dome Fire), I had collected data on vegetation composition at 19 of the 40 stations (Table 1). Some of the data sets are visual estimates of ground cover by canopies of perennial plant species, and several include point-intercept data of plant canopy cover by species. Two sites also included height measurements in 2016 of a sample of 100 Joshua trees at each site, along with estimates of Joshua tree density measured with the point-quarter method (*6*). Coupled with repeat photography, collection of various kinds of vegetation data at future dates will contribute substantially to the capacity to accurately document and track future vegetation changes.

Observations in November 2020. During six days of fieldwork on Cima Dome from November 1-6, I examined sites immediately northeast of Cima along Morning Star Mine Road, Cima Road, Valley View Ranch Road, Aiken Mine Road, and the road connecting Valley View Ranch to Cut Spring (Fig. 2). Additionally, overland trips on foot to the summit of Cima Dome and to remote sites located 6 km west of the summit gave me a wide-ranging view of the fire's aftermath. Although the intensity of the fire was variable from place to place (*1*), I observed that the uppermost branches of even the tallest Joshua trees throughout most areas were typically scorched by the fire, and few retained green leaves. Nevertheless, some damaged Joshua trees may resprout from the root crown as was observed after a wildfire in 1995 in Joshua Tree National Park, where 28% of burned plants produced sprouts at the base of the plant within 16 months of the fire (*7*). However, very few (2%) fire-damaged Joshua trees examined in that study exhibited regrowth of the fire-damaged stems. In most places on Cima Dome, all above-ground stems of woody shrubs were completely incinerated, reduced to dark smudges of fine charcoal and ash on the ground. Buckhorn cholla (*Cylindropuntia acanthocarpa*) and diamond cholla (*C. ramosissima*) were frequently reduced to standing skeletons of brown stems with spines burned away, and after more than two months since the fire, the scorched, succulent stems had

Table 1. Cima Dome repeat photography stations.

Station	Camera location (Lat. & Long.)	View direction	Dates of previous photos	2020 repeat photo date	Pre-fire vegetation data*
Cima-1	35.28907, -115.55703	N	20 Apr 2013	2 Nov	no
Cima-2	35.28986, -115.55784	N-NW	4 Mar 1998 29 Mar 2013 20 April 2013 18 Sep 2013	2 Nov	1
Cima-3	35.29950, -115.55761	N	21 Apr 2013	2 Nov	1
Cima-4	35.29502, -115.55550	W	21 Apr 2013	2 Nov	1
Cima-5	35.29759, -115.56046	NW	20 Apr 2013	2 Nov	1
Cima-6	35.29750, -115.56109	NE	20 Apr 2013	2 Nov	no
Cima-7	35.28777, -115.55717	N	19 Sep 2013	2 Nov	no
Cima-8	35.28925, -115.58334	N	19 Sep 2013	3 Nov	1
Cima-9	35.28932, -115.58334	E	19 Sep 2013	3 Nov	no
Cima-10	35.28952, -115.58542	N-NW	19 Sep 2013	3 Nov	no
Cima-11	35.28834, -115.58277	E	19 Sep 2013	3 Nov	1
Cima-12	35.28632, -115.56994	E	19 Sep 2013	3 Nov	no
Cima-13	35.28640, -115.56002	S-SE	19 Sep 2013	3 Nov	no
Cima-14	35.28656, -115.56020	S-SE	19 Sep 2013	3 Nov	no
Cima-15	35.28661, -115.55920	S-SW	19 Sep 2013	4 Nov	no
Cima-16	35.28712, -115.55852	S	19 Sep 2013	4 Nov	no
Cima-17	35.28703, -115.55842	S	19 Sep 2013	4 Nov	no
Cima-18	35.28705, -115.55819	S-SE	19 Sep 2013	4 Nov	no
Cima-19	35.28677, -115.55917	E-NE	19 Sep 2013	4 Nov	no
Cima-20	35.28561, -115.56329	NE	19 Sep 2013	4 Nov	no
Cima-21	35.28553, -115.56401	NE	19 Sep 2013	4 Nov	no
Cima-22	35.31253, -115.61727	N-NE	1 May 1993 19 Feb 2015	4 Nov	1
Cima-23	35.30723, -115.64418	W-NW	1 May 1993 19 Feb 2015	4 Nov	1
Cima-24	35.30705, -115.64420	N	1 May 1993 19 Feb 2015	4 Nov	1
Cima-25	35.29223, -115.66092	N-NW	14 Mar 2016	5 Nov	no
Cima-26	35.28099, -115.65427	N-NW	14 Mar 2016	5 Nov	no
Cima-27	35.27794, -115.65303	N-NW	15 Mar 2016	5 Nov	2, 4
Cima-28	35.27793, -115.65301	SE	15 Mar 2016	5 Nov	2, 4
Cima-29	35.27793, -115.65300	E-SE	15 Mar 2016	5 Nov	2, 4
Cima-30	35.32660, -115.57043	S-SW	30 Mar 2013	6 Nov	1, 3
Cima-31	35.32669, -115.57036	S-SE	30 Mar 2013	6 Nov	1, 3
Cima-32	35.32679, -115.57040	S-SW	30 Mar 2013	6 Nov	1, 3
Cima-33	35.32681, -115.57102	SW	Apr 2009	6 Nov	no
Cima-34	35.32681, -115.57102	NW	Apr 2009	6 Nov	no
Cima-35	35.32683, -115.57104	NE	Apr 2009	6 Nov	no
Cima-36	35.33032, -115.55817	NE	24 Jun 1992 29 Mar 2013	6 Nov	1, 3
Cima-37A-B	35.30899, -115.54276	W	16 Mar 2016	6 Nov	1
Cima-38A-B	35.30899, -115.54276	W	16 Mar 2016	6 Nov	1
Cima-39	35.30526, -115.54214	W-SW	16 Mar 2016	6 Nov	no
Cima-40	35.24913, -115.50935	NE	28 Oct 2004	6 Nov	1

* **Types of vegetation data:**

   1 – Species list & visual estimate of percent canopy cover (perennials only)

   2 – Point-intercept estimate of canopy cover

   3 – Plot data – frequency of occurrence (0.1 m² plots)

   4 – Point-quarter sampling estimate – Joshua tree density & height distributions

been reduced to brittle, dehydrated remains (Figs. 1 and 3).

At the northwest and southeast sides of the burned area along Aiken Mine Rd. and Morning Star Mine Rd., respectively, I examined unburned vegetation directly outside of the main footprint of the fire. I also examined multiple islands of unburned vegetation within the fire footprint that had escaped due to the effects of firebreaks such

as roads or natural bedrock surfaces. Dried remains of dense growths of red brome (*Bromus madritensis*) that grew during the previous winter-spring season (2019-20) were present in nearly all of these unburned places, from the base of Cima Dome to the summit (Fig. 4, A, B, and C). A notable exception was an area containing unburned blackbrush (*Coleogyne ramosissima*) between Teutonia Peak and Kessler Springs along Cima Road, where very little, if any red

brome was present within the dense stands of this shrub (Fig. 4D).

The densest accumulations of red brome frequently occurred beneath shrubs with loosely branched canopies, including *Ephedra nevadensis* and *Lycium* spp., and also amidst clusters of rosettes of banana yucca, *Yucca baccata* (Fig. 5, A and B). The tendency for denser growth of ephemeral plants, including red brome, beneath canopies of larger shrub-like perennials in this semi-arid setting is due partly to the shading effect of the canopy, which reduces evaporative losses from the soil, thereby enhancing local growth and productivity of ephemerals (*8*). Higher levels of plant nutrients, particularly nitrogen, in the "fertile islands" beneath larger plant canopies can also enhance ephemeral plant production (*9, 10*). Dried remains of native ephemeral plants, notably fiddleneck (*Amsinckia tesselata*) were also present in some of the unburned locations, but overall, red brome contributed the bulk of ephemeral plant fine fuels. This understory of fine fuels dominated by red brome was clearly enough to cause all above-ground parts to be nearly incinerated even in succulent plants, such as banana yucca, with living leaves and stems that are inherently non-flammable (Fig. 5C). Based on these observations, the complete combustion of above-ground stems of nearly all woody shrubs can at least be partly attributed to the dense accumulations of red brome on the landscape and beneath the shrub canopies. In stands of blackbrush where apparently little red brome was present, the relatively compact, dry, fine woody stems of the closely spaced shrubs were apparently sufficient in themselves to fuel fires that completely consumed the canopies of that shrub and other plants (Figs. 4D and 3).

At the time of the fire, there were no precipitation recording stations on Cima Dome, but NPS personnel described an isolated convective storm on August 22 that was restricted to the northeastern corner of the Dome Fire footprint (Fig. 2) (*11*). In that area, the rain dispersed and washed the ash and fine charcoal from the soil surface. This is also where I found the only plants that had resprouted from surviving underground parts and they were located in channels that received some runoff from that storm (Fig. 6). In

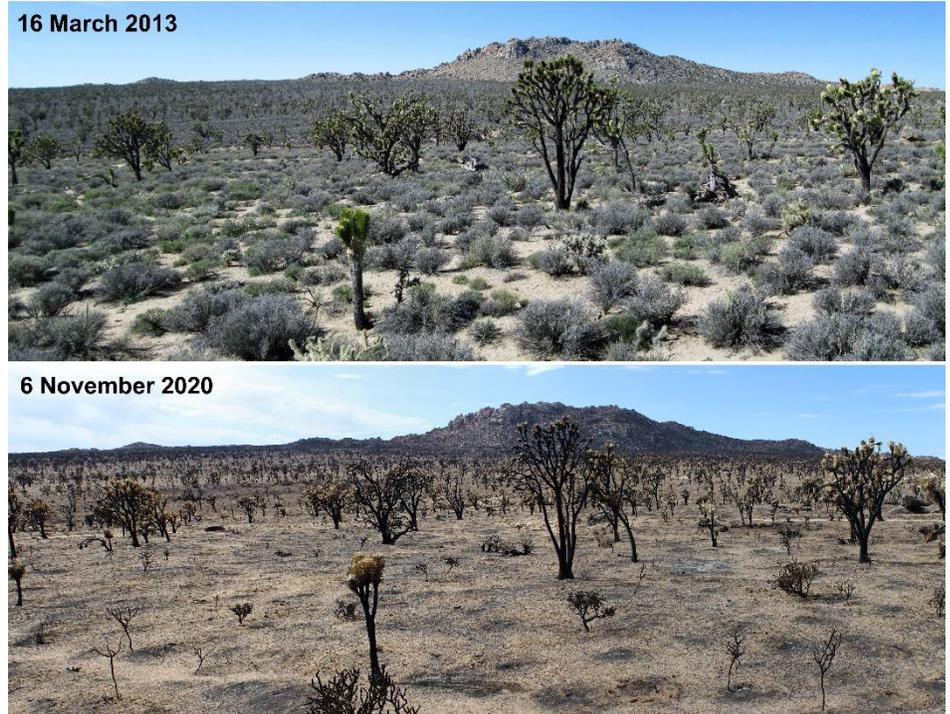
16 March 2013

6 November 2020

Figure 3. Photo station Cima-37 near Cima Road viewed toward Teutonia Peak. Blackbrush was the dominant plant at this locality; that species and all other shrubs were completely consumed by the fire. The smaller plants that remain standing after the fire are the dead, dehydrated remains of buckhorn cholla (*Cylindropuntia acanthocarpa*). Photographs on both dates consisted of a pair of overlapping frames to produce the wide panoramic view.

most other areas, the persistence of discrete patches of fine charcoal and ash marking the original locations of plants indicated a lack of rain from the time of the fire until the timing of my visit in the first week of November (Fig. 1). I observed no regrowth or resprouting by any perennial plants anywhere else on Cima Dome in early November, nearly three months after the fire. The elimination of ground cover by the fire and the delay in plant regrowth exposes the soil to rapid erosion by runoff after storms, potentially altering soil conditions, thereby potentially affecting future germination and seedling survival (Fig. 6).

