

Blackbrush (*Coleogyne ramosissima*: ROSACEAE) natural regeneration following fire in the Great Basin - Mojave Transition Zone

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Abstract

Blackbrush (*Coleogyne ramosissima*) has rarely been observed naturally regenerating following fire. It was historically considered a paleoendemic species because it did not recolonize following disturbance. In 2008, the Fossil and Jacob fires burned 241 ha of blackbrush in Basin and Range National Monument, Lincoln County, Nevada, USA in the Mojave-Great Basin Desert transition zone. These sites are at the northern boundary of the species range near the top of its current elevational band. Eighteen 5 x 30 m plots within the burned areas were monitored in 2009–2011 and 2018–2022 to assess plant foliar cover and woody plant density. Another 18 plots in adjacent unburned areas were monitored in 2022. Blackbrush seedlings emerged within the first year following fire at higher densities in the burned areas compared to adjacent unburned areas. After an initial flush of seedlings in 2009, there was high seedling mortality in 2010. By 2011, density in the burned areas was 0.35 blackbrush per m² (46% of density in adjacent unburned areas), but individuals were small and had less than 1% total cover. Upon returning in 2018, the blackbrush that established early following fire had grown, and showed a significant increase in cover to 5.83–10.80%. Cover continued to increase through 2020 peaking at a mean of 12.9% before slightly declining with drought in 2021–2022. The area now has nearly two-thirds the blackbrush density and one-third the cover that adjacent unburned areas have. Blackbrush redominated these burned areas in under 10 years following fire and continues to increase.

Introduction

In changing climate conditions, some evolutionary lineages that were once diverse and widespread are greatly reduced or nearly eliminated. Once broadly distributed species now restricted to a small portion of their historic range are considered paleoendemic species (Stebbins and Major 1965). Paleoendemics are also characterized by losses of diversity, high ploidy number, self-fertilization, difficulty reproducing, and range fragmentation (Kruckeberg and Rabinowitz 1985). Blackbrush (*Coleogyne ramosissima*) was the model used for paleoendemism when the biogeographers Stebbins and Major (1965) coined the term. Since then, the term has been applied to species worldwide, especially rare or localized plant species such as the famous paleoendemic *Ginkgo biloba*. The latter was once a diverse group distributed nearly worldwide, but now is the last remaining representative of a monotypic phylum and is restricted to a few refugia in East Asia (Tang et al. 2018). While concepts surrounding endemism have continued to change and expand, paleoendemism remains relevant in the conversation regarding how species adapt to changing climates.

The idea that *C. ramosissima* is a paleoendemic was proposed due to taxonomic isolation, historic reductions in distribution range, and the lack of observable recolonization after disturbance (Stebbins and Major 1965). This was the prevailing thought that guided what became the standard description of *C. ramosissima* ecology (Bowns 1973). *C. ramosissima* does not resprout and has only rarely been seen to recolonize at low densities after being burned (Callison et al. 1985). Redomination or something that appears on a trajectory towards resembling mature *C. ramosissima* stands has little been observed

following its disturbance, although mature stands can periodically recruit new individuals to maintain dominance (Brooks and Matchett 2003, Pendleton et al. 2015, Kitchen et al. 2015).

Blackbrush is a long-lived shrub that reproduces infrequently. It can be classified as a highly stress tolerant species using Grime's (1977) adaptive strategy theory. Like other stress tolerant species, it is particularly sensitive to disturbance. Following severe disturbance, the opened niche can go down one or more successional pathways which may or may not result in a vegetation community similar to the predisturbance community (Whisenant 1999). In the southwestern deserts of the United States, introduced species and fire have combined in some locations to create a grass-fire cycle where frequent burning inhibits the recovery of perennial species (D'Antonio and Vitousek 1992, Brooks et al. 2004). *C. ramosissima* shrublands are dominant on over three million hectares of the Mojave Desert and Colorado Plateau (Pendleton and Meyer 2004). They have been particularly susceptible to invasion by non-native annual species following fire, almost always converting to some other community type after stand replacing disturbances (Brooks and Matchett 2003; Pendleton et al. 2015).

Dominant species are the most common plant species on a site, making up at least 20% relative cover (FICWD 1989). *C. ramosissima* absolute cover on unburned sites ranges from 26 to 50% in near pure stands, with relative cover sometimes exceeding 90% (Brooks and Matchett 2003; Brooks et al. 2007). *C. ramosissima* is a non-clonal shrub known to maintain dominance on established sites through the regular recruitment of new individuals within clumps that appear to be a single shrub (Kitchen et al. 2015). While regular recruitment would suggest that the plant can in fact reproduce itself, requiring an adult host plant for new recruitments presents a classic chicken and egg problem, which hinders regeneration after mature stands are burned. It is unusual for a common species dominant across so many hectares to lack a mechanism for naturally regenerating after a stand-replacing disturbance.

C. ramosissima is a mast-seeding plant that may go five or more years between significant seed crops (Pendleton et al. 1995). Flower and fruit production are highly variable from year to year (Beatley 1974). *C. ramosissima* seeds require cold-stratification which may not be properly achieved on sites currently experiencing warmer than historic conditions (Pendleton and Meyer 2004). Germination requires wet rainy or snowy conditions during late winter, which do not occur every year (Meyer and Pendleton 2005). For there to be a successful germination, the timing of the mast-seeding year must match up with an unusually wet germination period while the seeds are still viable. One factor in favor of recovery after fire is that *C. ramosissima* seeds are fire tolerant (Zitser 2009).

A bioclimatic profile was produced for *C. ramosissima* by Richardson and Meyer (2012) who then used genetic sampling from across the regional population to show that genetic diversity was higher in the species than would be expected for a paleoendemic species. The populations that occur in the Mojave Desert were also genetically unique from the populations that occur on the Colorado Plateau. Richardson et al. (2014) went on later to propose specifically that *C. ramosissima* will expand up in elevation as the climate warms and dries.

The Fossil and Jacob fires were two stand-replacing wildfires through mature *C. ramosissima* stands that were selected for long-term monitoring because they were observed to have significant *C. ramosissima* seedling development in the first few years following fire. These fires sites are at the extreme northern range of *C. ramosissima* in the Mojave Desert, where natural regeneration might be expected to occur based on the bioclimatic profile. To test the hypothesis that blackbrush will not recruit after disturbance, we assessed blackbrush regeneration during a 14-year period following two wildfires in the northern Mojave Desert that burned in 2008.

Methods

The study area is on public land administered by the Bureau of Land Management (BLM) at the north end of the Pahrnagat Valley in Lincoln County, Nevada, USA. The study area is partially within Basin and Range National Monument, and is located in the Mojave-Great Basin Desert Transition Zone within Major Land Resource Area 29 – Southern Nevada Basin and Range (Soil Survey Staff 2006). The Fossil and Jacob fires were two lightning-ignited, high-severity, stand-replacing wildfires that together burned 241 ha through *C. ramosissima* shrublands in August 2008 (Fig. 1).

We monitored a total of 18 macroplots in the burned areas eight times each over 14 years (May 2009, June 2010, June 2011, December 2018, and June–July 2019, May 2020, June 2021, and July 2022). A set of 18 macroplots in adjacent unburned plots was monitored in 2022. The macroplots were grouped into demonstration plots with sets of three macroplots arranged in pinwheels with azimuths of 0°, 120°, and 240° and permanently monumented with rebar stakes and fiberglass fence post locators (Fig. 2). The macroplot and demonstration plot design combination was adapted from the National Park Service's Fire Monitoring Handbook (USDI National Park Service 2003). Each macroplot was a 5 × 30 m rectangle where quantitative data were collected for point-intercepts to yield cover, shrub density, shrub age, and species diversity. Along both 30 m long sides, point-intercept cover points were distributed every 0.5 m for a total of 120 cover points/plot. At each point, vegetation canopy cover by layer and soil surface cover were recorded. Mature shrub density included counts for all mature woody vegetation with bases partially or wholly within the 150 m² plot. Herbaceous density of plants and shrub seedlings was monitored from 2009–2011 with 10, 0.5 m² quadrats for a total of 5 m² of herbaceous density per plot. Shrub seedlings were counted within the entire 150 m² plot from 2018 to 2022. During the first three years of monitoring, shrubs were denoted as mature, resprout, seedlings, or burned dead. During the last five years of monitoring, shrubs were denoted as either mature or seedlings as time reduces the ability to identify resprouts or burned dead. Individuals were considered mature once they were firmly rooted. Additional species not found within the density or cover subsamples were searched for within the entire plot and listed to determine total species diversity. Repeat photographs were taken each year from the start and end of each transect.

