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Fire frequency effects on plant community characteristics in the Great Basin and Mojave deserts of North America

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Abstract

Background Wildfire regimes are changing dramatically across North American deserts with the spread of invasive grasses. Invasive grass fire cycles in historically fire-resistant deserts are resulting in larger and more frequent wild-fire. This study experimentally compared how single and repeat fires influence invasive grass-dominated plant fuels in the Great Basin, a semi-arid, cold desert, and the Mojave, a hyper-arid desert. Both study sites had identical study designs. In the summer of 2011, we experimentally burned half of each experimental block, the other half remaining as an unburned control. Half of the burned plots were reburned 5 years later to simulate increasing burn frequency. We estimated non-woody plant biomass, cover, and density in plots from 2017 to 2020.

Results Biomass did not vary between sites, but there was higher plant cover and lower plant density at the Mojave site than at the Great Basin site. Plant biomass, density, and cover varied significantly across the years, with stronger annual fluctuations in the Great Basin. At both desert sites, fire increased plant density and biomass but had no effect on the cover. The effect of fire on plant cover varied significantly between years for both deserts but was greater in the Great Basin than in the Mojave site. Repeat fires did not amplify initial fire effects.

Conclusions The results suggest that in general annual fluctuations in fine fuel production and fluctuations in response to fire were more apparent at the Great Basin site than at the Mojave site, with no immediate compounding effect of repeat fires at either site.

Keywords Bromus, Cheatgrass, Invasion, Invasive grass fire cycle, Red brome

Resumen

Antecedentes Los regímenes de fuego están cambiando dramáticamente a lo largo de los desiertos de Norteamérica con la propagación de pastos invasores. Los ciclos de fuego de pastos invasores en desiertos históricamente resistentes a los fuegos han resultado en incendios más grandes y frecuentes. Este estudio comparó experimentalmente cómo incendios individuales y repetidos influyen los combustibles vegetales dominados por pastos invasores en la región de la Gran Cuenca (the *Great Basin* en Inglés), un semi desierto árido y frío, y el Mojave, un desierto hiper-árido. Ambos sitios de estudio tuvieron los mismos diseños de estudio. En el verano de 2011, quemamos experimentalmente la mitad de cada uno de los bloques experimentales, y la otra mitad permaneció como el control sin quemar. La mitad de las parcelas quemadas fueron re- quemadas 5 años después para simular un incremento en

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la frecuencia de quemas. Estimamos la biomasa de plantas no leñosas, la cobertura, y densidad en parcelas desde 2017 a 2020.

Resultados La biomasa no varió entre sitios, aunque hubo más cobertura vegetal y menor densidad de plantas en el sitio de Mojave que en el sitio de la Great Basin. La biomasa de plantas, densidad y cobertura varió significativamente entre años, con una mayor fluctuación anual en la Great Basin. En ambos desiertos, el fuego incrementó la densidad de plantas y la biomasa, pero no tuvo efectos en la cobertura. El efecto del fuego en la cobertura vegetal varió significativamente entre distintos años para ambos desiertos, aunque fue mayor en la Great Basin que en el desierto de Mojave. Los fuegos repetidos no amplificaron los efectos iniciales de los fuegos.

Conclusiones Los Resultados sugieren que en general, la fluctuación anual en la producción del combustible fino, y fluctuaciones en respuesta al fuego, fueron más aparentes en el sitio de la Great Basin que en el sitio del desierto de Mojave, con ningún efecto compuesto de fuegos repetidos en ninguno de los sitios.

Background

Plant invasions are increasingly becoming more problematic (Rejmánek and Richardson 1996; Callaway and Ridenour 2004; Levine et al. 2004; Enders et al. 2019) particularly in areas where human activities are increasing ecological disturbance (Seabloom et al. 2006; Bishop et al. 2019). Wildfires in particular have opened niche space for plant invasions globally (D'Antonio and Vitousek 1992). Desert ecosystems have historically been relatively resistant to frequent wildfires, but increased fine fuel infill between native shrubs by invasive annual grasses has resulted in larger and more frequent fires in deserts of North America (St. Clair and Bishop 2019, Fusco et al. 2019). Following a wildfire, a reduction in native plant cover significantly reduces biotic resistance from native plants (Pyke 1986; Levine et al. 2003, 2004, St. Clair et al. 2016). In the post-fire absence of competition from native plants, invasive grasses proliferate, increasing fine fuels that can lead to secondary fires (Whisenant 1989, St. Clair and Bishop 2019). The proliferation of invasive annual grasses has shortened the fire return interval from century to decadal time scales in some desert ecosystems making it hard for native vegetation to successfully regenerate (D'Antonio and Vitousek 1992; Balch et al. 2013; Bukowski and Baker 2013). This cycle of fire and invasive grass production can ultimately create vegetation state transitions resulting in invasive grass monocultures that leads to losses of native plant diversity (Brown and Heske 1990, St. Clair et al. 2016).