Vegetation responses. The amount and timing of future precipitation will have the greatest impact on resprouting from surviving underground portions of some plants or establishment of new plants from undamaged seed. The exceptionally dry soil conditions that persisted for months after the fire could significantly affect the survival of any remaining, underground portions of plants and their ability to resprout from the base. For example, black grama stores the bulk of its energy reserves in the above-ground culms; the below-ground portions have very limited storage capacity (Figs.

7 and 8). Although this perennial grass can regrow after above-ground portions have burned or been otherwise removed (*12*), the small below-ground storage reserves limit regrowth and how long the remaining dormant tissues can survive. Even during dormancy, the surviving tissues continue to respire, but without replenishing their energy stores through regrowth and photosynthesis, these plants can eventually succumb to carbon "starvation" and die (*13*). The relative amounts of cool- versus warm-season precipitation received in the immediate future will exert a strong control on which species recover and predominate in the burned areas. Warm-season precipitation will benefit the native C_4 perennial grasses, whereas most deeper-rooted shrubs with a C_3 photosynthetic pathway rely more on moisture delivered in the cool season (*14*). The first substantial widespread precipitation on Cima Dome after the fire came as snowfall during the last week of January, 2021. I received a report from Drew Kaiser of the NPS that a storm on January 25, 2021 delivered 4-6 inches (10-15 cm) of snow in the vicinity of Cima, and perhaps as much as 12 inches (30 cm) in the upper elevations of Cima Dome (Fig. 9). The water derived from this snow will begin
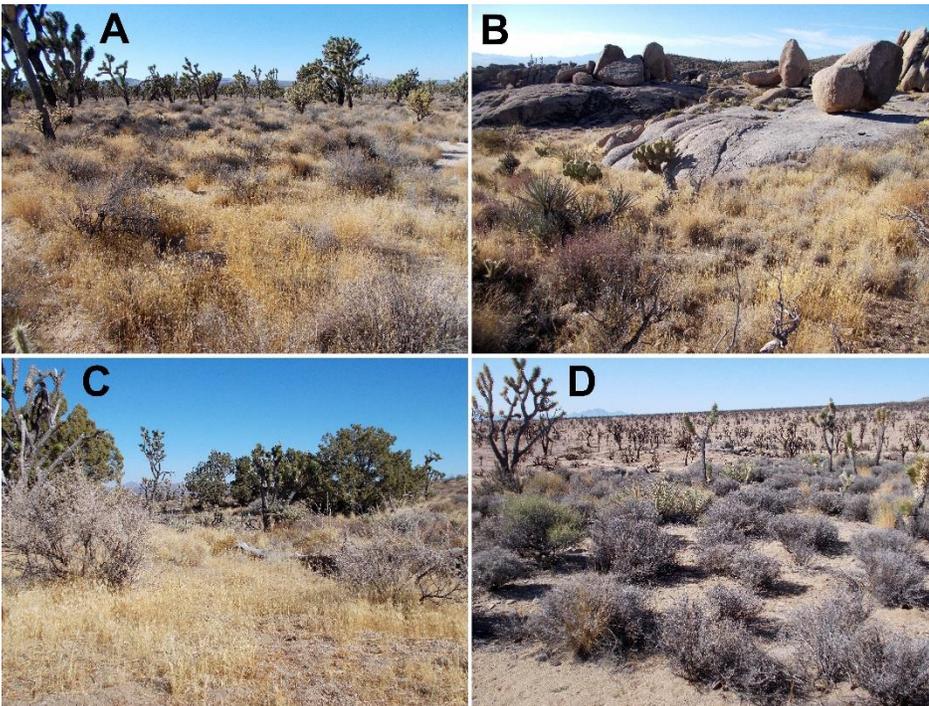
Figure 4. A. Unburned vegetation ~ 160 m from the northwest boundary of the Dome fire footprint, along Aiken Mine Road, 35.30531° N, 115.65186° W, 1385 m elev. Mixed shrub –Joshua tree vegetation with abundant red bome beneath shrub canopies and areas between shrubs. The straw-colored vegetation is red brome produced during the winter-spring season of 2019-20. 4 November 2020.

B. Unburned patch ~ 2 km east of the Cima Dome summit and 1.5 km south of Teutonia Peak, 35.28748° N, 115.56204° W, 1620 m elev. Abundant red brome (straw-colored) in area protected from fire spread by surrounding, barren bedrock surfaces. 3 November 2020.

C. Unburned patch ~ 50 m directly east of Cima Dome summit, 35.28912° N, 115.58452° W, 1750 m elev. Dense growth of red brome (straw-colored) in a broad swale. The high density of brome here is attributed to deeper soils and receipt of moisture as runoff from surrounding areas. Nevertheless, although production was less, red brome was present throughout those surrounding areas. 3 November 2020.

D. Unburned patch of blackbrush (*Coleogyne ramosissima*) on the west side of Cima Road, ~ 1.4 km northwest of Kessler Spring Ranch, 35.30781° N, 115.54290° W, 1527 m elev. Unburned areas of blackbrush in this vicinity were the only places in which very little, if any, red brome was produced in the 2019-20 winter-spring season. 17 May 2021.
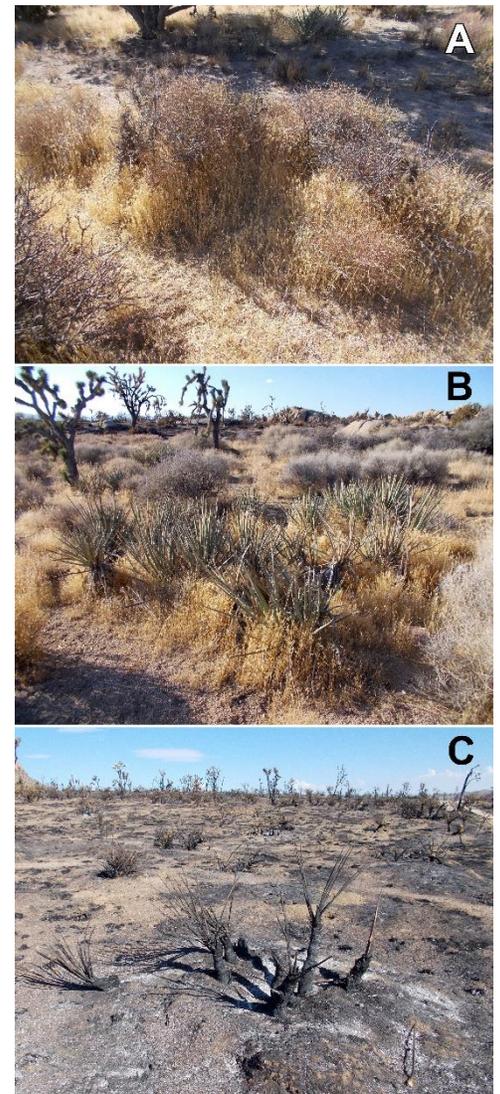

Figure 5. A. Dense growth of red brome within and beneath canopy of *Ephedra nevadensis*, near Cima Dome summit, 0.5 km southeast of Cima Dome summit, 1730 m elev. 3 November 2020.

B. Dense growth of red brome beneath cluster of banana yucca (*Yucca baccata*) rosettes, 1.5 km south of Teutonia Peak, 1520 m elev. 2 November 2020.

C. Burned remains of banana yucca, 1 km south-southeast of Tuetonia Peak, 1595 m elev. 2 November 2020.

recharging soil moisture after the nearly rainless summer and fall. Repeat visits in May and October 2021, will provide more data to assess the regrowth of various plant species following both the winter-spring and summer rains.

Knowledge about how vegetation has responded after past wildfires helps to inform us about what to expect in the future in the aftermath of the Dome Fire. In early afternoon on July 5, 2006, a lightning strike on Cima Dome, approximately 1 km east of the Valley View Ranch, ignited the Valley View Fire. That fire burned 65.5 acres (0.265 km^2) before it was brought under control by firefighters (Fig. 10) (*15*). Seven years after the fire, I compared vegetation composition in adjacent burned vs. unburned areas. In addition to the reduction of density of Joshua trees due to

fire-caused mortality, the fire significantly altered the relative predominance of some native shrubs and native, warm-season perennial grasses. In particular, the fire nearly eliminated Cooper's goldenbush (*Ericameria cooperi*), a small shrub that originally dominated the burned area before the fire. The persistence of the dead, charred basal portions of the small shrubs throughout the footprint of the fire demonstrated that this shrub occurred in both the burned and unburned areas at equivalent densities, but did not regrow after fire consumed above-ground portions. At the time of data collection in March 2013, recruitment of new Cooper's goldenbush from seed had not occurred in the burned area, but combined canopy cover of the two native perennial grasses, black grama and galleta, were more than double that observed in the adjacent

unburned area (Fig. 10) (*4*). The original dominance of Cooper's goldenbush at this site located only a kilometer from the Valley View Ranch headquarters is likely attributed, at least in part, due to the sustained influence of livestock grazing, which suppressed the native perennial grasses. This small, short-lived shrub is a colonizer of disturbed vegetation. For example, it often occupies abandoned fields at comparable elevations that were cleared by homesteaders in the early 1900s in Lanfair Valley (*4, 16*). It is

Figure 6. View to the south from Valley View Ranch Road near the intersection with Cima Road within the area receiving isolated rain on 22 August 2020. With ground cover completely destroyed by the fire, runoff and fine gravelly-sandy sediments accumulated in first order channels as above. Sparse regrowth of galleta (*Hilaria jamesii*) occurred along these areas of runoff collection (center, foreground), but regrowth away from channels in areas shedding water had not occurred by early November, 2020.

possible that the increased abundance of native perennial grasses within the footprint of the Valley View Fire more closely represents the original ground cover that existed in the area before the advent of livestock grazing in the 1890s. In contrast to the inability of Cooper's goldenbush to regrow after the fire, some perennial species found at the site such as *Ephedra nevadensis*, *Lycium* spp., *Scutellaria mexicana*, and *Yucca baccata* regrew from surviving underground portions.