The burned areas were treated by the BLM Ely District with a seed mix that broadcasted forage kochia (*Bassia prostrata*), bottlebrush squirreltail (*Elymus elymoides*), blue flax (*Linum perenne*), Sandberg bluegrass (*Poa secunda*), salad burnet (*Sanguisorba minor*), sand dropseed (*Sporobolus cryptandrus*),

and Indian ricegrass (*Stipa hymenoides*) at a total rate of 11 kg pure live seed per ha. *Sanguisora minor* and *Linum perenne* were the only species that established, and they did so at low density and cover, so seeding was considered to have only a minor influence on post-fire vegetation dynamics.

Data were analyzed using IBM SPSS Statistics for Windows, Version 23.0 (IBM Corp. 2015) to perform descriptive statistics, summaries, and statistical tests. Precipitation and temperature data were remotely sourced from the nearest operating weather station (37.5581, -115.2236), 15 km south of the burned areas, in Hiko, NV (National Weather Service 2022). Daily data from the weather station were available for September 1989 through October 2022. This range was trimmed to include only the 30 full years from 1992 to 2021 to calculate 30 annual means. The recent averages for the 14 years since the fire occurred were compared with the 30-year averages to create indices showing the percent divergence from mean annual precipitation, mean annual maximum temperature, and mean annual minimum temperature. For cover and density data, we performed a repeated measures ANOVA (Girden 1992) blocked using the two fires as a between-subject factor. We used Mauchly's Test of Sphericity (Mauchly 1940) to check for normality and homogeneity of variance together. If sphericity was violated, we used the method described by Greenhouse and Geisser (1959) to correct the degrees of freedom. A regression (Galton 1886) was used to model the rate of change of cover increase and predict convergence time with published values of 26–50% for unburned *C. ramosissima* cover (Brooks and Matchett 2003; Brooks et al. 2007).

Results

The climate data show that the 14 years from 2008 to 2021 were 13 mm wetter than the 30-year mean with a 0.5°C higher maximum temperature and 0.1°C higher minimum temperature (Table 1). The critical years just before, during, and just after the fire (2007, 2008, and 2009) had 45 to 73 mm less precipitation than normal, with no more than 141 mm of precipitation in any year. Wetter years occurred in 2006, 2010, 2016, and 2019, with 28–55% more precipitation than normal.

Table 1
Climate data from Hiko, Nevada weather station 2006–2022.

Year	Ppt ^a	Δ Ppt ^b	T _{max} ^c	Δ T _{max} ^d	T _{min} ^e	Δ T _{min} ^f
2006	272	48.6	23.1	1.8	5.1	-7.2
2007	133	-27.4	23.9	5.2	5.0	-9.1
2008	141	-22.8	23.3	2.6	4.8	-12.7
2009	113	-38.5	23.4	3.1	5.0	-9.1
2010	272	48.9	22.6	-0.4	5.1	-7.2
2011	108	-40.9	22.9	0.8	4.1	-25.5
2012	169	-7.5	24.4	7.4	6.3	14.5
2013	181	-1.3	22.9	0.8	5.2	-5.5
2014	168	-8.1	23.6	4.0	6.2	12.7
2015	187	2.2	23.2	2.2	6.5	18.1
2016	234	27.6	22.9	0.8	5.9	7.2
2017	186	1.8	23.6	4.0	6.3	14.5
2018	119	-35.0	23.4	3.1	6.1	10.9
2019	283	54.6	21.3	-6.1	5.1	-7.2
2020	98	-46.5	23.8	4.8	5.2	-5.5
2021	121	-33.9	23.4	3.1	5.6	1.8
2022 through July	38					
14-year mean ^g	199	6.9	23.2	2.2	5.5	1.9%
30-year mean^h	186		22.7		5.4	

Year	Ppt ^a	Δ Ppt ^b	T _{max} ^c	Δ T _{max} ^d	T _{min} ^e	Δ T _{min} ^f
^a Mean annual precipitation in mm						
^b Percent difference between Ppt and the 30-year mean						
^c Mean annual maximum temperature in °C						
^d Percent difference between T _{max} and the 30-year mean						
^e Mean annual minimum temperature in °C						
^f Percent difference between T _{min} and the 30-year mean						
^g 14-year mean calculated from 2008 to 2021						
^h 30-year mean calculated from 1992 to 2021						

In the burned areas, *C. ramosissima* mean density was 1.06 clumps/m² in 2009, 0.30 clumps/m² in 2010, 0.35 clumps/m² in 2011, 0.36 clumps/m² in 2018, 0.41 clumps/m² in 2019, 0.64 clumps/m² in 2020, 0.41 clumps/m² in 2021, and 0.48 clumps/m² in 2022 (Fig. 3). *C. ramosissima* seedlings were already present the first year following fire at all but one plot. Seedlings were observed to have germinated in 2009, 2010, 2011, 2019, and 2020. In 2022, *C. ramosissima* density was 0.76 clumps/m² in the adjacent unburned areas. Total shrub density was 0.81 per m² in the adjacent unburned areas. The adjacent unburned areas contained ten shrub species including two species that were not represented in the post-burn community.

A repeated measures ANOVA using Greenhouse-Geisser corrections blocked by fire determined the mean total (mature and seedling) *C. ramosissima* density significantly differed between years ($F_{1,223,19.573} = 7.338$, $p = 0.01$). However, there was no significant effect due to fire ($F_{1,16} = 0.908$, $p = 0.355$), implying the results were consistent between fires. There was no significant interaction between year and fire ($F_{1,223,19.573} = 0.535$, $p = 0.508$). Post-hoc tests using a Bonferroni correction revealed that year 2020 was significantly different from years 2010, 2011, 2018, 2019, and 2021 ($p = 0.002$ to $p = 0.038$), 2010 different than 2018, 2019, 2021, and 2022 ($p = 0.002$ to $p = .035$), and 2011 different than 2022 ($p = 0.011$).

A repeated measures ANOVA using Greenhouse-Geisser corrections blocked by fire determined that the mean *C. ramosissima* cover differed between years ($F_{1,173,18.764} = 35.574$, $p < 0.001$). However, there was no significant effect from comparing the two fires ($F_{1,16} = 2.338$, $p = 0.146$) or the interaction between year and fire ($F_{1,173,18.764} = 1.967$, $p = 0.177$). Post-hoc tests using a Bonferroni correction revealed that years 2009, 2010, and 2011 were similar. Years 2018 and 2021 were similar. Years 2019, 2020, 2021, and 2022 were similar (Fig. 4).

Mean cover increased each year from 2009 to 2020. Mean cover regressed slightly in 2021 but remained high and increased slightly again in 2022. A significant regression equation ($F_{1,142} = 120.2$, $p < 0.001$), with an R^2 of 0.458, fit with the *C. ramosissima* cover increase since the fires (Fig. 5). The *C. ramosissima* predicted cover is equal to $-1.54 + 1.06 \times [\text{years since fire}]$. By 2018, cover was at least 2.5% at every plot monitored.

The repeat photography sequences show visible change in the shrub community at the permanently established plots (Figs. 6 and 7). Small seedlings are present in 2009 and 2010. By 2011, growing *C. ramosissima* are visible in the photos. The individuals continue to grow through 2020 and persist through 2022. The change in individuals can be directly observed from year to year in the photos.

Total vegetation cover ranged from 2.6% in 2009 to 81% in 2019 in the burned areas (Table 2). Annual cover was highly variable based on precipitation. Dominant functional groups on the burned area varied from year to year. Annual forbs dominated cover in 2009, 2010, 2019, and 2020. Annual grasses had the most cover for a single year in 2011. Shrubs dominated in 2018 when monitoring occurred in the winter. Shrubs also dominated in 2021 and 2022 which were dry years. Non-native species were present in the post-burn community and accounted for 20–73% of total cover.