A common characteristic of novel fire regimes is increased fire frequency (Brooks et al. 2004; Underwood et al. 2019), which can strongly affect patterns of plant community assembly (Klinger and Brooks 2017). A study in the Mojave Desert by Klinger and Brooks (2017) suggests that herbaceous plant productivity can increase with fire frequency. The fuel characteristics of repeat fires tend to be different than initial fires, primarily because of the fuel that perpetuates them. Woody native shrubs and other plants tend to burn hotter in initial fires than finer

fuel species that tend to drive secondary fires (Fuentes-Ramirez et al. 2016), creating higher burn severity that can drastically reduce soil organic matter (Allen et al. 2011) and alter soil crusts and soil microbial communities (Aanderud et al. 2019). Repeat fires fueled by annual grasses tend to burn faster and at lower temperatures than initial fires occurring in perennial shrublands (Jones et al. 2015; Fuentes-Ramirez et al. 2016). Repeat fires can still have a significant impact on the available nutrients in a system as they reduce the carbon and nitrogen stored in the plant tissue to ash, which can then be lost through erosion (Ojima et al. 1994; Jones et al. 2015). While there may be an initial pulse of nitrogen following a fire (Esque et al. 2010), over time, with as few as two burns, there can be reductions in soil organic nitrogen, microbial biomass and nitrogen availability, and increases in the C:N ratios of soil organic matter (Ojima et al. 1994). This kind of post-fire condition continues to favor invasive grasses over native communities (Underwood et al. 2019), further perpetuating the invasive grass fire cycle (Whisenant 1989; Salo 2004; Bradley et al. 2017).

Ecosystems show varying degrees of susceptibility to invasions and sensitivity to fire (Balch et al. 2013), but few studies have compared the impact of wildfire on fuel load production in different deserts. The Great Basin and Mojave deserts, which are adjacent to one another, provide an opportunity to compare invasion and fine fuel responses to fire frequency in an arid and semi-arid desert. The Great Basin Desert is a semi-arid, cold desert in the Intermountain West. The Mojave Desert is a hyper-arid desert in the southwestern US. The vegetation of both deserts is dominated by native perennial woody shrubs, interspersed with forbs and grasses. The Great Basin is mostly sagebrush steppe, whereas the Mojave is home to a diverse shrub community made up of iconic plant species such as Joshua trees (*Yucca brevifolia* Engelm.) and creosote bushes (*Larrea tridentata* (DC.) Coville). Cheatgrass (*Bromus tectorum* L.) is an aggressive plant invader of the Great Basin, and the closely

related red brome (*Bromus rubens* L.) dominates in the Mojave Desert (Mack 1981; Salo 2005). Both actively compete with native plant communities for limiting soil moisture and nitrogen (Young et al. 1972) and increase fire frequency and extent (St. Clair and Bishop 2019; Bishop et al. 2020a).

Researchers have conducted studies that focus on the effects of fire on fine fuel load production (Salo 2004; Bradley et al. 2017), but less is known about the impacts of reburns, a phenomenon that is becoming more common (Bishop et al. 2020a). Very little is known about how the effect of fire on plant productivity and the accumulation of fine fuel loads differs between desert types over time (Horn and St. Clair 2017). The purpose of this study was for the first time to experimentally assess how fire and repeat fires influence the production of fine plant fuels, consisting of grass and forb species, in the Great Basin and Mojave Deserts. We explored the following questions: (1) Do fire and repeat fire differentially affect the production of fine plant fuel? and (2) How do the effects of fire vary across time in different desert types? We hypothesized that fire and repeat fire would increase fine plant fuels and that cooler and less water-limited Great Basin Desert would produce more fine fuels than the Mojave Desert.

Methods

Study sites

The Great Basin study site was located just east of Vernon, Utah (40° 05′ 26.17″ N 112° 18′ 18.01″ W, elevation: 1650 m) in the sagebrush-steppe ecosystem of western North America. The area's average temperature is 8.6 °C, with the average January temperature being -3.2 °C and average July temperatures being 22.3 °C (Vernon GHCN: COOP, Utah Climate Center). Precipitation falls as both rain and snow at a rate of approximately 257 mm per year spread relatively evenly across all seasons. Soils have been classified as silty, mixed mesic Haplic Natrargid, and Taylors Flat Loam. Native plants that are common to the area include Wyoming big sagebrush (*Artemisia tridentata* Nuttall) and bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey). Several invasive plants common to the area include cheatgrass (*Bromus tectorum*) and bur buttercup (*Ceratocephala testiculata* Crantz. Bess.). There was no evidence of recent grazing or fire at the field site since the native shrub community is mature and the soil crusts are well developed. Wire fences surround the whole site to prevent cattle grazing.