Native perennial grasses similarly increased in abundance in some places in the aftermath of the 1995 Hackberry Complex Fires. For example, 18 km southeast of the Cima Dome summit, northern and westward spread of that fire was halted at Cedar Canyon Road and a small intersecting road to the south. Before the fire, the vegetation of this area consisted of a mixed assemblage of shrubs and perennial grasses (primarily big galleta with lesser amounts of black grama) within a moderately dense stand of Joshua trees. A decade after the fire, cover provided by those perennial grasses had approximately doubled in the burned areas and shrub cover was much reduced as was the population of Joshua trees (Fig. 11).

Figure 8. A tuft of black grama uprooted from the Cima-2 photo station, showing the very limited amount of underground storage tissue. The plant stores most of its energy reserves during dormancy in the above-ground culms. Loss of above-ground tissues due to either fire or other removal can limit subsequent regrowth.

Native, warm-season perennial grasses occur widely over Cima Dome, and if adequate summer precipitation occurs in the coming years, many burned areas on Cima Dome will probably experience a similar increase in the predominance of perennial grasses. However, some locations on Cima Dome lacked these perennial grasses before the fire. For example, the area occupied by blackbrush (*Coleogyne ramosissima*) to the east of Teutonia Peak and extending to the southern flank of the Ivanpah Mountains in the vicinity of the Kessler Spring

Figure 7. Photo station Cima-2 located approximately 1 km south-southeast of Teutonia Peak (shown here in center of background). In 1998, perennial vegetation was dominated by shrubs, including *Salvia dorrii*, *Ephedra nevadensis*, *Menodora spinescens*, *Ericameria cooperi*, *Thamnosma montana*, and *Prunus fasciculatus*. The short tufts are the bases of black grama (*Bouteloua eriopoda*) and smaller amounts of galleta (*HIlaria jamesii*), consumed by livestock to within 2 cm of the soil surface. This extreme level of utilization of native perennial grasses was typical across most of Cima Dome before removal of livestock circa 2000. The 2013 photograph shows the substantial response of the perennial grasses more than a decade after the removal of livestock. The increased predominance of grasses was accompanied by mortality of approximately half of all *Salvia dorrii* that were alive in 1998. The November 2020 photo shows the charred bases of individual tufts of perennial grasses; the residual fine charcoal remains on the surface due to lack of rain since the August fire. All above-ground stems of woody shrubs were completely consumed by the fire.

Ranch generally lacks grasses such as galleta and black grama. The Dome Fire destroyed much of this blackbrush-dominated vegetation (Fig. 3). Fire readily eliminates this shrub and plants burned to the ground do not resprout (*17, 18,* pers. obs.). Recruitment by seedlings is exceptionally slow, therefore burned areas exhibit negligible recolonization by this shrub

after many decades (*19*). In the ecological vacuum that ensues after elimination of blackbrush, a variety of species with wind-dispersed seeds, including small, short-lived shrubs such as wire lettuce (*Stephanomeria* spp.), snakeweed (*Gutierrezia microcephala*), and groundsel (*Senecio flaccidus*) often predominate for a decade or more (pers. obs.).

Potential long-term changes. Although red brome may have contributed to the rapid spread and size of the Dome Fire, there is evidence that wildfires occurred on Cima Dome long before this non-native species became prevalent throughout the region. For example, in the upper elevations between Teutonia Peak and the summit of Cima Dome where scattered Utah junipers occur, in 2017 I observed fire-hollowed and extremely weathered juniper stumps. The considerable degree of weathering of the stumps indicated the fires that consumed those trees likely occurred well over a century ago (Fig. 12). I have documented similar remains of old fire-hollowed juniper stumps on the eastern side of the New York Mountains; preliminary radiocarbon dating from that site indicates some of those stumps were trees that had died several centuries ago (*20*). The presence of old fire-hollowed stumps on Cima Dome provides unequivocal evidence of the occurrence of fire at those locations long ago, but the timing and areal extent of those fires is unknown. The fire-hollowed stumps I observed in 2017 may have been destroyed or partially consumed in the Dome Fire, making it difficult, if not impossible, to derive any further specific information from them regarding the timing or extent of past fires.

However, there is other evidence for a sizeable wildfire that occurred slightly more than a century ago on the western flank of Cima Dome. Aerial images taken before the Dome Fire revealed a large, contiguous area of contrasting, lighter color that I suspected was the footprint of a wildfire that had not been historically recorded (Fig. 13, A and B). I examined this area in detail on the ground in March 2016. The western boundary of this area was very sharply defined and separated a dense stand of tall, older Joshua trees to the west from considerably lower densities of shorter, younger Joshua trees to the east (Figs. 13C and 14). The area containing the shorter Joshua trees

Figure 9. Snowfall near Cima from the 25 January 2021 storm. Photo by Drew Kaiser, NPS.
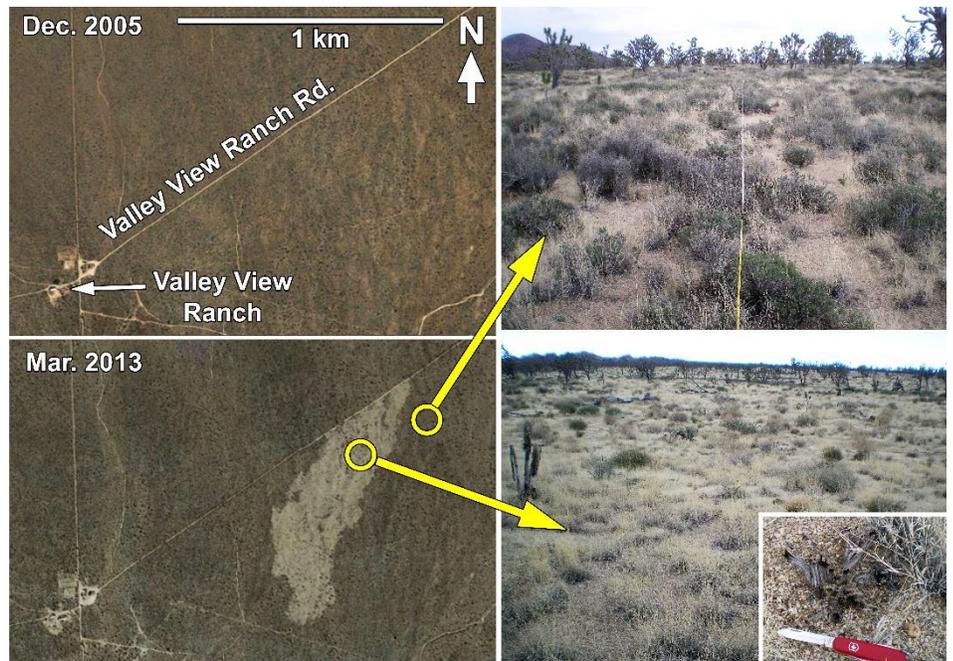

Figure 10. Left side – matched Google Earth ™ views showing the location of the July, 2006 Valley View Fire. The footprint of the fire (lower left panel) appears light-colored in the 2013 view due to the greater abundance of native perennial grasses, in a dried, dormant state. Right side – ground-level views on 30 March 2013 showing the unburned vegetation (upper panel) and burned area (lower panel). Most of the small, dark canopies in the unburned area are *Ericameria cooperi*. The inset in the lower right shows the charred, dead base of *E. cooperi* from the burned area. Density of these dead remains was equivalent to the density of living plants in the unburned area; none of the burned plants exhibited regrowth.

apparently represents the footprint of a wildfire that nearly completely replaced the original stand of Joshua trees. The maximum ages of Joshua trees within that footprint can provide an estimate of the minimum amount of time that elapsed since that wildfire. Trunks of Joshua trees lack decipherable tree-rings that could be used to determine age, but I estimated maximum ages in another way. I compared the measured heights of Joshua trees in the old, burned area on Cima

Dome with those that had established after known dates at two other localities in Lanfair Valley. Those localities were an agricultural field cleared in 1915 but abandoned around 1920 (oldfield) and thick piles of earthen fill that were excavated and dumped along the route of the Nevada Southern Railroad during its construction in 1893 (Fig. 15). Joshua trees from the oldfield achieved maximum heights of 4 m, which was approximately a meter less than those from the

old wildfire footprint on Cima Dome or those growing on the piles of earthen fill created in 1893 (Fig. 16). Annual height increase in Joshua trees measured over a 25-year period on Cima Dome was reported as 3.3 cm/year (*21*), and the approximately 1 m difference in maximum heights of Joshua trees from the abandoned oldfield versus those that occupy the railroad excavation fill and the old wildfire footprint represents an approximately 30-year difference. This information derived from the heights of Joshua trees suggests the stand-replacing wildfire on the west side of Cima Dome probably occurred around or somewhat before 1900. Yet despite the passage of more than a century, the estimated density of the Joshua tree population within the burned area (92 plants/ha) is only 58% of that in the adjacent, unburned area (158 plants/ha) (Fig. 14). This information reveals that regeneration of a population of Joshua trees from seed is a slow process. In my work on Cima Dome in November 2020, I frequently observed intact, unburned fruits in the uppermost branches of Joshua trees, even though those branches had been killed by the fire. Fruits that had fallen to the ground contained what appeared to be viable seed, so it appears that a prospect for new seedling establishment probably exists in even severely burned areas. However, several human generations will pass before the population of Joshua trees across Cima Dome might once again approach the appearance of the pre-fire stand, providing wildfires do not, once again, intervene.

Although red brome was probably introduced to the Central Valley of California as early as the mid-1800s, its spread was first concentrated along transportation corridors in California and most likely was either absent or rare in more remote parts of the Mojave Desert such as Cima Dome before 1900 (*22*). Rather than being fueled by this non-native species, the fire that occurred on Cima Dome around 1900 was probably fueled by native plants, including the native perennial grasses, which has also been suggested for wildfires that occurred in pre-Eurosettlement times in similar vegetation in Lanfair Valley (*20*). However, individual wildfires long ago may have been far less extensive than the Dome Fire. The footprint of the wildfire that occurred more than a century ago on the west flank of Cima Dome as

Figure 11. Photos taken from single point along a small road that functioned as a firebreak, stopping the westward advance of the June 2005 Hackberry Fire. Camera view is to the north at a location 0.2 km south of Cedar Canyon Road (35.16174° N, 115.46288°W; elev. 1345 m). Top photo is the western (unburned) side; lower photo shows the eastern side burned in 2005. Photos were taken 20 February 2015, nearly 10 years after the fire. Cover provided largely by the native perennial grass big galleta (*Hilaria rigida*) and lesser amounts of black grama (*Bouteloua eriopoda*) on the burned side is double that on the unburned side. Joshua tree and shrub densities on the burned side are markedly reduced. The large shrub in the center of the lower photograph is a catclaw acacia (*Senegalia = Acacia greggii*), a plant that readily regrows from the base following wildfire.