Table 2

Mean vegetation cover ^a by native status and functional group for Fossil and Jacob Fires combined

		2009	2010	2011	2018	2019	2020	2021	2022
Non-native	Annual Graminoid	0.4	2.9	9.7	2.9	3.7	16.9	1.1	6.3
	Annual Forb	0.8	1.7	2.2	7.4	32.7	12.2	0.1	0
Native	Annual Graminoid	0.4	0.6	7.2	0	0.1	0.3	0	0
	Annual Forb	0.6	17.5	4.5	1.8	5.4	34.3	0.1	3.5
	Perennial Graminoid	0.0	0.0	0.0	0.1	0.2	0.3	0.1	0.2
	Perennial Forb	0.1	0.6	2.6	2.1	1.0	1.4	0.3	0.8
	Shrub	0.2	0.7	1.1	10.4	12.8	15.5	13.2	14.7
Subtotals	Annual Graminoids	0.8	3.5	16.9	2.9	3.8	17.3	1.1	6.3
	Annual Forbs	1.4	19.3	6.7	9.1	38.1	46.5	0.1	3.5
	Perennials	0.3	1.4	3.7	12.5	14.3	17.2	13.5	15.7
	Non-natives	1.2	4.8	12.3	10.3	36.4	59.5	1.2	9.5
	Natives	1.3	19.3	15.1	14.3	19.7	21.5	13.5	16.1
TOTAL		2.6	24.1	27.4	24.6	56.1	81.0	14.7	25.6
^a Values given in percent									

There were 117 plant species recorded during the study, but just five species comprised 52–88% of the relative vegetation cover during monitoring (Table 3). The annuals were highly variable with primary dominants storksbill filaree (*Erodium cicutarium*), an invasive annual forb; whitestem blazingstar (*Mentzelia albicaulis*), a native annual forb; red brome (*Bromus rubens*), an invasive annual grass; and sixweeks fescue (*Vulpia octoflora*), a native annual grass. *C. ramosissima* increased in absolute cover from 2009 to 2020 before decreasing slightly in 2021. During winter monitoring in 2018, *C. ramosissima* was dominant with 37% relative cover. During summer monitoring in 2019, *C. ramosissima* (20% relative cover) was codominant with *E. cicutarium* (50% relative cover). In 2020, *B. rubens* (21% relative cover) and *E. cicutarium* (37% relative cover) were codominant. In 2021, *C. ramosissima* was dominant again (77% relative cover). In 2022, *C. ramosissima* (46% relative cover) and *B. rubens* were codominant. In 2022, *C. ramosissima* absolute cover was 35.3% in the adjacent unburned areas. Total cover was 49.1% in the adjacent unburned areas.

Table 3

Absolute and relative cover^a of the most common species on the burned area: blackbrush (*Coleogyne ramosissima*), red brome (*Bromus rubens*), storksbill filaree (*Erodium cicutarium*), whitestem blazingstar (*Mentzelia albicaulis*), and sixweeks fescue (*Vulpia octoflora*)

		2009	2010	2011	2018	2019	2020	2021	2022
<i>Coleogyne ramosissima</i>	AbsCV ^b	0.0	0.3	0.7	9.1	11.0	12.9	11.3	11.7
	% of Perennial	0.0	23.0	18.6	72.7	78.6	75.0	87.7	74.5
	RelCV ^c	0.0	1.3	2.5	37.0	19.6	15.9	76.9	45.7
<i>Bromus rubens</i>	AbsCV ^b	0.4	2.9	7.1	2.5	3.7	16.7	1.0	6.3
	RelCV ^c	15.4	12.0	25.9	10.1	6.6	20.6	6.8	24.6
<i>Erodium cicutarium</i>	AbsCV ^b	0.8	1.6	2.0	1.3	26.9	30.3	0.1	3.1
	RelCV ^c	30.1	6.6	7.3	5.3	47.9	37.4	0.7	12.4
<i>Mentzelia albicaulis</i>	AbsCV ^b	0.6	15.9	0.1	0	0.1	0.1	0	0.1
	RelCV ^c	23.1	66.0	0.4	0	0.2	0.1	0	0.4
<i>Vulpia octoflora</i>	AbsCV ^b	0.4	0.5	7.2	0	0.1	0.3	0	0
	RelCV ^c	15.4	2.1	26.3	0	0.2	0.4	0	0
All Others Combined	RelCV	14.7	2.9	10.3	11.8	14.3	20.9	2.4	4.6
^a Values given in percent									
^b Absolute cover									
^c Relative cover									
Bold values indicate dominant species with relative cover equal to or exceeding 20%									

Discussion

In areas burned by the Fossil and Jacobs fires in 2008, *C. ramosissima* became established the first year after fire, mostly persisted, and increased in cover and density during the 14-year period after fire. *C. ramosissima* seedlings in the Fossil and Jacob fire areas were observed to have germinated in the first year following fire. Density in 2009 was 40% higher than in adjacent unburned areas during this first wave of germination, but not all individuals survived. Mean density dropped to 55% lower than adjacent unburned areas in 2010 before slowly trending upward. Additional seedling recruitment was noted in

2010, 2011, 2019, and 2020, while some die back occurred in 2021. By 2022, *C. ramosissima* density was at two-thirds the density of adjacent unburned plots. By winter 2018, the cover had reached a point where *C. ramosissima* would be considered a dominant species according to the 50/20 rule (FICWD 1989). In 2019 and 2020, at the height of significant annual blooms, *C. ramosissima* again maintained 16–20% relative cover overall and accounted for three-quarters of the relative perennial cover. During drought years in 2021 and 2022, when annuals were suppressed by lack of precipitation, *C. ramosissima* was dominant or codominant overall. This sort of redominance of *C. ramosissima* following a stand-replacing disturbance has not been documented in previous literature (Brooks and Matchett 2003; Pendleton et al. 2015). Although this site is still not fully revegetated having less than half the cover of the adjacent unburned plots, the rapid rate of cover increase on the burned areas was unexpected, especially for a species that has so rarely recolonized following severe stand-replacing disturbance. If the trend continues, *C. ramosissima* cover on these sites will reach unburned values of 26–50% after 26–49 years following fire.

Qualitatively, the plots were representative of the burned areas overall, but were not in the locations with the most *C. ramosissima* natural regeneration either. Compared to a view of the macroplot found to have the highest blackbrush cover in 2019 (Fig. 8a), other areas of the Jacob fire appear to have even higher cover and density numbers (Fig. 8b). Seedling development was common immediately after the fire and new seedlings were observed throughout monitoring. *C. ramosissima* seedlings tended to have several nodes developed by the time of monitoring but were not yet firmly rooted (Fig. 8c).

The Jacob fire was also the subject of research by Miller et al. (2013) and Clifford et al. (2018) on post-fire soil erosion. These researchers conducted vegetation surveys from 2009 to 2011 at 450, 50 cm x 50 cm plots established across the burned area at locations different than those used in this study. They identified blackbrush at 22 of the 40 burned upland plots in 2009, 24 of the 35 burned upland plots and 3 of the 40 burned drainage plots in 2010, and 22 of the 40 burned upland plots in 2011 (Miller et al. 2013). They found that blackbrush was four times more common in burned uplands than unburned uplands, but was not recovering significantly in burned drainages. Three years after fire, the blackbrush continued to recruit (Clifford et al. 2018). Their results confirm the observations of this study.

The flashes of dominance by annuals observed in this study reflect the highly variable nature of ephemeral Mojave Desert species (Beatley 1969). Dominance switched among invasive annual forbs, native annual forbs, invasive annual grasses, and native annual grasses whose populations oscillate with precipitation pulses. All the while, the perennials, most notably *C. ramosissima*, have steadily increased. This area has so far avoided reburning and falling into a grass fire cycle where perennials decrease as annuals increase (D'Antonio and Vitousek 1992). Instead, this area appears to be on a path towards natural regeneration of the *C. ramosissima* community type despite occasional periods of annual dominance. Why this is such a rarely observed pattern remains unclear, but this example of *C. ramosissima* naturally regenerating provides an excellent opportunity to increase our knowledge about *C. ramosissima* communities with implications for land managers interested in restoration of the species.

Richardson and Meyer (2012) proposed that *C. ramosissima* should be able to recover given the right climate conditions which now only occur in the wetter, cooler parts of its range. The Fossil and Jacob fires burned along the Mojave-Great Basin transition zone near the northern boundary of *C. ramosissima*'s current range, in the area where they proposed regeneration should occur. Furthermore, these fires were both relatively small burns surrounded by large healthy *C. ramosissima* populations, which provided a potential seed source for the disturbed areas.