The Mojave field study area was located near Lytle Ranch Preserve in the Beaver Dam Wash region of the Mojave Desert, approximately 40 km West of St George, Utah (37° 8′ 53.46″ N, 114° 0′ 49.59″ W, elevation 915 m). The average temperature is 17.3 °C, with the

average January temperature being 7.2 °C and the average July temperature being 29.4 °C (Lytle Ranch GHCN: COOP, Utah Climate Center). An average of 206 mm of precipitation falls per year, with a large portion of that falling in the winter months between October and April. The soil is a young alluvium with a gravelly, sandy-loam texture. Common native plants in the area include Joshua trees (*Yucca brevifolia* Engelm.), white bursage (*Ambrosia dumosa* (A. Gray) Payne), and creosote bush (*Larrea tridentata* (DC.) Coville). Several invasive plants are common at the study site: cheatgrass (*Bromus tectorum*), red brome (*Bromus rubens*) and Arabian schismus (*Schismus arabicus* Nees). Wire fences surrounding the study site have prevented grazing from cattle for at least the last 30 years, and there is no evidence of a recent fire.

Experimental design

An identical experimental design was used at both the Great Basin and Mojave study sites to test the effects of fire frequency on fine plant fuel production. Five replicate blocks were installed at both sites, each consisting of two 30 m × 30 m plots. Each plot was randomly selected as either a burn plot or an unburned control. In 2016, burned plots at both study sites were split in half, with one side being randomly selected to serve as a reburn treatment and the other remaining in the single-burn condition so that unburned, single-burned, and twice-burned plots could be compared.

The initial burn treatments at the Great Basin site were conducted on 20 September 2011. Because the site was uninvaded prior to this experiment, there was insufficient fine fuel to carry fire between native shrubs across the plots. We, therefore, spread wheat straw (300 g m⁻²) between the shrubs to facilitate the spread of fire between native shrubs (Esque et al. 2010). Drip torches were used to initiate the experimental burns. Nitrogen released into the system by burning straw was comparable to nitrogen released by burned cheatgrass (St. Clair and Bishop 2019). Consumption of the straw fuel across the experimental plots was very rapid, within a few minutes, which is similar to burn rates of invasive brome grasses (St. Clair and Bishop 2019). The burn treatment was classified as high severity as measured by more than 99% plant cover loss. The reburn treatment was conducted on the 27th of October 2016. During the reburn treatment, the cheatgrass cover was sufficient to carry the fire across the experimental burn plots. Drip torches were used to facilitate the burn.

Initial burn treatments at the Mojave site were conducted on 18 June 2011, using a drip torch. Because invasive grasses had already started to invade the site prior to the experiment, fine fuels from red brome, growing at a rate of 1319 stems m⁻² in the intershrub spaces,

were sufficient to carry the fire treatment across the burn plots. The severity of the burn was high, resulting in a 90% reduction in plant cover (Sharp Bowman et al. 2017a). Reburn treatments at the Mojave site occurred on 6 October 2016. Because of low fine fuel loads at our Mojave study site that year, wheat straw (300 g m^{-2}) was used to carry flames from drip torches across the designated reburn area.

Vegetation surveys

We conducted vegetation surveys annually in May–June of 2017–2020 when herbaceous plants reach their vegetative peak but before seeds dropped. We randomly placed four parallel 30 m transects in each plot at least 2 m away from the edge of the plots to prevent biases due to edge effects. The direction of the transects (North to south or east to west) alternated annually. Along transect lines, vegetation biomass, vegetation cover, and vegetation density were measured.

We measured vegetation biomass by placing four frames along each transect line. We used scissors to collect all above-ground plant matter from grasses and forbs rooted within each frame and sorted it into bags labeled by species. The biomass samples were taken back to the lab, dried in a drying oven for at least 72 h at approximately $40 \text{ }^{\circ}\text{C}$, and weighed using a balance (Denver Instrument, Bohemia, New York, USA).

Plant cover was measured using the line-point intercept method (Herrick et al. 2006). We dropped a vertical pin systematically every 0.5 m along each transect line. For each vertical pin drop, we recorded the canopy layer (tallest plant that intersected the pin) or bare soil where plant cover was absent (Helm and Mead 2004).