Figure 12. Top – View toward the summit of Cima Dome from the southwest-facing slopes of Teutonia Peak. The elevation in the foreground is approx. 1630 m; Utah juniper (*Juniperus osteosperma*) occurs all the way to the summit (~1750 m). Lower – two extremely weathered, fire-hollowed juniper stumps from the northeastern side of Cima Dome pictured above. 23 April 2017.

interpreted from aerial imagery is approximately 1,656 acres (6.7 km²), which is less than 4% of the area burned in the Dome Fire. The dense accumulations of fine fuel generated by red brome following the extremely wet 2019-2020 cool season probably contributed to the

devastating spread and size of the Dome Fire. Unfortunately, red brome is here to stay and the future of vegetation change and vegetation composition on Cima Dome and other areas in the Mojave Desert will continue to be influenced by the presence of this introduced, non-native

species.

A look to the future. Although knowledge about vegetation change and recovery after past wildfires suggests what might be expected on Cima Dome in the future, many questions remain. How will future climate changes influence the trajectory of vegetation recovery and the plant species that reestablish and predominate? Mojave National Preserve is located near the western margin of regular incursions of summer monsoonal rainfall. If the geographic position of monsoonal moisture influx shifts in the future, how will that affect the vegetation? Long-term changes in the relative amounts of cool- versus warm-season precipitation will likely promote the establishment and success of different species. If wildfires repeatedly occur, what will be the consequences? Detailed documentation of vegetation change over time is required to understand these relationships and to better predict the consequences of environmental changes in the future. Decades from now, this information will also provide the National Park Service with an important resource for interpreting and communicating the ecological consequences of the Dome Fire to future generations. Repeat photography paired with vegetation data collection at locations distributed across Cima Dome provides a powerful means to track, document, and better understand future changes.

As mentioned previously, I will revisit Cima Dome periodically in the coming years to continue this work. However, I realize that I will merely witness the beginning of changes that will continue long into the future. Once I have completed my contribution to this effort, I will pass on the entire repeat photograph collection together with associated data and information on vegetation for use by others in the future. I intend to archive duplicate sets of those materials in two locations – at my home institution, the Desert Botanical Garden's Schilling Library, and with the National Park Service.
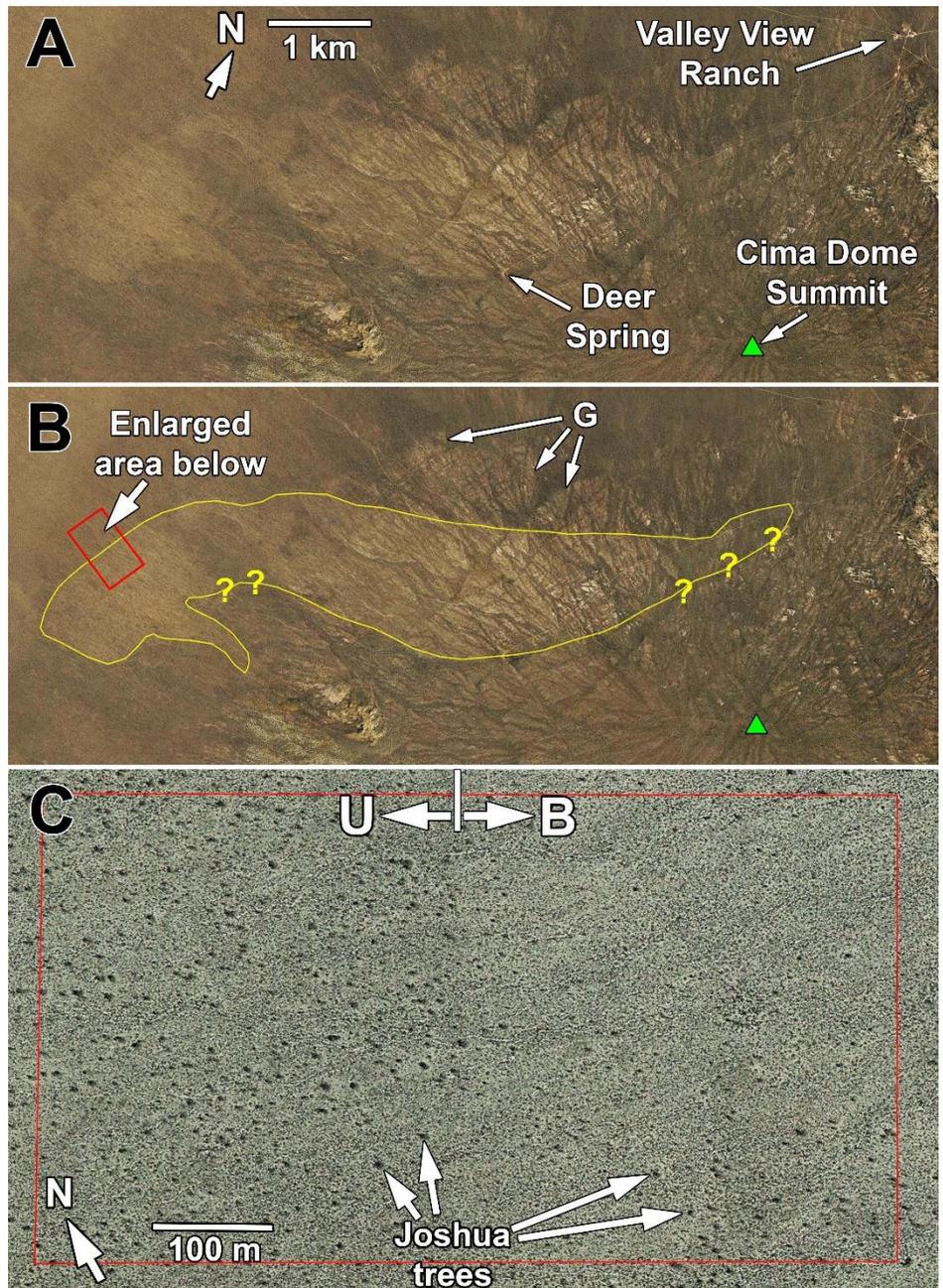

Figure 13. A- Google Earth ™ aerial view of an area of the western flank of Cima Dome with place names indicated.

B – identical view showing outline of footprint of old wildfire scar (thin yellow line) as indicated by contrast in color and ground inspection. Indistinct boundaries indicated with question marks. The outlined area has an area of 6.67 km². The areas labeled "G" are boundaries of geologically varying substrates, rather than margins of formerly burned areas.

C – enlarged view of the area enclosed in the red rectangle in B that straddles the margin of the burned area showing the sharp border of the burned area. The view is oriented with the unburned side (U) on the left and burned side (B) on the right. The distinct, near-absence of large Joshua trees typifies the burned area.

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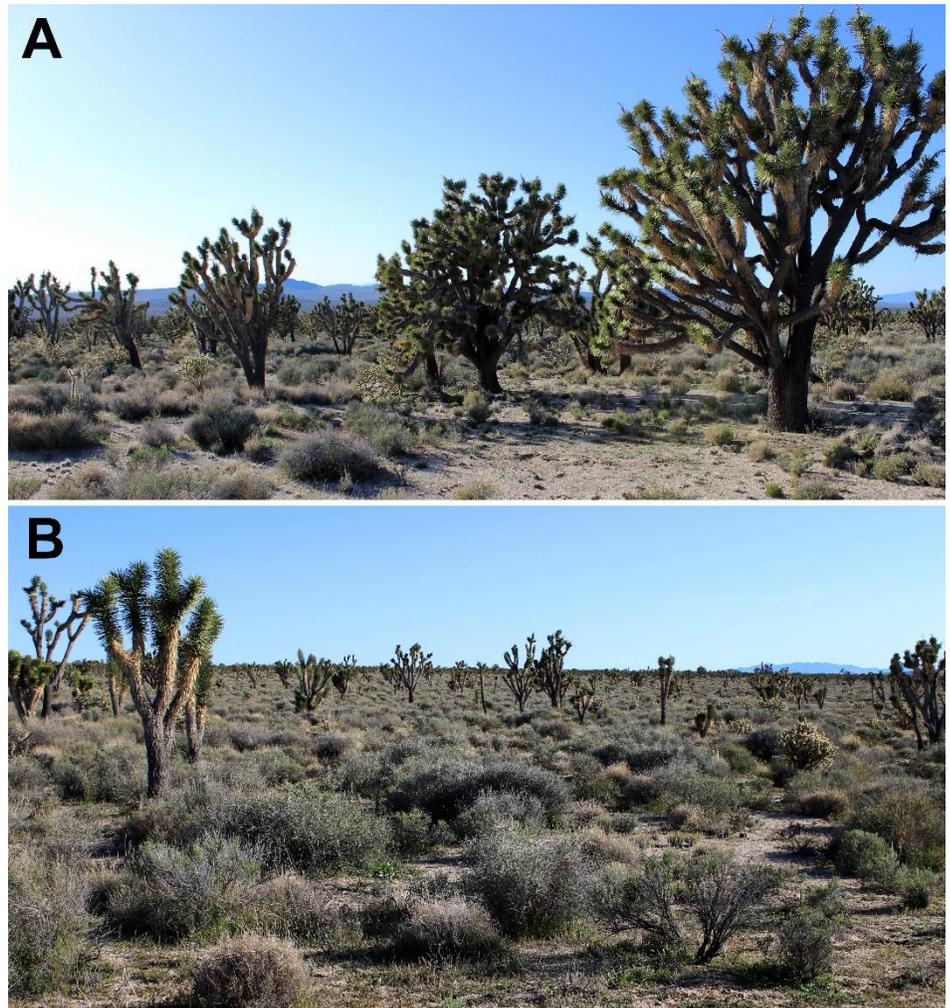
Figure 14. Contrast in densities and sizes of Joshua trees in the unburned vs. burned areas within the red rectangle pictured in Fig. 12B.

A – view of unburned area with Joshua trees commonly exceeding 6 m height.

B – view towards interior of burned area showing considerably lower densities and lower maximum heights (< 5 m) of Joshua trees. Densities of Joshua trees were estimated using the point-quarter method (*6*), with point-to-plant distance measurements taken at 25 points spaced at 50 pace intervals within each area. Joshua tree density for the unburned area = 158/ha (95% confidence interval = 129-192/ha) and for the burned area = 92/ha (95% confidence interval = 75-112/ha).