C. ramosissima shares many of the characteristics of a paleoendemic species, but not all of them. It is a monotypic genus that used to be more widely distributed. Lincoln County, NV had more than 40% of its blackbrush lost in fires from 2005 to 2006 (Pendleton et al. 2015), but the shrub remains broadly distributed in the county and elsewhere in its range. *C. ramosissima* is diploid (McArthur and Sanderson 1985), not the high polyploidy typical of a paleoendemic. It does have several unusual features for members of the Rosaceae including lacking petals, which reflects its past adaptation to the loss of its pollinator, but it remains self-incompatible (Pendleton and Pendleton 1998). The Mojave Desert and Colorado Plateau have distinct subpopulations of *C. ramosissima*, each with higher genetic diversity than would be expected of a paleoendemic. (Richardson and Meyer 2012). It may even be in the process of speciation into distinct Mojave and Colorado Plateau taxa. Calling *C. ramosissima* a paleoendemic may still be accurate by some measures, but this resilient species is resisting this label as it continues to adapt and survive. The rapid recolonization of the Fossil and Jacob fire areas provides additional evidence that *C. ramosissima* is still regenerating in some sites, which is inconsistent with it being a paleoendemic. If the species is currently moving due to climate change, it would not be the first time it has done so. It previously migrated from lower elevations and more southerly latitudes to reach its current habitat (Phillips and VanDevender 1974; Spaulding 1990).

Species facing changing climatic conditions must either adapt, migrate, or both to ensure their continued survival. Particularly stress-tolerant species with lifespans measured in centuries may not appear to be doing much on a human timescale, but they survive nonetheless. Many of the *C. ramosissima* individuals that Stebbins and Major (1965) wrote about are still alive and reproducing over 50 years later. Species with patient reproduction strategies may continue to be successful over the long-term even if recolonization events remain rare.

Declarations

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Competing Interests

The Author is the owner of Ericameria LLC who funded the project in 2020 and 2021.

Author Contribution

The author preformed field monitoring all years (2009-2011 and 2016-2022), analyzed the data, wrote the original monitoring close-out report after 2011, proposed the remonitoring efforts, obtained funding for the remonitoring 2016-2022, preformed statistical analyses, and drafted the manuscript. The original study design was done by Neil Frakes at Eastern Nevada Landscape Coalition. The author received support and guidance from multiple field assistants, academic advisors, peers, technical editors, reviewers, and agency staff. The author read and approved the final manuscript.

References

1. Beatley JC (1969) Biomass of desert winter annual plant populations in southern Nevada. *Oikos* 20(2):261-273
2. Beatley JC (1974) Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology* 55(4):856-863
3. Bowns JE (1973) An autecological study of blackbrush (*Coleogyne ramosissima* Torr.) in southwestern Utah. Unpublished M.S. thesis. *All Graduate Theses and Dissertations*. 1442. <https://digitalcommons.usu.edu/etd/1442>. Accessed 20 Nov 2022. Utah State University, Logan, Utah
4. Brooks ML, Matchett JR (2003) Plant community patterns in unburned and burned blackbrush (*Coleogyne ramosissima* Torr.) shrublands in the Mojave Desert. *Western North American Naturalist* pp 283-298
5. Brooks ML, D'antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant, Pyke D (2004) Effects of invasive alien plants on fire regimes. *BioScience* 54(7):677-688

6. Brooks ML, Esque TC, Duck T (2007) Creosotebush, blackbrush, and interior chaparral shrublands [Chapter 6]. In: Hood, Sharon M.; Miller, Melanie, editors. Fire ecology and management of the major ecosystems of southern Utah. Gen. Tech. Rep. RMRS-GTR-202. Fort Collins, Colorado: US Department of Agriculture, Forest Service, Rocky Mountain Research Station 202:97-110
7. Callison J, Brotherson JD, Bowns JE (1985) The effects of fire on the blackbrush [*Coleogyne ramosissima*] community of southwestern Utah. J Range Mgmt 38(6):535-538
8. Clifford M., Etyemezian V, Chen L, Nikolich G (2018) Synthesis of Post-fire Monitoring Activities in the Great Basin Desert, Mojave Desert, and Transition Zones. No. 45282; DOE/NV/0003590-11. Submitted to U.S. Department of Energy Environmental Management Nevada Program by Desert Research Institute. Las Vegas, Nevada
9. D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual review of ecology and systematics 23(1):63-87
10. Federal Interagency Committee for Wetland Delineation (FICWD) (1989) Federal Manual for Identifying and Delineating Jurisdictional Wetlands. Cooperative Technical Publication. U.S. Army Corps of Engineers, U.S. Environmental Protection Agency, U.S. Fish and Wildlife Service, and USDA Soil Conservation Service, Washington, DC
11. Galton F (1886) Regression towards mediocrity in hereditary stature. J Anthropological Institute of Great Britain and Ireland 15(1886):246-63
12. Girden ER (1992) ANOVA: Repeated measures. Sage university paper series on the quantitative applications in the social sciences, 07-084. Newberry Park, California
13. Greenhouse SW, Geisser S (1959) On methods in the analysis of profile data. Psychometrika, 24:95-112
14. Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111(982):1169-1194
15. IBM Corp. (Released 2015) IBM SPSS Statistics for Windows, Version 23.0. Armonk, NY: IBM Corp
16. Kitchen SG, Meyer SE, Carlson SL (2015) Mechanisms for maintenance of dominance in a nonclonal desert shrub. Ecosphere, 6(12):Article 252
17. Kruckeberg AR, Rabinowitz D (1985) Biological aspects of endemism in higher plants. Rev Ecol Syst 16:447-479
18. Mauchly JW (1940) Significance test for sphericity of a normal n-variate distribution. The Annals of Mathematical Statistics 11(2):204-209
19. McArthur ED, Sanderson SC (1985) A cytotaxonomic contribution to the western North American Rosaceous flora. Madroño 32:24–28
20. Meyer SE, Pendleton BK (2005) Factors affecting seed germination and seedling establishment of a long-lived desert shrub (*Coleogyne ramosissima*: Rosaceae). Plant Ecol 178:171-187
21. Miller J, Etyemezian V, Cablk ME, Shillito R, Shafer D (2013) Monitoring Soil Erosion on a Burned Site in the Mojave-Great Basin Transitional Zone: Final Report for the Jacob Fire Site. No. 45253;

- DOE/NV/0000939-13. Submitted to U.S. Department of Energy National Nuclear Security Administration Nevada Field Office by Desert Research Institute. Las Vegas, Nevada
22. National Weather Service (2022) NOWData – NOAA Online Weather Data, Hiko, Nevada Weather Station. <https://www.weather.gov/wrh/Climate?wfo=vef>. Accessed 20 Nov 2022
 23. Pendleton BK, Meyer SE (2004) Habitat-correlated variation in blackbrush (*Coleogyne ramosissima*: Rosaceae) Seed Germination Response. *J Arid Environments* 59:229-243
 24. Pendleton BK, Meyer SE, Pendleton RL (1995) Blackbrush biology: insights after three years of a long-term study. In *Proceedings: Wildland shrub and arid land restoration symposium*, compiled by Roundy BA, McArthur ED, Haley JS, Mann DK, 223-27. General Technical Report INTGTR-315. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, Utah
 25. Pendleton BK, Pendleton RL (1998) Pollination biology of *Coleogyne ramosissima* (Rosaceae). *The Southwestern Naturalist* 43:376-380
 26. Pendleton RL, Pendleton BK, S.E. Meyer SE, Richardson B, Esque T, Kitchen SG (2015) Blackbrush (*Coleogyne ramosissima* Torr.) State of Our Knowledge and Future Challenges. *The Colorado Plateau VI: Science and Management at the Landscape Scale*. University of Arizona Press, Tucson
 27. Phillips III AM, VanDevender TR (1974) Pleistocene packrat middens from the lower Grand Canyon of Arizona. *J Arizona Academy of Sci* 9:117–119
 28. Richardson BA, Kitchen SG, Pendleton RL, Pendleton BK, Germino MJ, Rehfeldt GE, Meyer SE (2014) Adaptive responses reveal contemporary and future ecotypes in a desert shrub. *Ecol App* 24(2):413-427
 29. Richardson BA, Meyer SE (2012) Paleoclimate effects and geographic barriers shape regional population genetic structure of blackbrush (*Coleogyne ramosissima*: Rosaceae). *Botany* 90(4):293-299
 30. Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture (2006) Land Resource Regions and Major Land Resource Areas of the United States, the Caribbean, and the Pacific Basin. Agricultural Handbook 296 digital maps and attributes. Available online. Accessed 15 Dec 2017
 31. Spaulding WG (1990) Vegetation dynamics during the last deglaciation, south-eastern Great Basin. *U.S.A. Quaternary Research* 33: 118–203
 32. Stebbins G, Major J (1965) Endemism and speciation in the California flora. *Ecol Mono* 35(1):1-35
 33. Tang CQ, Matsui T, Ohashi H, Dong YF, Momohara A, Herrando-Moraira S, Qian S, Yang Y, Ohsawa M, Luu HT, Grote PJ (2018) Identifying long-term stable refugia for relict plant species in East Asia. *Nat Comm* 9(1):Article 4488
 34. USDI National Park Service (2003) Fire Monitoring Handbook. Fire Management Program Center, National Interagency Fire Center. Boise, Idaho
 35. Whisenant S (1999) Repairing damaged wildlands: a process-orientated, landscape-scale approach (Vol. 1). Cambridge University Press, Cambridge

36. Zitzer SF (2009) Recruitment of native and non-native annual and perennial plant species following wildfire in a blackbrush (*Coleogyne ramosissima*) Community in south central Nevada. Poster Session 67-113. In 94th annual meeting of the Ecol Soc of America.