We placed a $25 \text{ cm} \times 50 \text{ cm}$ modified Daubenmire frame every 2 m along each transect line to measure the vegetation density. We identified and counted every grass and forb rooted within the frame to get an average count of plant density per m^2 . For cheatgrass and bur buttercup in the Great Basin and red brome and Arabian schismus in the Mojave, we measured density within a $10 \text{ cm} \times 25 \text{ cm}$ subframe of the larger Daubenmire frame.

Statistical analysis

As outlined by Zuur et al. (2010), we conducted data exploration to ensure that the data met the assumptions for normality and equal variances. We modeled plant biomass, cover, and density using mixed-effects models in the program JMP[®]. For each measurement, site, year, and burn were assigned as fixed effects with block as a random effect (JMP[®] Pro 1989–2021). Pairwise analysis to compare unburned, single burn, and repeat burn treatments was conducted using the Tukey HSD test in the

program R, using the package emmeans (Lenth 2021; R Core Team 2018).

Results

Plant biomass

Plant biomass was consistent across the two study sites when averaged across years ($F_{1,71} = 0.01$, $p = 0.91$) but varied dramatically between years ($F_{3,71} = 130$, $p < 0.0001$). In the Great Basin, the highest biomass year was in 2019 (219 g m^{-2} , $\text{SE} = 17$), which was 37-fold higher than the lowest biomass year in 2020 (6 g m^{-2} , $\text{SE} = 2.39$) (Fig. 1). In the Mojave, the highest biomass year, also in 2019 (185 g m^{-2} , $\text{SE} = 18$), was nearly an order of magnitude greater than 2018 (19 g m^{-2} , $\text{SE} = 2.04$), which had the lowest biomass. Fluctuation in biomass across years was greater in the Great Basin than the Mojave as evidenced by a significant site by year interaction term ($F_{3,71} = 6.4$, $p = 0.0007$). When averaged across sites and years, fire increased plant biomass from 71 g m^{-2} ($\text{SE} = 15$) in the unburned plots to 88 g m^{-2} ($\text{SE} = 15$) in the burned plots ($p = 0.08$), but there was no statistically significant difference between the biomass in the burned and the reburned plots ($p = 0.61$; $F_{2,71} = 2.41$, $p = 0.10$) (Fig. 1). The fire by site interaction ($F_{2,71} = 2.19$, $p = 0.12$), the fire by year interaction ($F_{6,71} = 0.90$, $p = 0.50$), and fire by year by site interaction terms ($F_{6,71} = 0.73$, $p = 0.63$) were not statistically significant (Fig. 1; Table 1).

Plant cover responses

There was 12% greater plant cover in the Mojave study plots (61%, $\text{SE} = 1.96$) than the Great Basin study plots (49%, $\text{SE} = 4.35$; $F_{1,71} = 26$, $p < 0.0001$) when averaged across years. Plant cover also varied between years ($F_{3,71} = 42$, $p < 0.0001$). In the Great Basin, the highest cover year was in 2019 (70%, $\text{SE} = 6.31$), with the lowest plant cover occurring in 2020 (16%, $\text{SE} = 3.09$). In the Mojave, the lowest cover year was 2017 (47%, $\text{SE} = 2.00$), and 2019 was the highest cover year (82%, $\text{SE} = 2.12$). Fluctuation in percentage cover across years was greater in the Great Basin than in the Mojave, as evidenced by a significant site by year interaction term ($F_{3,71} = 24$, $p < 0.0001$). The main effect of burn and reburn did not impact plant cover when averaged across site and year ($F_{2,71} = 1.50$, $p = 0.23$). The fire by site interaction was not statistically significant ($F_{2,71} = 0.45$, $p = 0.64$), but there was a fire by year interaction ($F_{6,71} = 2.14$, $p = 0.06$) with the effects of fire being greatest in 2019. There was evidence that the effects of fire on plant cover were more variable in the Great Basin across time than in the Mojave Desert as indicated by the three-way interaction term ($F_{6,71} = 2.05$, $p = 0.07$; Fig. 1; Table 1).