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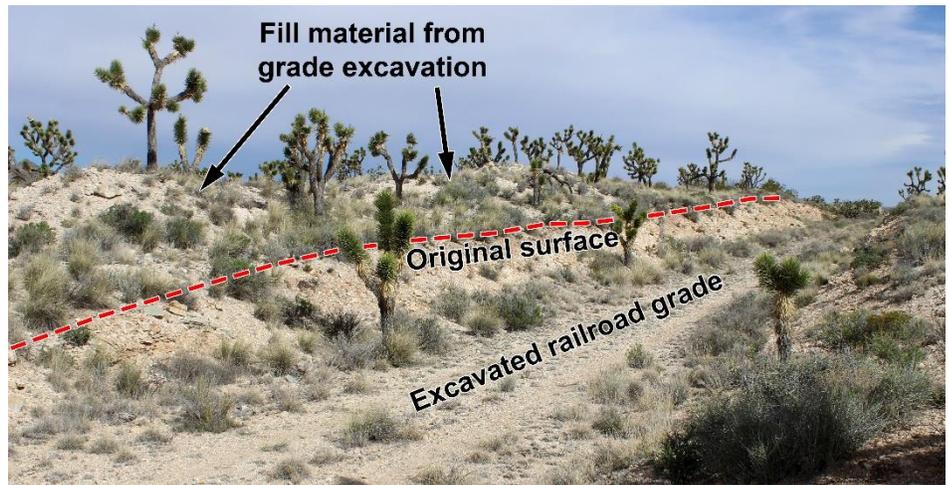
Figure 15. One of two excavated cuts created in Lanfair Valley during the 1893 construction of the Nevada Southern Railroad between Goffs and Barnwell. Excavated materials were piled along the margins of the cut to depths exceeding 2 m in some places. Heights of a sample of 100 Joshua trees that had established on top of this fill material were measured on 20 March 2017 in two locations: 35.25091°N, 115.21286°W and 35.24676°N, 115.21242°W (1400 m and 1390 m elevation, respectively).
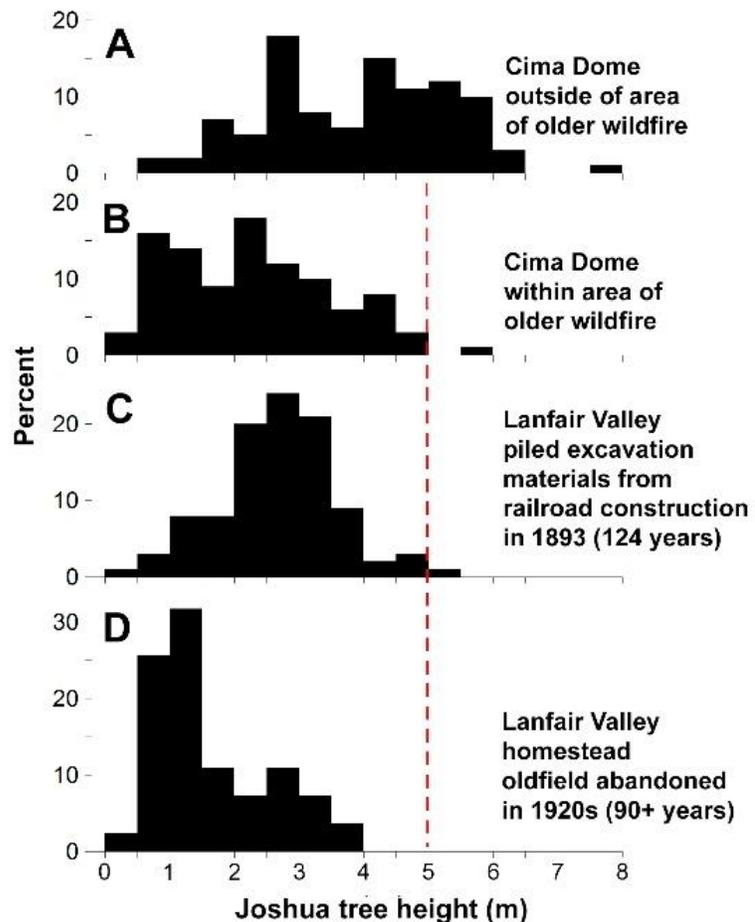

Figure 16. Height distributions of Joshua trees in unburned and adjacent burned area on Cima Dome (A, B) and two localities in Lanfair Valley where maximum plant age is constrained by human-caused clearing or piling of material (C, D). A sample of 100 Joshua trees was measured at all sites, except the homestead oldfield, where the sample contained 82 Joshua trees due to the limited number in the area sampled. The rectangular oldfield, 20 acres in area, is centered on 35.13305° N, 115.29329° W, and ranges in elevation from 1408 -1419 m. It was recorded as being entirely cleared and planted for the first time in 1915, with the last recorded planting in 1918 (*23*). Height measurements used in A, B, and D were collected in March, 2016; those in C were taken in March 2017.

The Impact of *Schismus* on Biodiversity in Mojave Desert Winter Annual Communities

Timothy Ohlert[1], Alesia Hallmark[2], Gregor Hamilton[1], Jade Mclaughlin[1], Mariah Patton[1], Scott Collins[1]

Biodiversity is a fundamental building block of ecosystems and is often indicative of ecosystem health. Deserts are hotspots of biodiversity, and the Mojave Desert is no exception (*1*). The Mojave Desert features an astounding number of endemic plant species and is known not only for its iconic species, such as Joshua tree (*Yucca brevifolia*), but also for the biodiversity of winter annual plants, short-lived species that emerge in spring and typically die by mid-summer. Occasionally, annual plants will emerge in such abundance they cover the desert floor, creating a "super bloom," an alignment of flowering that brings a rare burst of color to the desert (*2*).

Because of the many facets of biodiversity, ecologists quantify biodiversity in several ways. One metric of biodiversity is species richness, a count of observed species. In the scientific community, the effect of species richness on productivity, the amount of aboveground plant growth, has been an evolving research topic for decades (*3*). Another metric of biodiversity is species "evenness," a measure of similarity in the abundances of species. In most plant communities, a few species are very common, and many are relatively rare. Such a community would have low evenness because of the large disparity in abundances among the species.

Productivity in plant communities is important for its connection with food for animals, carbon capture, soil stability, and soil fertility (*4*). Biodiversity and productivity are typically tightly linked (*5*), with some exceptions. That is, more diverse communities are generally more productive than less diverse communities. In diverse plant communities, evenness also tends to be related to productivity (*6*). However, when a single or a few species are dominant, high productivity of the dominant species can result in

[1] Department of Biology, University of New Mexico, Albuquerque, New Mexico.

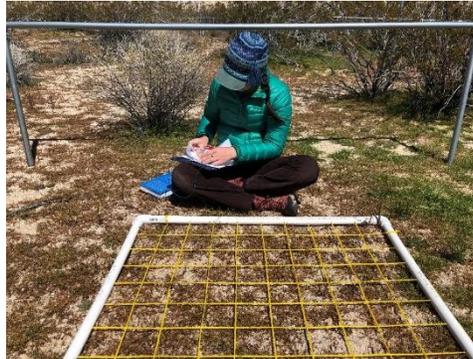[2] National Ecological Observatory Network (NEON), Boulder, Colorado.

Figure 1. Jade McLaughlin measures plant community composition in a 1x1m plot at Sweeney Granite Mountains Desert Research Center.

Figure 2. Creosote shrubland field site at Sweeney Granite Mountains Desert Research Center.

the greatest productivity occurring at low evenness (*7*). While ecosystems in wetter climates, such as grasslands and forests, tend to demonstrate higher productivity with greater biodiversity (*8*), deserts remain more of a mystery, in part, because studies focusing on plant productivity in the Mojave Desert are noticeably lacking. Therefore, little is known about how the biodiversity of annual plant communities might affect productivity. As deserts make up a third of the Earth's terrestrial surface

and are expanding under climate change (*9, 10*), it is imperative that we research and understand fundamental aspects of desert ecosystems. Here we ask whether winter annual plant communities of the Mojave Desert express similar properties to more mesic grassland and forest

What is the observed relationship between biodiversity and productivity in Mojave Desert winter annual plant communities? To answer this question, we measured plant species composition, productivity, and percent ground cover of all native and non-native species in 28 1x1m plots at the Sweeney Granite Mountains Desert Research Center in April 2019 (Figs. 1 and 2, Table 1). We placed each plot in the intershrub space of a creosote (*Larrea tridentata*) shrubland. We defined intershrub spaces as being a minimum of 0.75 m from the dripline of the nearest shrub canopy and we only placed plots in areas where no identifiable rooted woody perennials occurred (note: one plot included a single *Acacia greggii* seedling). With these data, we calculated species richness, species evenness, and aboveground productivity metrics for each plot. We first assessed the relationship between species richness to productivity. Surprisingly, we did not find the positive relationship between species richness and productivity that we expected based on previous studies in forest and grassland ecosystems. Instead, we found a strong negative relationship, indicating that the plots with the fewest species were actually the most productive (Fig. 3a).

When species evenness was compared to productivity within each plot, we found that the least even plots - those with the greatest disparity of abundances between species - were the most productive (Fig. 4a). This is similar to the dynamic observed in ecosystems with high dominance where the most productive plots are the least even. Although this evenness metric is calculated independent of species richness (*11*), there was a stark relationship between the two at

our study site (Fig. 5). In effect, the plots with fewer species were also those with the greatest disparity between abundant and rare species.

What can account for the negative biodiversity-productivity relationship?

Though the biodiversity-productivity relationship is well-studied and documented, counterexamples are common, and many factors could contribute to an observed negative biodiversity-productivity relationship. When communities have a single, ultra-productive dominant species, that species alone accounts for most of the production in a community (*12*). For example, the southeastern US is invaded by kudzu (*Pueraria montana*), which is an infamously productive and abundant invasive plant. Like many invasive species that have evolved in a different context, here in the US, kudzu is relatively free from organisms that might keep it in check, such as pathogens or herbivores. These advantages allow kudzu to be ultra-productive. The most productive communities then are those with an abundance of kudzu, not those with the most diverse mix of native species (*13*).

Similar processes could be at work in the Mojave Desert. When only native species are included in the analysis, we find a positive, rather than negative, relationship between species richness and productivity (Fig. 3b). Note that this is the exact same data from Figure 3a but excludes non-native species. The native plants exhibit the positive biodiversity-productivity relationship that we expect, but the incursion of non-native plants has interrupted that relationship.