Figures

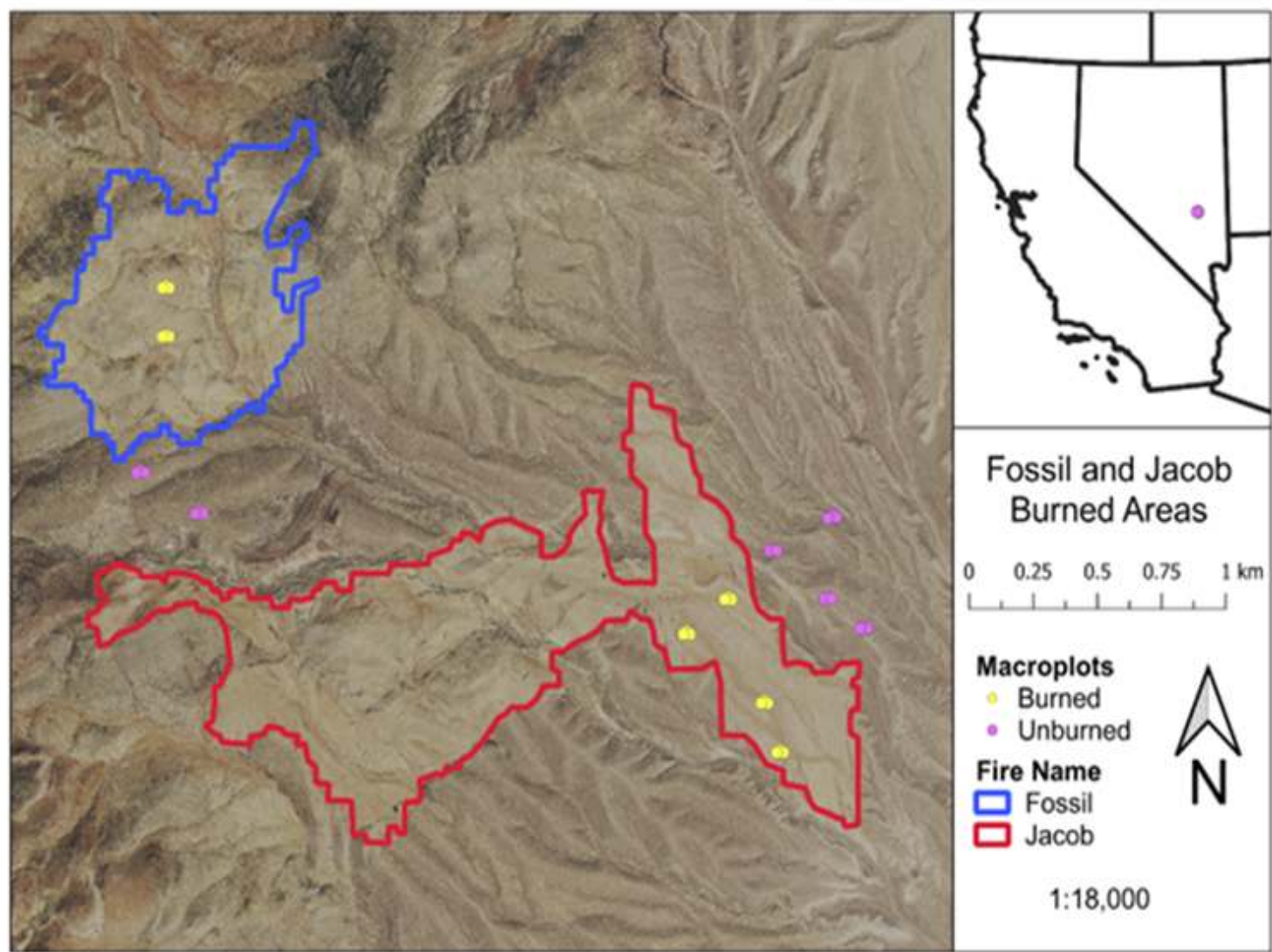


Figure 1

Map of Fossil and Jacob Burned Area. The Fossil (76 ha) and Jacob (165 ha) fires burned in 2008, in the northern Mojave Desert, southern Nevada, USA. Fossil has 2 demonstration plots (6 macroplots) in the burned area and 2 demonstration plots (6 macroplots) in the adjacent unburned area. Jacob has 4 demonstration plots (12 macroplots) in the burned area and 4 demonstration plots (12 macroplots) in the unburned area. There is a total of 18 burned macroplots and 18 unburned macroplots across two fires

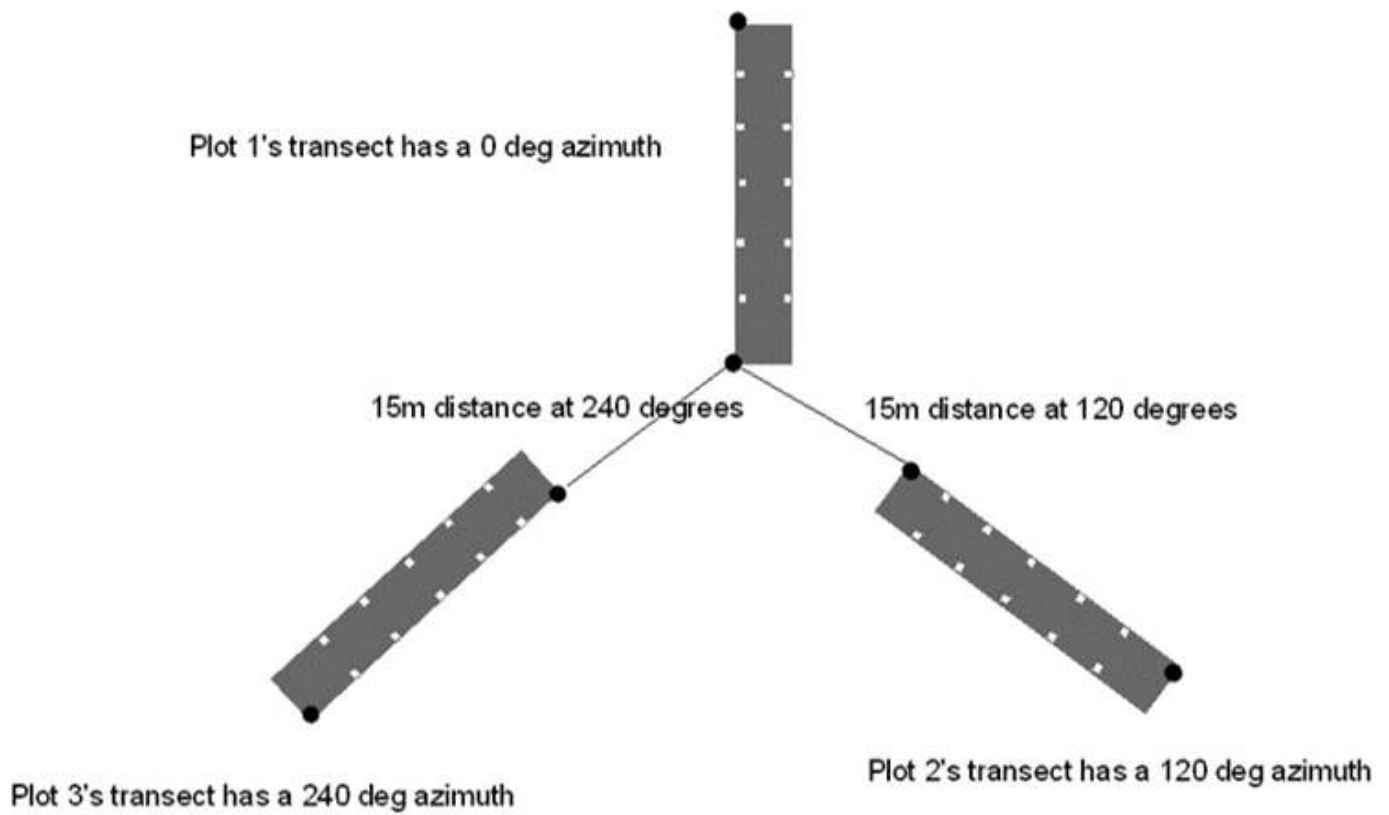


Figure 2

Overview of a demonstration plot. Each demonstration plot contains three 5 x 30 m macroplots (gray rectangles) arranged in a pinwheel with azimuths of 0°, 120°, and 240°. Each macroplot has ten 0.5 m² herbaceous and shrub seedling density quadrats (white squares).