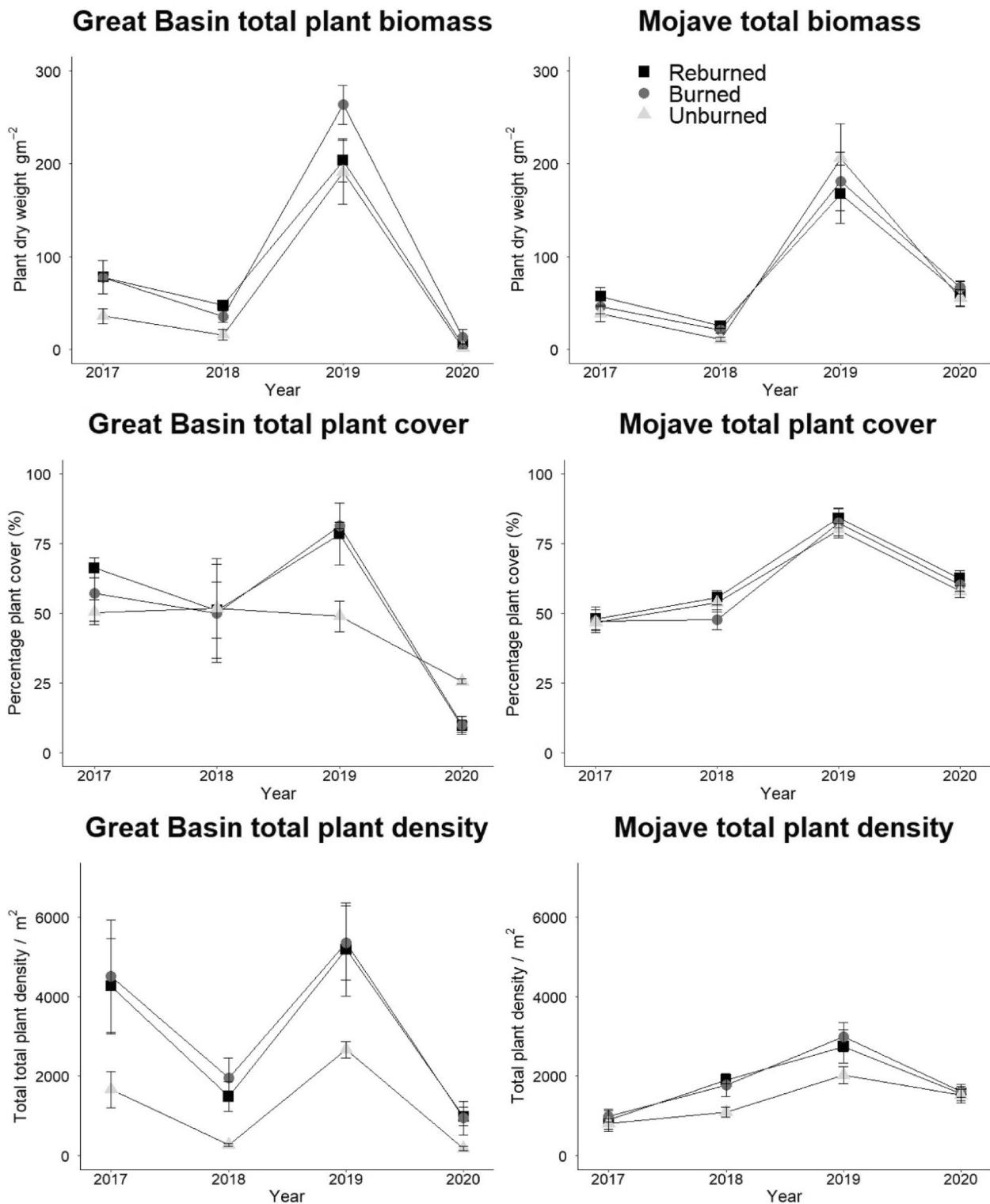


Fig. 1 Time series showing how the main and interactive effects of fire (unburned, burned, reburned), field site (Great Basin or Mojave) and year (2017–2020) influence fuel load production in the form of total plant biomass, cover, and density. Light gray triangles represent our control areas left unburned, dark gray circles represent plots burned once in 2011, and black squares represent plots that have been reburned or burned twice, in 2011 and again in 2016. Error bars are ± S.E.; for significance values, see Table 1

Table 1 The main and interactive effects of fire frequency (unburned, burned, reburned), year (2017–2020), and site (Mojave or Great Basin) on forb and grass biomass, cover, and density

	Biomass		Cover		Density	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Fire frequency	2.41	0.08	1.5	0.23	18	<0.0001
Site	0.01	0.91	26	<0.0001	20	<0.0001
Year	131	<0.0001	42	<0.0001	33	<0.0001
F×S	2.19	0.12	0.45	0.64	6.9	0.002
F×Y	0.9	0.5	2.14	0.06	1.03	0.42
S×Y	6.4	0.0007	24	<0.0001	20	<0.0001
F×S×Y	0.73	0.63	2.05	0.07	0.74	0.62