In the early 1900's, *Schismus barbatus* (common Mediterranean grass) (Fig. 6) was introduced to the intershrub spaces of the Mojave Desert (*14*). By the mid-1990's, *Schismus* was dominant in the area between shrubs (*15*). This species is native to the Mediterranean region where the climate is similar to the Mojave Desert: defined by high temperatures and low rainfall, most of which comes in the winter rainy season. In the absence of competition from plants in its native region (*16*), *Schismus* fits the profile of a species capable of upending the typical biodiversity-productivity relationship just as kudzu can in the Southeast.
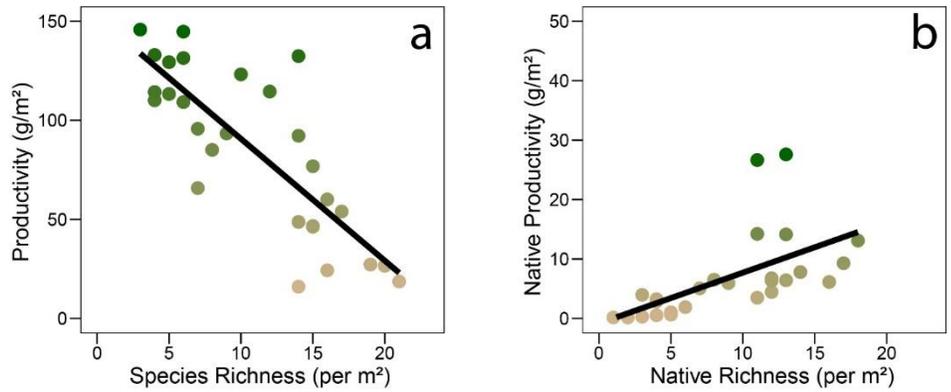

Figure 3. (a) Species richness-productivity relationship for all species (non-native and native). p-value < 0.001, r² = 0.64. (b) Species richness-productivity relationship for only native species. Dots are colored by productivity: tan dots are less productive plots and green dots are more productive. p-value < 0.001, r² = 0.33.
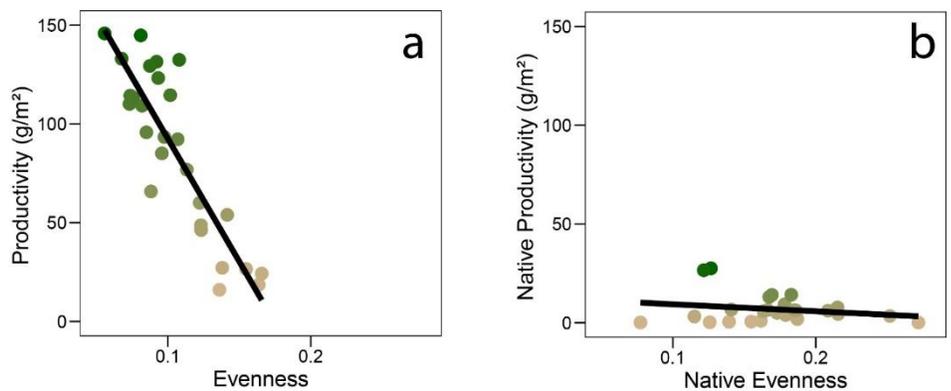

Figure 4. (a) Evenness-productivity relationship for all species (non-native and native). p-value < 0.001, r² = 0.76. (b) Evenness-productivity relationship for only native species. Higher evenness values indicate more similar species abundances whereas low evenness means that one or a few species are common and most others are rare. Dots are colored by productivity: tan dots are less productive plots and green dots are more productive. p-value = 0.002, r² = 0.31.
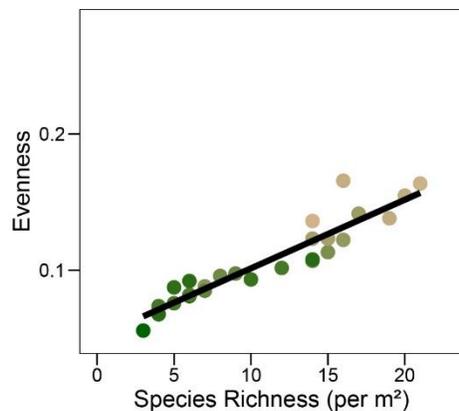

Figure 5. Species richness-evenness relationship for all species (non-native and native). Higher evenness values indicate more similar species abundances. Dots are colored by productivity: tan dots are less productive plots and green dots are more productive. p-value < 0.001, r² = 0.88. The most productive plots were those with the lowest values for species evenness and species richness.

Is Schismus the kudzu of the Mojave Desert?

To test this, we compared plots across a gradient of *Schismus* influence. We found a strong, positive relationship between the percentage of *Schismus* in the plots and the productivity of each plot. This indicates that the plots dominated by *Schismus* are most productive (Fig. 7). For example, plots with > 75% ground cover of Schismus averaged around 100 g/m² aboveground biomass, while plots with <30% ground cover of *Schismus* averaged < 50 g/m² aboveground biomass.

Another aspect of the negative biodiversity-productivity pattern potentially affecting the winter annual community in the Mojave Desert is the impact of *Schismus* on biodiversity, or rather, competitive interactions between *Schismus* and other plant species. Dominance by non-native species is often attributed to their ability to outcompete native species (*15, 17*). If *Schismus*

had a competitive advantage over other species in this community, we would expect the number of species in each plot to decrease as the abundance of *Schismus* increases. In fact, our data show this negative relationship between amount (percent cover) of *Schismus* and species richness in a plot (Fig. 8) and therefore provides circumstantial evidence for the competitive dominance of *Schismus*. Some common mechanisms of competition attributed to desert plants include competition for water and soil nutrient acquisition; both of which could be altered in the modern era via climate change or increased atmospheric pollution (Fig. 9) (*18*).

The composition of plant communities in deserts changes dramatically from year-to-year (*19*). Many species can lay dormant as seeds in the soil for years before emerging in great abundance during a year with optimal conditions (*2, 20*). This fact makes desert plant communities both compelling and challenging to study for a plant ecologist. With that in mind, this study was performed in a single year when *Schismus* was especially prolific. High *Schismus* abundance in 2019 might be attributable to higher than average winter precipitation or periodic cycles of seed germination. Whatever the reasons may be, 2019 brought far more *Schismus* than we observed in 2020 or 2021. *Schismus* cover in 2019 reached a maximum of 90%, but the highest *Schismus* cover observed in 2020 was just 12%. In years with less *Schismus*, another native or non-native species could perform the same dominant role and maintain the negative relationship we observed. Or, in the absence (or reduced dominance) of *Schismus*, perhaps the biodiversity-productivity principles observed elsewhere would emerge just as we observed with our "natives only" data in 2019. Perhaps the high native diversity in Mojave Desert winter annual communities can sustain high functioning ecosystems in the long-term either due to species richness and/or the turnover in dominant species from year to year (*21*). As we continue observations in this ecosystem over the next few years, we will track how these communities change over time with different climate conditions. Furthermore, our study is paired with a drought experiment in its third year of treatment as of 2021. By experimentally inducing drought conditions, we will be able to test direct effects of

Figure 6. *Schismus barbatus* in the foreground.

climate on the biodiversity and productivity of these communities.

Finally, plants are but a single facet of desert ecosystems which are dynamic and rich with interactions. To address this challenge, our team will be collecting data on many more components of desert ecosystems including soil chemistry, biological soil crust, microbes, and fungi. With these data, we hope to provide a better understanding of the many mysteries of desert ecosystems while providing critical information for conservation and preservation of the Mojave Desert.

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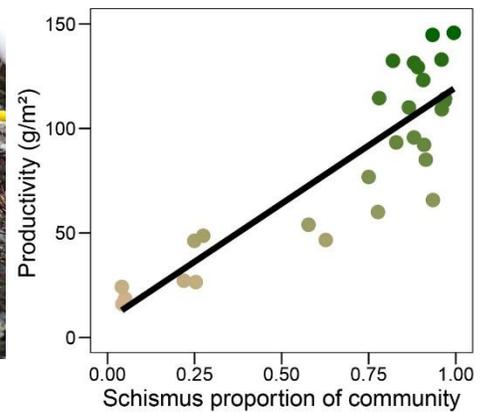
Figure 7. *Schismus* abundance as a percentage of total vegetative cover and its relationship to productivity. Dots are colored by productivity: tan dots are less productive plots and green dots are more productive. p-value < 0.001, r² = 0.75.
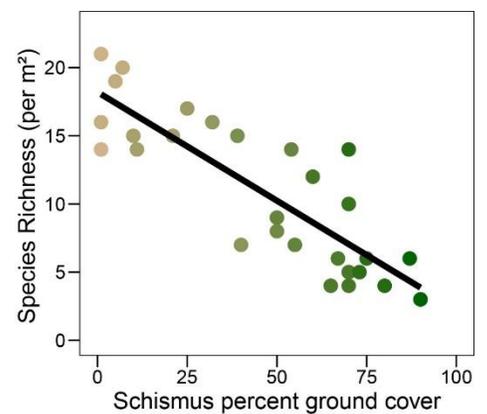

Figure 8. Percent cover of *Schismus* (max 100%) and its correlation with species richness. Dots are colored by productivity: tan dots are less productive plots and green dots are more productive. p-value < 0.001, r² = 0.70.

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Table 1. Summary table of all species found in the 28 plots sampled at the Granite Mountains; they are listed in order of frequency (highest to lowest), then alphabetically. A total of 34 species were observed: 28 winter annuals (A), three herbaceous perennials (HP), and one seedling of a woody perennial (WP). The number of plots in which each species was recorded (N) is used to calculate the average percent cover, as well as the average productivity value (g/m²). NA denotes species for which destructive samples for productivity were not collected.
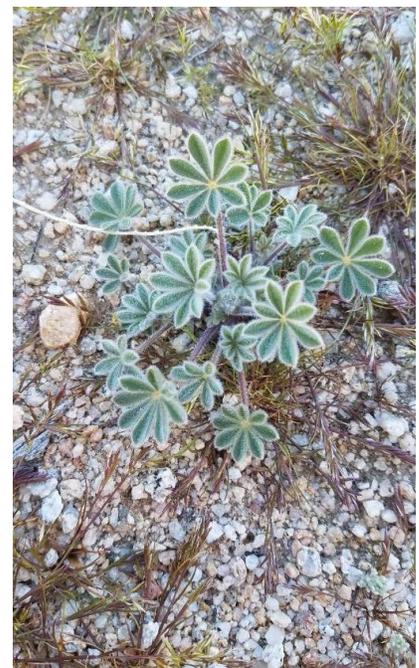
Species	Native vs. Non-Native	Habit	# of plots (N)	Avg. % Cover	Avg. Productivity (g/m²)
Schismus barbatus	Non-Native	A	28	45.68	73.66
Erodium cicutarium	Non-Native	A	28	3.66	4.67
Acmispon strigosus	Native	A	26	2.40	1.69
Pectocarya heterocarpa	Native	A	23	1.40	2.14
Cryptantha circumscissa	Native	A	19	0.42	0.61
Pectocarya recurvata	Native	A	17	1.46	2.08
Pectocarya platycarpa	Native	A	15	0.64	0.85
Eriophyllum wallacei	Native	A	14	1.72	1.04
Cryptantha pterocarya	Native	A	13	0.75	0.29
Bromus rubens	Non-native	A	13	0.74	0.51
Eriastrum eremicum	Native	A	13	0.43	0.21
Dichelostemma capitatum	Native	HP	12	0.44	0.13
Lepidium lasiocarpum	Native	A	12	0.43	0.45
Eriogonum maculatum	Native	A	11	0.17	0.09
Amsinckia tesselata	Native	A	10	0.71	1.36
Pectocarya setosa	Native	A	8	1.03	0.93
Logfia depressa	Native	A	6	0.47	0.80
Camissonia palmeri	Native	A	5	0.34	0.43
Descurania pinnata	Native	A	4	1.35	2.47
Eriogonum pusillum	Native	A	4	0.13	0.06
Centrostegia thurberi	Native	A	3	0.30	NA
Plagiobothrys arizonicus	Native	A	3	0.10	0.08
Salvia columbariae	Native	A	3	0.27	0.71
Stylocline psilocarphoides	Native	A	3	0.15	0.15
Gilia sinuata	Native	A	2	0.25	NA
Lupinus concinnus	Native	A	2	0.35	0.57
Acacia greggii	Native	WP	1	0.10	NA
Chamaesyce albomarginata	Native	HP	1	0.20	0.32
Leptosiphon aureus	Native	A	1	0.30	NA
Toxicoscordion brevibracteatum	Native	HP	1	0.50	0.76
Tropidocarpum gracile	Native	A	1	0.10	NA