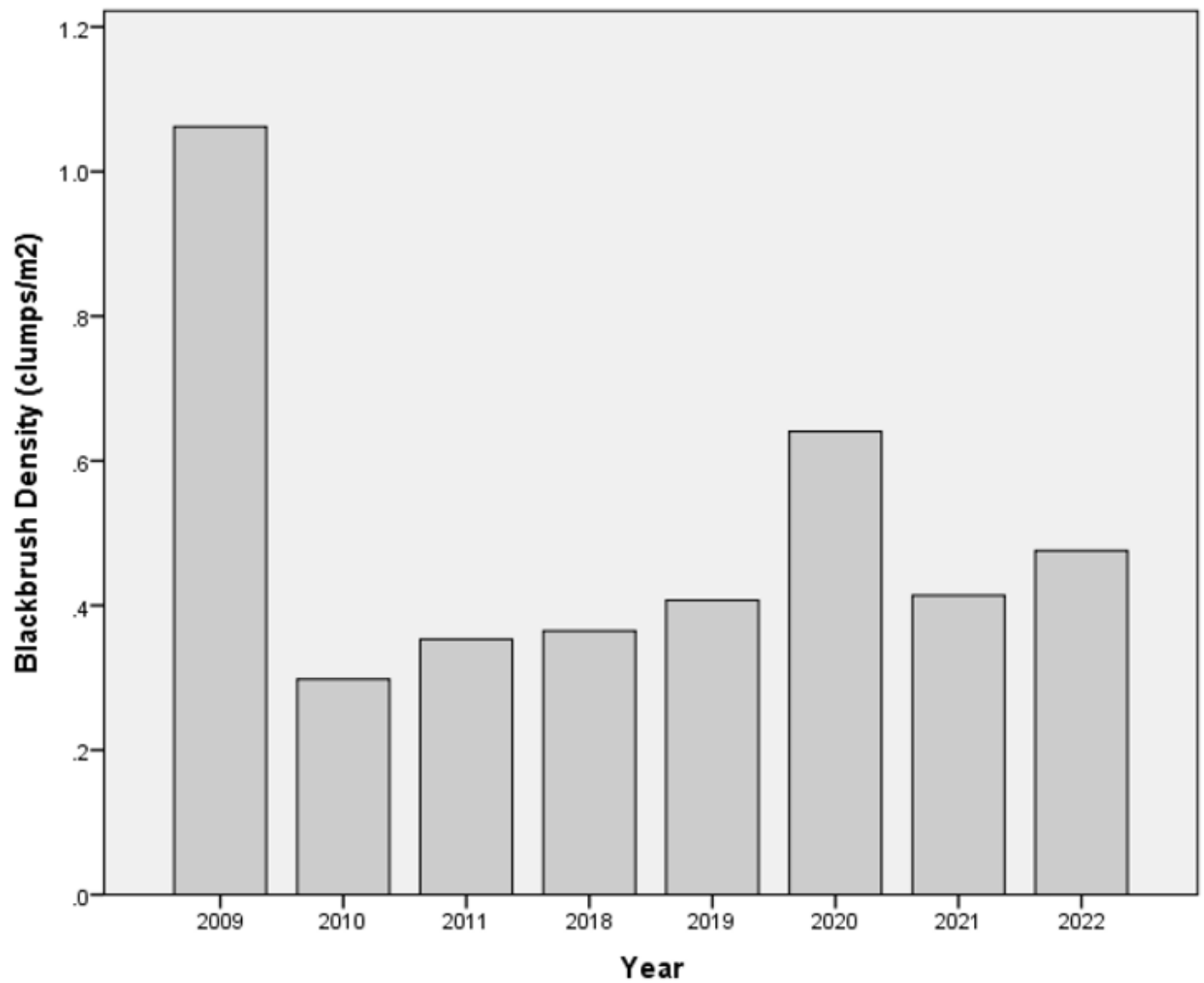


Figure 3

Coleogyne ramosissima total density at the Fossil and Jacob fires. Density at adjacent unburned areas was 0.76 clumps per m²

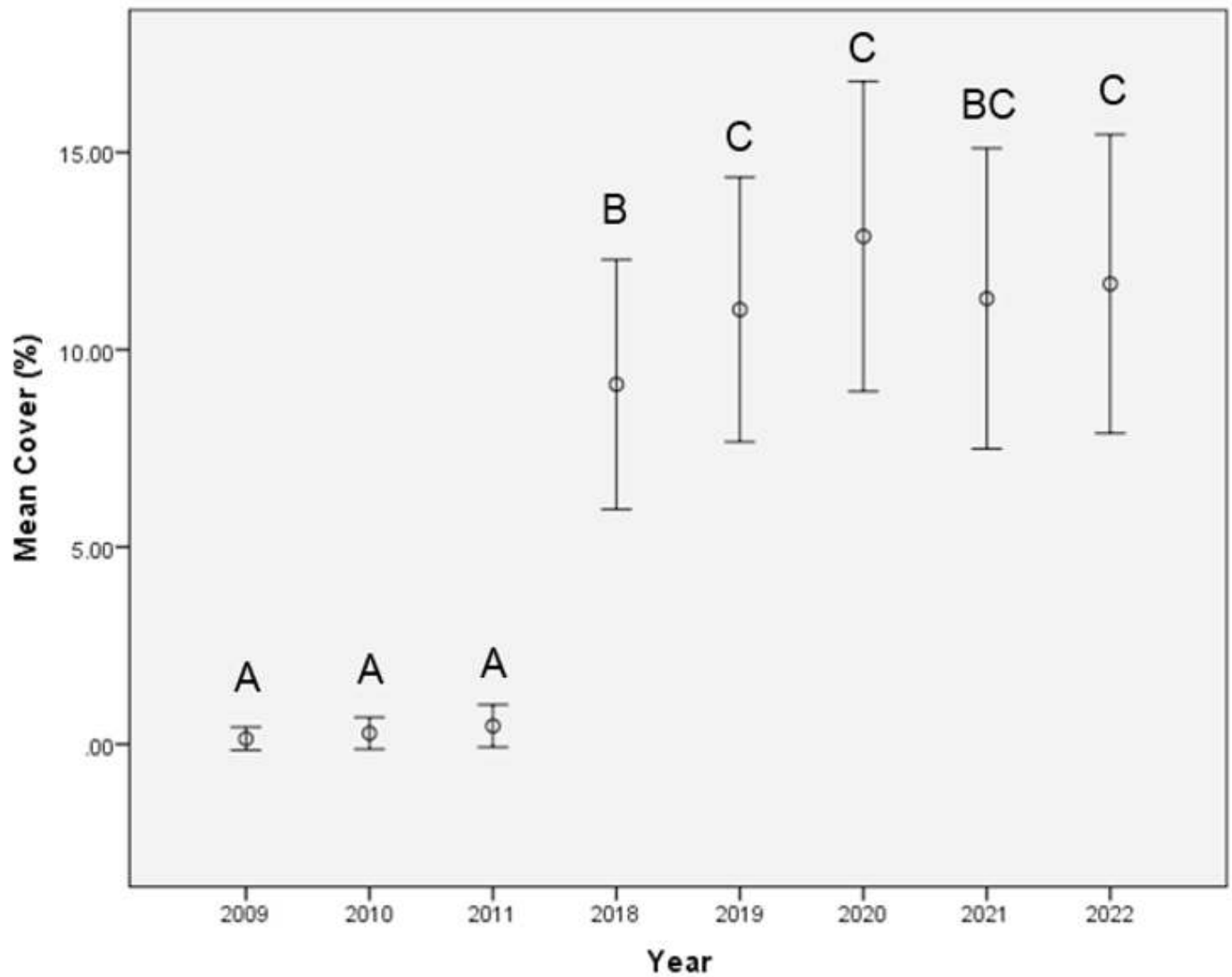


Figure 4

Coleogyne ramosissima mean cover (circles) with 95% confidence error bars from one year (2009) to 14 years (2022) after wildfire in the northern Mojave Desert, USA. Letters indicate Bonferroni post-hoc significance groups (repeated measure ANOVA ($F_{1.173, 18.764} = 35.574, p < 0.001$)). In 2022, *C. ramosissima* cover was 35.3% in the adjacent unburned areas