Plant density responses

There was a larger density of plants at our Great Basin site (2500 individuals m^{-2} , $\text{SE}=361$) than at our Mojave site (1661 individuals m^{-2} , $\text{SE}=106$) when averaged across years ($F_{1,71}=20$, $p<0.0001$). Plant density also varied between years and sites, resulting in a significant year by site interaction ($F_{3,71}=33$, $p<0.0001$). The highest density year in the Great Basin was in 2019 (4403 plants m^{-2} , $\text{SE}=615$), which decreased 6.5-fold the following year in 2020 (675 plants m^{-2} , $\text{SE}=181$), which was the lowest density year. In the Mojave, the lowest density year was 2017 (895 plants m^{-2} , $\text{SE}=107$), while 2019 was the highest density year (2590 plants m^{-2} , $\text{SE}=215$). When averaged across years, the effects of the initial fire increased the density of plants by 1.8-fold ($p<0.0001$), from an average of 1302 individuals per m^2 ($\text{SE}=145$) in the unburned plots to 2393 individuals m^{-2} ($\text{SE}=303$) in the burned plots. However, there was no significant difference between the density of plants in the burned and the reburned plots when averaged across years ($p=0.82$). There was a significant fire by site interaction term, indicating that the fire effect on plant density was stronger in the Great Basin than in the Mojave ($F_{2,71}=6.90$, $p=0.002$). The fire by year ($F_{6,71}=1.03$, $p=0.42$) and fire by year by site interaction terms ($F_{6,71}=0.74$, $p=0.62$; Fig. 1; Table 1) were not statistically significant for plant density.

Discussion

Fire frequency, site, and year all had varying influences on plant biomass, cover, and density. We hypothesized that greater fire frequency would increase fine plant fuels that promote fire. While fire increased plant biomass and density, particularly in the Great Basin Desert, repeat fire had no amplifying effect on fine fuels contrary to our prediction (Fig. 1). Great Basin vegetation showed stronger fluctuations across years and more responsiveness to fire

than the Mojave Desert vegetation consistent with our second hypothesis (Fig. 1).

Effects of fire and repeat fire

Our data show that a second fire occurrence did not significantly alter plant biomass, cover, or density, when compared to the effects of the initial fire (Fig. 1). Initial desert fires remove significant shrub cover, leaving space and soil resources that promote invasion success that leads to loss of plant community diversity (Brooks 2000, DeFalco et al. 2003; Mahood and Balch 2019). The secondary fires occurred 5 years after the initial burns, which is within the potential fire frequency window being observed in these deserts (Balch et al. 2013). Short fire return intervals likely reduce the re-establishment success of perennial native species (Keeley and Brennan 2012). A combination of burn severity and frequency plays a prominent role in determining the amount of fuel available for subsequent fires, with peak invasive grass cover being reached between 10 and 20 years following a burn (Klinger and Brooks 2017). In our study systems, invasive annual grasses dominate in post-fire conditions meaning secondary fires would burn cooler with lower severity, which could have a stabilizing influence on post-fire invasive grass re-establishment (Ojima et al. 1994; Fuentes-Ramirez et al. 2016). Furthermore, subsequent fires can cause nutrient loss through the wind erosion of ash (Jones et al. 2015). Taken together, we hypothesize that additional fire occurrence at short intervals in these desert systems is unlikely to promote dramatic increases in fine fuel beyond the initial fire (Ojima et al. 1994).

Our data show a significant fire by year interaction for plant cover (Fig. 1), indicating that the effects of fire varied across years. Weather conditions in the Great Basin and the Mojave Deserts fluctuate dramatically across seasons and years, which can amplify or dampen fire effects (Hereford et al. 2006; Soulard 2012; Horn et al. 2017). Sensitivity to fire tended to be greater at the Great Basin

study site and was particularly strong in 2019 (Fig. 1) a year preceded by Utah's tenth wettest water year in recorded history (NOAA 2023). Productivity of invasive grasses is strongly regulated by fire history and precipitation timing and quantity (Horn and St. Clair 2017, Kerns and Day 2017). Invasive annual grasses exhibit strong responses to precipitation in deserts due to water limitation (Salguero-Gomez et al. 2012) particularly in the fall period (Horn et al. 2017; Bishop et al. 2020b). This increase in cover in high precipitation years, and in the years that follow, likely increases fire probability by increasing fuel continuity (Pilliod et al. 2017).