Figure 9. *Lupinus concinnus*, a native winter annual, surrounded by the non-native annual grass, *Schismus barbatus*.

The Polarizing Nature of Shrubs: Species-specific Associations of Annual Plants with Creosote Bush (*Larrea tridentata*)

Stephanie M. Haas-Desmarais[1] and Christopher J. Lortie[1]

The large shrub, creosote bush (*Larrea tridentata*), is commonly found throughout the Mojave Desert, and is an important determinant of the distribution of annual plants (Fig. 1) (*1*). In the harsh environment of deserts, positive interactions between shrubs and other species are ubiquitous (*2*). These shrubs can impact other species in three ways: amelioration of abiotic stress, biotic stress, and through resource addition (*3*). Each shrub can act as a refuge from harsh abiotic conditions for a host of plants and animals (*2, 4*). Shrubs, like creosote bush, are one of the only sources of shade in the desert. Because shrubs provide protection from the sun, animals are frequent visitors for the purpose of cooling (*4*) and plants are often more successful when under the canopy of a shrub (*5*). Beyond protection from the sun, shrubs also provide shelter from the wind (*3*). While heat may be the most obvious threat in the desert, wind can be just as great of a threat as the sun to annual plants and small animals.

Figure 1. Creosote bush (*Larrea tridentata*) is a dominant cover at the study site in the Mojave Desert; this photo was not taken the same year of sampling. The effect of facilitation is evident by the increased annual growth under the shrub in comparison to the open areas. Photo by T. La Doux, May 2020.

In a similar way to how shrubs block the sun and wind, they can also block the sight of predators (for animals) (*4*) and herbivores (for plants) (*6–8*). Animals use shrubs to hide from predators and even plants will be far less obvious to herbivores in the face of a large shrub (*4*). However, benefactor shrubs can also protect annual plants from herbivores in other ways. Shrubs are generally well-defended from herbivores by being distasteful or by using active deterrents such as thorns or toxic chemicals (*9–12*). For instance, the leaves and stems of creosote bush are coated in phenolic resins that herbivores tend to avoid (*13, 14*). By acting as a large patch of unappetizing vegetation, shrubs can deter herbivores from the surrounding annual plants just by sheer proximity (*15*). This phenomenon, known as associational resistance, is commonly

[1] Department of Biology, York University, Toronto, Ontario, Canada.

seen in plant-plant interactions (*16*). Vulnerable plants will receive the same benefit when growing near species that have good defenses, and therefore, will grow more successfully (*16–18*). However, this strategy can backfire. Rather than avoiding the patch, herbivores may avoid the distasteful plant (e.g. creosote bush) and instead focus on the unprotected annual plants nearby (*19*). Thus, rather than receiving reduced levels of herbivory under this scenario, some annual plants may experience more attention from herbivores than if they were surrounded by equally palatable plants.

Another way in which shrubs can benefit species growing near them, is by providing resources. For instance, many shrubs are nitrogen fixers and therefore increase the amount of nutrients available to the surrounding plants (*3, 20, 21*).

Shrubs can also increase the amount of water in the soil surrounding them by shading the soil and decreasing evapotranspiration (*3*), dripping water at the dripline, or through hydraulic lift (moving groundwater up closer to the surface) (*3*). In addition to providing resources for plants, shrubs can provide important resources for animals, whether it is for nesting or a place to make a burrow (*4, 15*). Similarly, shrubs can attract pollinators by providing nesting habitat or increasing the density of flowers; this interaction goes both ways between the shrub and the annuals growing under its canopy (*22–24*).

With all of these ways in which shrubs benefit the surrounding plants and animals, they are foundation species that shape the communities around them. It is common to see annuals aggregated around shrubs (Fig. 1), making

islands of fertility dotting the landscape (*1, 5, 25*). However, despite these numerous, well-documented positive effects, shrubs can also negatively affect some plant species (*26–29*). Many annual plants are well-adapted to the heat and thrive in the open spaces between the shrubs and may perform better away from the competition found under the shrub canopy (*30, 31*). In some cases, plants compete directly with the shrub itself (*32*); shrubs may increase some resources while depleting others. The nature of how a shrub will interact with any possible neighbor is highly dependent on the characteristics of the neighbor and upon the specific environmental conditions they are both experiencing.

In this study we tested the hypothesis that shrub facilitation is species-specific for annuals. We predicted that some annual plants would be more abundant under shrubs than in the open, but also that the degree of association would vary between annual species.

In April 2019 we visited the Mojave Desert (34.72, -115.68) and explored the association of annual plants with creosote bush. We chose a total of 100 creosote shrubs along five 50-m transects; the first 20 shrubs (at least 5-m apart) located along each transect were chosen. A square 0.25-m^2 quadrat was placed under the canopy of the north side of each shrub and then again at least 1.5-m away from the shrub dripline in the nearest open space. These locations were used to compare microsites: 100 'shrub' quadrats represent those influenced by the shrub canopy versus 100 'open' quadrats represent those not influenced by the shrub canopy, i.e., shrub vs. open. We recorded the number and identity of each annual plant (excluding grasses) within each quadrat (Table 1).

A total of 13 species were found during the census; however, only six species were found in at least 20 (≥10%) quadrats. The most abundant species, which were also the most frequent, are (from most to least frequent): *Eriophyllum wallacei*, *Chaenactis fremontii*, *Cryptantha circumscissa*, *Malacothrix glabrata*, *Chylismia claviformis* subsp. *aurantiaca*, and *Cryptantha angustifolia* (Fig. 2). A complete species list is provided in Table 1.
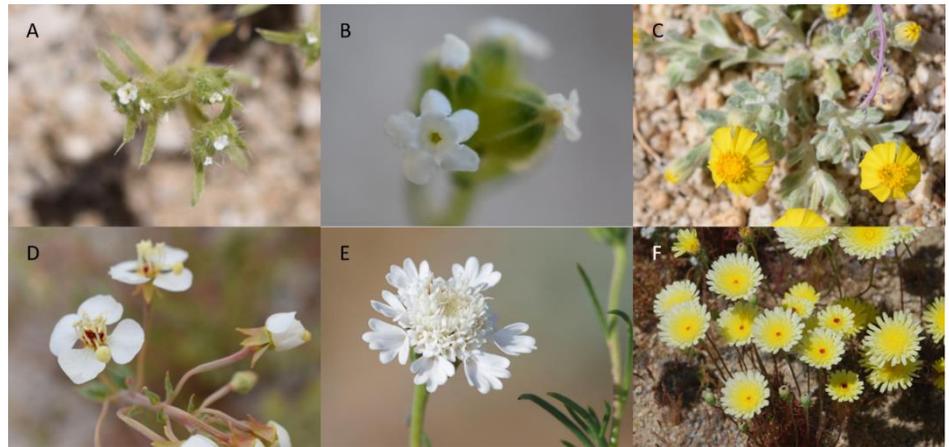

Figure 2. The six most common species in the study area. A) *Cryptantha angustifolia*, B) *Cryptantha circumscissa*, C) *Eriophyllum wallacei*, D) *Chylismia claviformis* subsp. *aurantiaca*, E) *Chaenactis fremontii*, F) *Malacothrix glabrata*. Photos E and F were taken by Jim André.

Table 1. A complete list of flowering annuals found during the 2019 census, listed in order of highest to lowest quadrat frequency (total quadrats = 200). The number of unique quadrats each species was found in per microsite type is shown; then the number of individual plants counted in all 100 quadrats of each microsite. 'Open' sites are ≥1.5-m from the dripline of any *Larrea tridentata* shrub and 'shrub' sites are under *Larrea tridentata* canopies.

	# Quadrats		# of Individuals			
Species	**Open**	**Shrub**	**Open**	**Shrub**	**Total Abundance**	**Total Freq.**
Eriophyllum wallacei	53	25	187	77	264	**39.0%**
Chaenactis fremontii	20	54	28	176	204	**37.0%**
Cryptantha circumscissa	55	15	389	48	437	**35.0%**
Malacothrix glabrata	15	47	22	83	105	**31.0%**
Chylismia claviformis subsp. *aurantiaca*	21	18	66	39	105	**19.5%**
Cryptantha angustifolia	25	6	57	9	66	**15.5%**
Loeseliastrum schottii	10	1	14	1	15	**5.5%**
Pectocarya heterocarpa	9	1	16	1	17	**5.0%**
Leptosiphon aureus subsp. *decorus*	3	4	3	5	8	**3.5%**
Plantago ovata	7	0	8	0	8	**3.5%**
Eremothera boothii subsp. *condensata*	2	1	2	1	3	**1.5%**
Nama demissum	3	0	7	0	7	**1.5%**
Acmispon strigosus	1	0	1	0	1	**0.5%**
Total	**100**	**100**	**800**	**440**	**1240**	

We modelled total plant density as a function of microsite (shrub-open) and we modelled individual species density as a function of both microsite and species, using total plant density as the offset term (Figs. 3, 4, and 5). In both cases we used a generalized linear mixed model with a negative binomial distribution (*33*). We also included shrub-open pairing as a random factor.