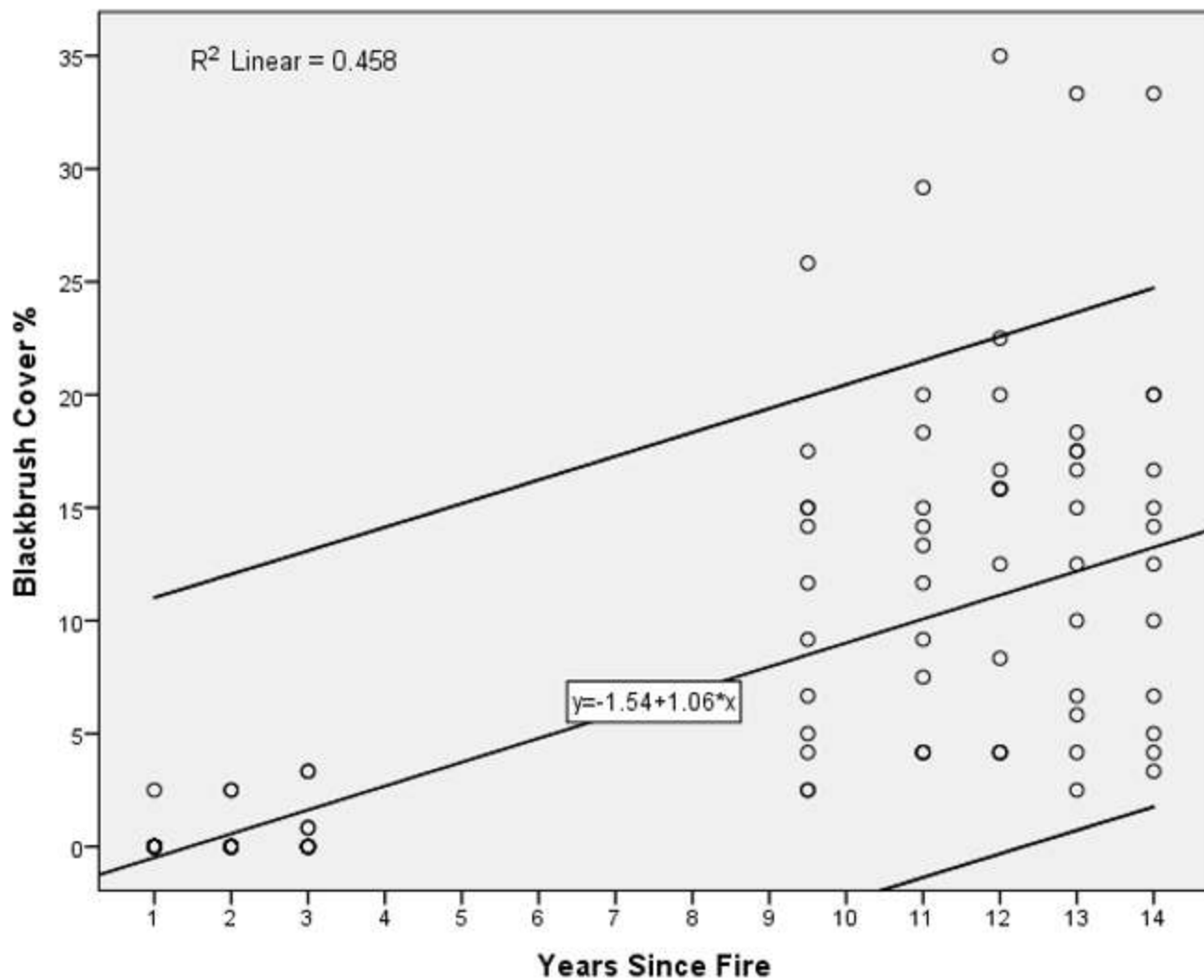


Figure 5

Coleogyne ramosissima cover as a function of time since fire. Year 1 = 2009, Year 14 = 2022. Circles represent burned macroplots with $n = 144$ (18 plots monitored 8 times). Outer lines show 95% confidence intervals

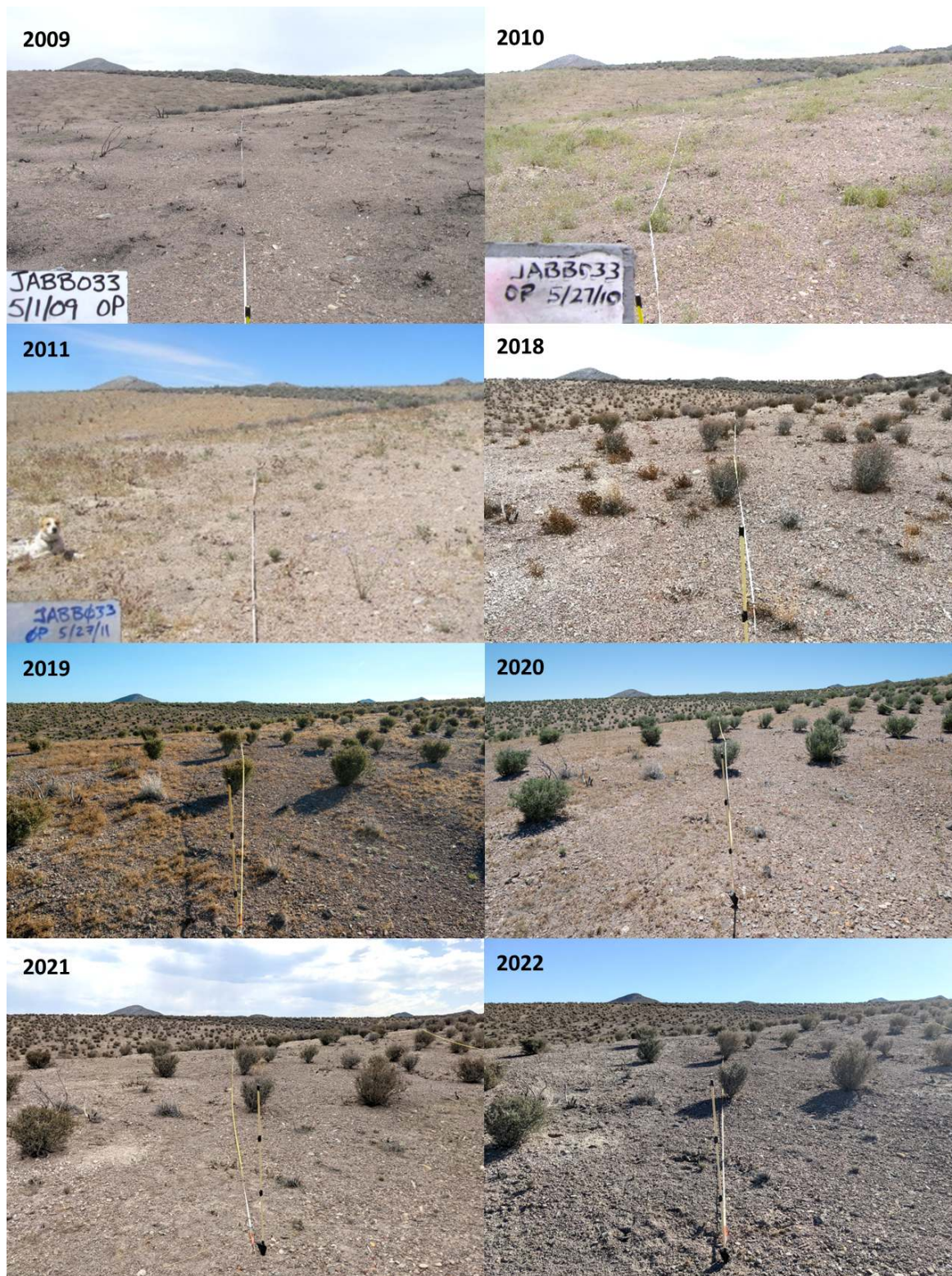


Figure 6

Photo sequence from the Jacob Fire. This plot, JABB033, had blackbrush cover of 2.5, 2.5, 3.3, 15.0, 14.2, 15.8, 15.0, 15.0%; and density of 0.18, 0.13, 0.19, 0.31, 0.41, 1.01, 0.49, 0.64 blackbrush per m² for the years 2009-2011 and 2018-2022. Photos by D.M. Gentilcore.