Contrasting responses of the two desert systems to fire

Both our Great Basin and Mojave Desert study systems demonstrate distinct differences in cover, density, and biomass in response to fire over time (Fig. 1) (Horn and St. Clair 2017, Bishop et al. 2020b) which is likely influenced by both abiotic and biotic differences between the two deserts. The Mojave Desert is a hyper-arid system with most precipitation falling in the cooler months between October and April, but it also experiences unpredictable monsoonal rain events in the summer (Wells 1979; Hereford et al. 2006). The Great Basin Desert is at a higher elevation and latitude than the Mojave (Hunter 1991) resulting in cooler conditions (Soulard 2012). Most of the precipitation in the Great Basin falls as snow in the winter (Soulard 2012). Invasive *Bromus* species form a large part of the plant community in these two deserts. Despite being closely related and having similar traits, cheatgrass in the Great Basin and red brome in the Mojave also show important differences in their characteristics, which likely contributed to the different responses of the two desert systems. Young red brome plants struggle with oscillations in colder temperatures that occur in the Great Basin but thrive in the warmer climate of the Mojave, while cheatgrass is adapted to cooler conditions (Bykova and Sage 2012).

Our data show that fire had a greater effect on the plant density in the Great Basin than in the Mojave (Fig. 1). This may be partially related to the burn characteristics at the two study sites. While both sites experienced a significant loss of vegetation in response to fire, burn severity was greater at the Great Basin site (>99%) compared to the Mojave site (~80%) for the 2011 burn treatments (St. Clair et al. 2016, Bishop et al. 2020a, b) resulting in some inherent differences in burn patchiness and intensity. We also used straw to carry the fire at the Great Basin site in 2011 and the Mojave site in 2016 to standardize fine fuels between sites, which gave us more consistent burn patterns but cheatgrass straw and wheat straw do have some inherent differences that we carefully tried to account for (see the "Methods" section).

Differences in the biological communities between the two deserts, including plant and consumer communities and soil properties (Bahr 2013, St. Clair et al. 2016, Bishop et al. 2020a, b) also have the potential to explain some of the differences in sensitivity to fire observed in this study (Fig. 1). Brooks (2002) and Korfmacher et al. (2003) identified that the peak temperatures of fires at ground level tended to be hotter in Great Basin shrublands than in the Mojave Desert resulting in more damage to soil crusts at our Great Basin than Mojave sites (Bahr 2013; Aanderud et al. 2019). We hypothesize that stronger plant fuel responses to fire at our Great Basin site (Fig. 1) may partially be driven by greater soil crust damage and associated losses of biotic resistance to invasive grass establishment (Belnap et al. 2006; Ponzetti et al. 2007).

Fire effects on plant fuels may also be partially driven indirectly through trophic interactions that can vary between deserts (St. Clair et al. 2016, Bishop et al. 2020a, b). For example, Mojave rodent populations dominated by bi-pedal rodent species tend to show greater resilience to fire than Great Basin rodent communities dominated by quadrupedal species (Horn et al. 2012; Sharp Bowman et al. 2017b). Differential responses of rodent communities to fire can indirectly affect plant fuels by altering rates of rodent seed predation and seedling herbivory (Borchert and Jain 1978, Sharp-Bowman et al. 2017c).

Conclusions and implications

This study suggests that the effects of fire on fine fuel production dominated by invasive grasses vary by desert and year, with a greater effect in the Great Basin Desert than in the Mojave Desert. The Mojave and the Great Basin Deserts both span multiple US states and experience variability in topography, climate, and biological composition. Our results provide a strong cross-desert comparison and multi-year temporal inference with data collected over a 4-year period that spanned variation in both the abiotic and biotic environments at our study sites. Key conclusions for fire management of deserts include initial fires having a bigger impact on subsequent fire potential than secondary fires and fuel potential varying between years, sometimes dramatically.

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Authors' contributions

RS organized the field work, analyzed the data, and wrote the manuscript. BN, KC, TB, BW, and DA conducted field surveys and lab analysis of samples and provided feedback on the manuscript. SS conceived, funded, designed, and set up the study and helped write the manuscript.

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Availability of data and materials

After acceptance for publication, data will be made available in Figshare.