Overall, there were more plants (regardless of species) in the open than under shrubs (x^2 = 10.7, p = 0.0011; Fig. 3, Table 1). Similarly, for the six most frequent species, microsite significantly impacted plant density for each species (x^2 = 5.63, p = 0.018; Fig. 4). However, plant density also greatly varied between these six species (x^2 = 70.5, p < 0.0001) and the effect of microsite varied between species (x^2 = 126, p < 0.0001) (Fig. 4). *C. angustifolia* (t = 4.06, p = 0.0001), *C. circumscissa* (t = 7.16, p < 0.0001), and *E. wallacei* (t = 3.71, p = 0.0002) were all denser in the open than under shrubs (Fig. 4). However, *C. fremontii* (t = -5.81, p < 0.0001) and *M. glabrata* (t = -4.29, p < 0.0001) were each denser under shrubs than in the open while *C. claviformis* subsp. *aurantiaca* (t = 1.50, p = 0.13)

was equally dense in the open and under shrubs (Fig. 4). Of the species that were not frequent enough to perform statistics, most tended to be more abundant in the open than under shrubs (Fig. 5, Table 1).

As predicted, we found that certain annual species were strongly associated with creosote bush canopies, while others were strongly associated with open spaces. Only one of the six most frequent species was found equally in both microsites (shrub and open). This polarization of association supports the notion that some annuals may experience either strong facilitation or strong competition with the shrub. Or it could be that those species not associated with shrubs have an overt preference for the conditions found in the open. For instance, some species require high levels of light for germination (*34*) and heat-tolerant plants may prefer the increased temperatures generally found in the open (*35*). Alternatively, those species found preferentially under shrubs may be out-competing other species under shrubs but not in the open.

The positive effect of shrubs on annuals is often species-specific (*36–38*) and therefore it was unsurprising when we found plants both associated with creosote bush and distinctly dissociated with it. Several studies have previously found that the benefit of shrubs not only varies between species (*36–39*) but also between years (*8, 40, 41*). It may be true that *C. angustifolia*, *C. circumscissa*, and *E. wallacei* consistently compete with creosote bush or otherwise prefer conditions in the open and are always disassociated with creosote (or other dominant shrubs), but it is also possible that the environmental conditions of 2019 were such that these species were better off disassociated with shrubs while in years of higher stress they would be found associated with creosote bush. The stress gradient hypothesis states that positive interactions increase with levels of stress (*40, 42*). That is, facilitation is more common when stress is high. A common stressor in deserts is drought and given that 2019 was not a drought year it is not surprising that positive interactions were not ubiquitous. This change in the association of plants with shrubs based on external factors such as stress is supported by the fact that *C. claviformis* (found here

unassociated with creosote bush) has been previously found associated with creosote bush (*43*). Similarly, both *M. glabrata* (here associated with shrubs) and *E. wallacei* (here disassociated with shrubs) have been previously found unassociated (neither associated nor disassociated) with creosote bush (*44*). Perhaps in a more stressful year more than two species would be positively associated with creosote bush.

Our findings provide further evidence of shrub facilitation, but also reinforce the species-specificity of facilitation. We showed that while facilitation is one outcome of the interaction between shrubs and annuals in deserts, the truth is that annuals can have polar opposite experiences when associated with shrubs. While our study provides a single look at relationships between plants in the Mojave Desert, understanding the relationship between plant
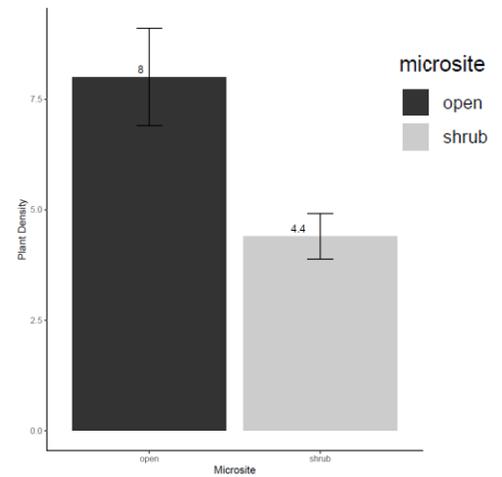

Figure 3. Mean total plant density per microsite (total number of all plants per quadrat ±standard error, with 100 quadrats per microsite) in open versus shrub microsites. 'Open' microsites are ≥1.5-m from the dripline of any *Larrea tridentata* shrub whereas 'shrub' microsites are under *Larrea tridentata* canopies.

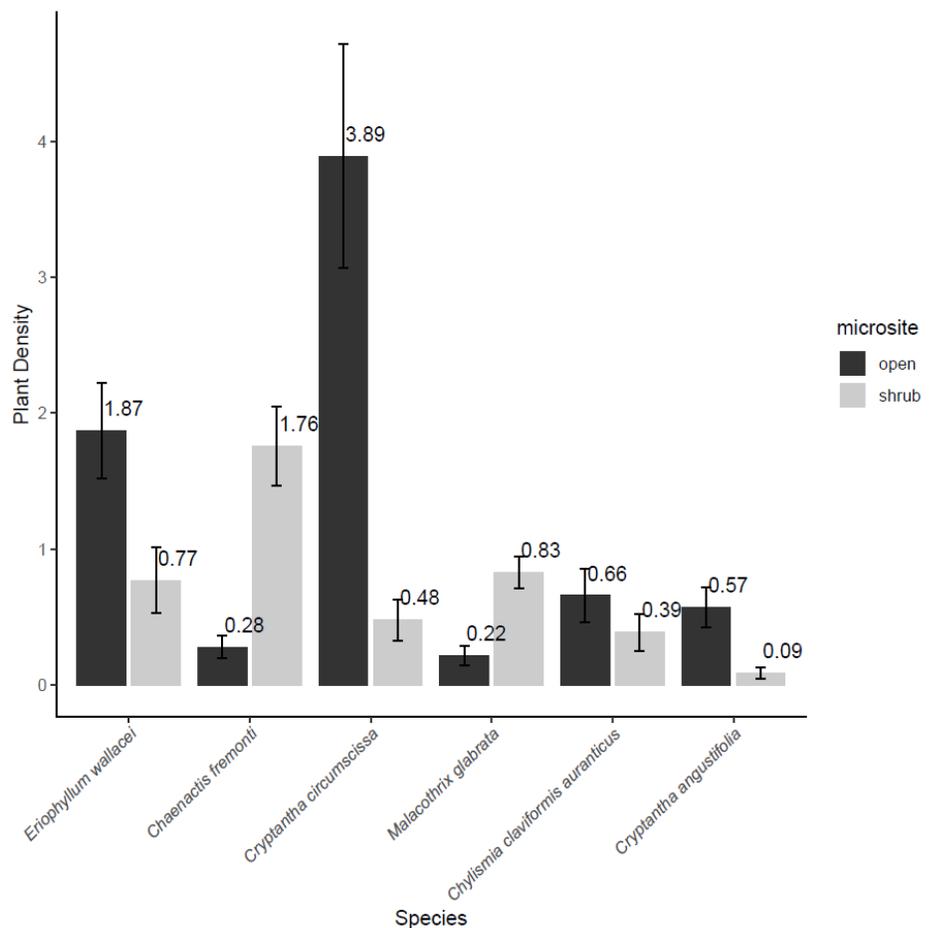**Figure 4. Individual plant density (number of plants per quadrat ± standard error, with 100 quadrats per microsite) for each of the six most frequent species in open versus shrub microsites. 'Open' sites are ≥1.5-m from the dripline of any *Larrea tridentata* shrub and 'shrub' sites are under *Larrea tridentata* canopies.**

interactions and stress requires multi-year studies, likely including both drought and non-drought years as well as further details on abiotic conditions such as temperature, moisture, and soil conditions to determine the mechanism behind association and disassociation.
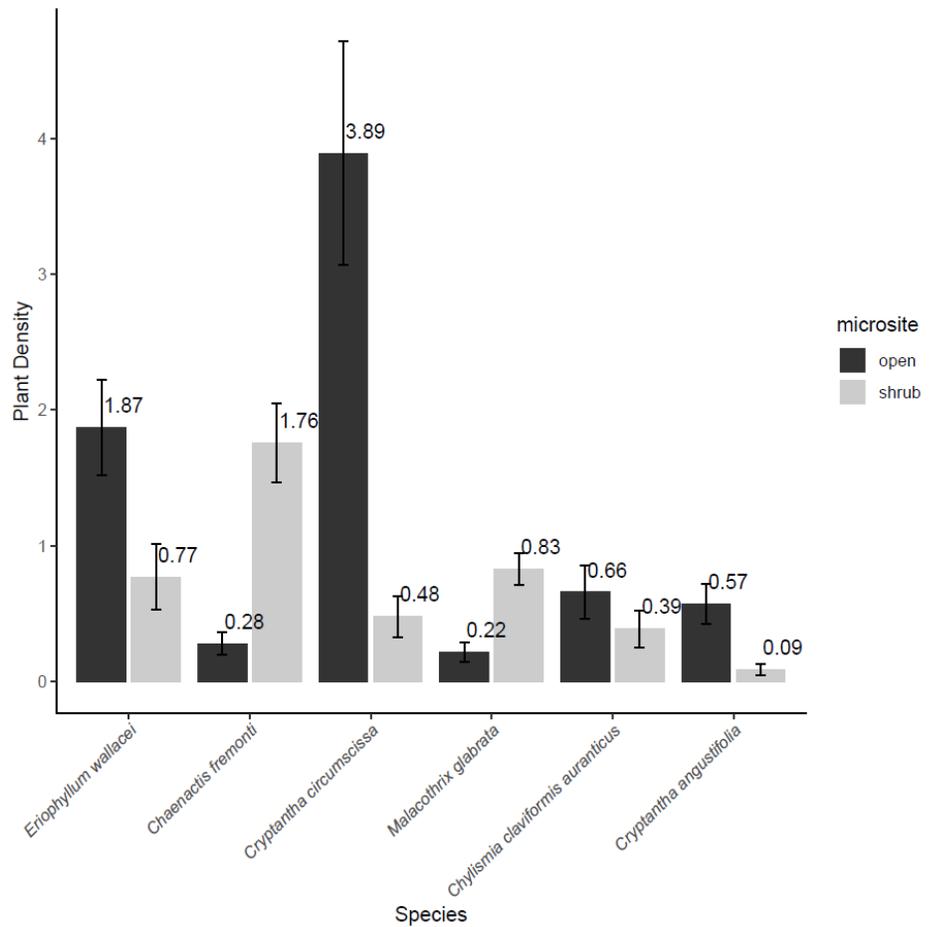

Figure 5. Individual plant density (number of plants per quadrat ±standard error, 100 quadrats per microsite) for each of the less frequent species not shown in Figure 4. 'Open' sites are ≥1.5-m from the dripline of any *Larrea tridentata* shrub and 'shrub' sites are under *Larrea tridentata* canopies.

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