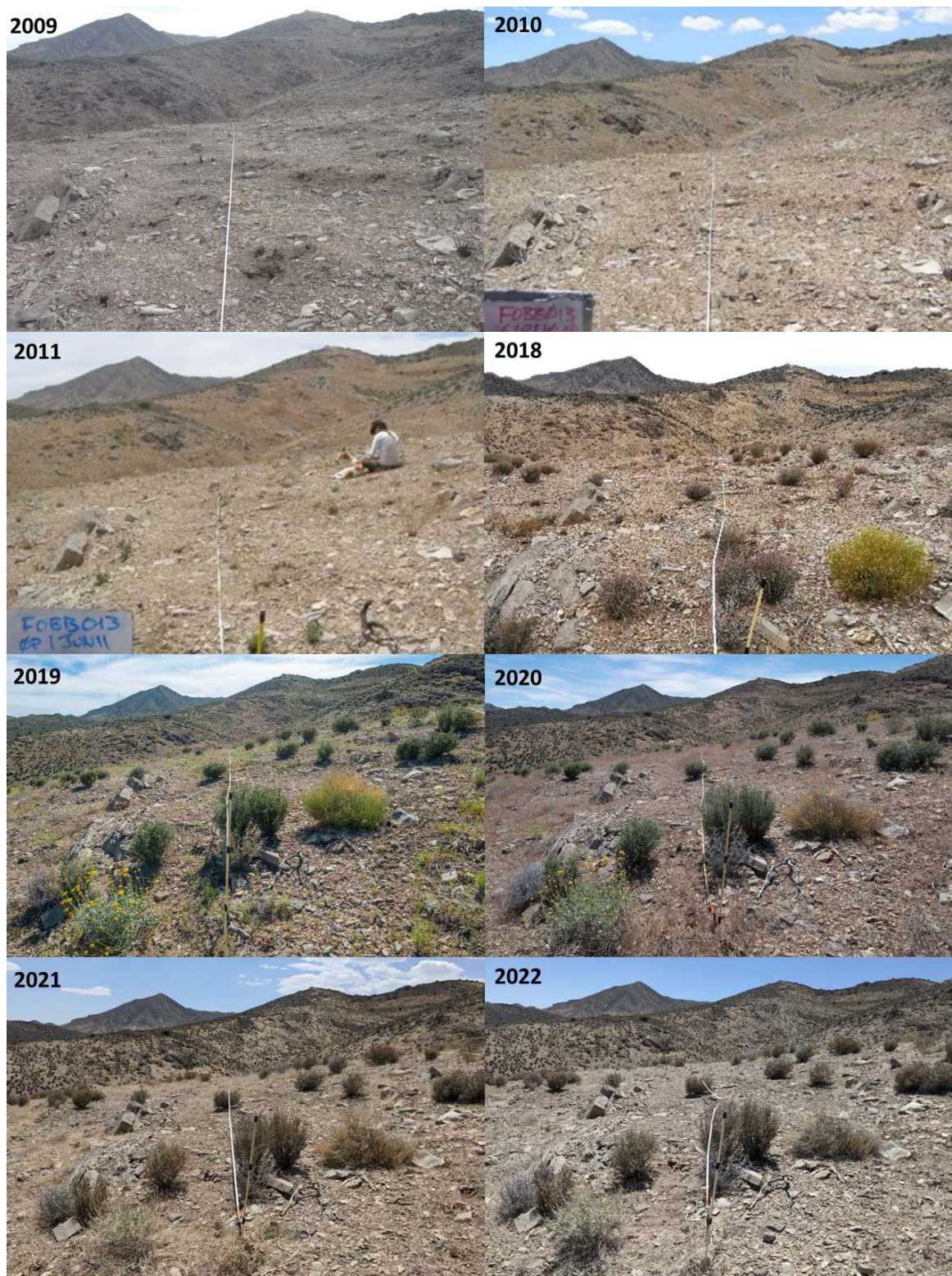


Figure 7

Photo sequence from the Fossil fire. This plot, FOBB013, had blackbrush cover of 0, 0, 0, 10.8, 15.0, 16.7, 13.3, 15.0%; and density of 0.01, 0.11, 0.10, 0.19, 0.25, 0.30, 0.25, 0.29 blackbrush per m² for the years 2009-2011 and 2018-2022. Photos by D.M. Gentilcore

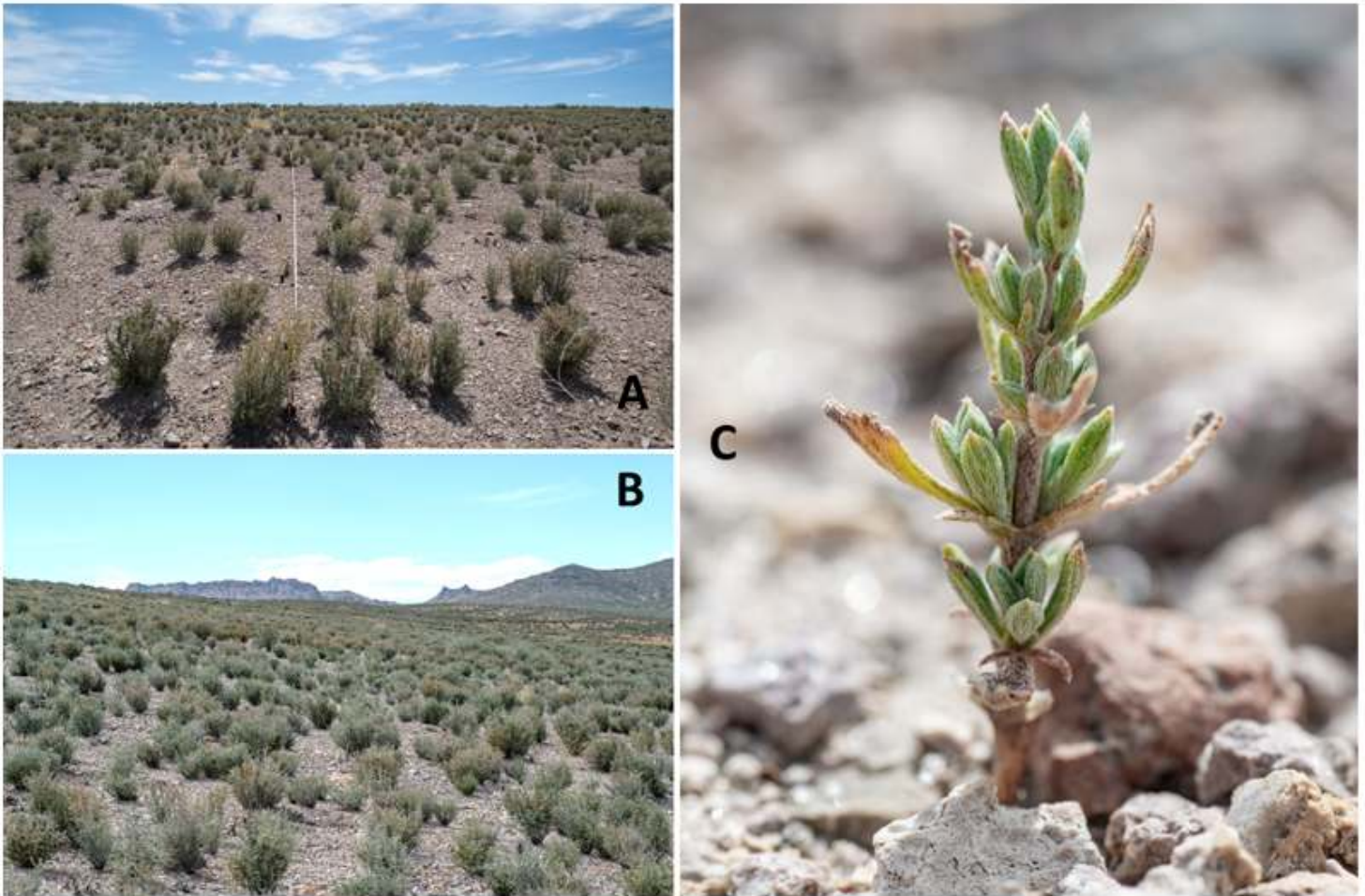


Figure 8

Coleogyne ramosissima natural regeneration on the Jacob fire. 8a: The macroplot with the highest blackbrush cover in 2019 (29%). 8b: An image of dense blackbrush regeneration in an unmonitored portion of the fire. 8c: A first year *C. ramosissima* seedling with cotyledons withered, but not yet firmly rooted