Declarations**Ethics approval and consent to participate**

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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References

- Allen, E.B., R.J. Steers, and S.J. Dickens. 2011. Impacts of fire and invasive species on desert soil ecology. *Rangeland Ecology & Management* 64: 450–462.
- Aanderud, Z.T., et al. 2019. The burning of biocrusts facilitates the emergence of a bare soil community of poorly-connected chemoheterotrophic bacteria with depressed ecosystem services. *Frontiers in Ecology and Evolution* 7: 467.
- Bahr, J.R. 2013. *Exploring post-fire recovery of biocrusts and desert ecosystem services*. Brigham Young University Thesis.
- Balch, J.K., B.A. Bradley, C.M. D'Antonio, and J. Gomez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global Change Biology* 19: 173–183. <https://doi.org/10.1111/gcb.12046>.
- Belnap, J., S.L. Phillips, and T. Troxler. 2006. Soil lichen and moss cover and species richness can be highly dynamic: The effects of invasion by the annual exotic grass *Bromus tectorum*, precipitation, and temperature on biological soil crusts in SE Utah. *Applied Soil Ecology* 32: 63–76. <https://doi.org/10.1016/j.apsoil.2004.12.010>.
- Bishop, T.B., et al. 2019. Spatiotemporal patterns of cheatgrass invasion in Colorado Plateau National Parks. *Landscape Ecology* 34: 925–941.
- Bishop, T.B., R.A. Gill, B.R. McMillan, and S.B.S. Clair. 2020a. Fire, rodent herbivory, and plant competition: Implications for invasion and altered fire regimes in the Mojave Desert. *Oecologia* 192: 155–167.
- Bishop, T.B., B.C. Nusink, R. Lee Molinari, J.B. Taylor, and S.B. St.Clair. 2020b. Earlier fall precipitation and low severity fire impacts on cheatgrass and sagebrush establishment. *Ecosphere* 11: e03019.
- Borchert, M.I., and S. Jain. 1978. The effect of rodent seed predation on four species of California annual grasses. *Oecologia* 33: 101–113.
- Bradley, B.A., et al. 2017. Cheatgrass (*Bromus tectorum*) distribution in the intermountain Western United States and its relationship to fire frequency, seasonality, and ignitions. *Biological Invasions*. <https://doi.org/10.1007/s10530-017-1641-8>.
- Brooks, M.L. 2000. Competition between alien annual grasses and native annual plants in the Mojave Desert. *The American Midland Naturalist* 144 (1): 92–108.
- Brooks, M.L. 2002. Peak fire temperatures and effects on annual plants in the Mojave desert. *Ecological Applications* 12: 1088–1102.
- Brooks, M.L., et al. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54: 677–688.
- Brown, J.H., E. Heske, and J. 1990. Rodent effects on plant communities. *Science* 250: 1705–1707.
- Bukowski, B.E., and W.L. Baker. 2013. Historical fire regimes, reconstructed from land-survey data, led to complexity and fluctuation in sagebrush landscapes. *Ecological Applications* 23: 546–564.
- Bykova, O., and R.F. Sage. 2012. Winter cold tolerance and the geographic range separation of *Bromus tectorum* and *Bromus rubens*, two severe invasive species in North America. *Global Change Biology* 18: 3654–3663.
- Callaway, R.M., and W.M. Ridenour. 2004. Novel weapons: Invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* 2: 436–443.
- D'Antonio, C.M., and P.M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23: 63–87.
- DeFalco, L.A., D.R. Bryla, V. Smith-Longozo, and R.S. Nowak. 2003. Are Mojave-Desert annual species equal? Resource acquisition and allocation for the invasive grass *Bromus madritensis* sp. *rubens* (Poaceae) and two native species. *American Journal of Botany* 90: 1045–1053.
- Enders, M., F. Havemann, and J.M. Jeschke. 2019. A citation-based map of concepts in invasion biology. *NeoBiota* 47: 23–42.
- Esque, T.C., J.P. Kaye, S.E. Eckert, L.A. DeFalco, and C.R. Tracy. 2010. Short-term soil inorganic N pulse after experimental fire alters invasive and native annual plant production in a Mojave Desert shrubland. *Oecologia* 164: 253–263.
- Fuentes-Ramirez, A., J.W. Veldman, C. Holzapfel, and K.A. Moloney. 2016. Spreaders, igniters, and burning shrubs: Plant flammability explains novel fire dynamics in grass-invaded deserts. *Ecological Applications* 26: 2311–2322.
- Fusco, E.J., J.T. Finn, J.K. Balch, R.C. Nagy, and B.A. Bradley. 2019. Invasive grasses increase fire occurrence and frequency across US ecoregions. *Proceedings of the National Academy of Sciences* 116 (47): 23594–23599.
- Helm, D.J., and B.R. Mead. 2004. Reproducibility of vegetation cover estimates in South-Central Alaska forests. *Journal of Vegetation Science* 15: 33–40.
- Hereford, R., R.H. Webb, and C.I. Longpré. 2006. Precipitation history and ecosystem response to multidecadal precipitation variability in the Mojave desert region, 1893–2001. *Journal of Arid Environments* 67: 13–34. <https://doi.org/10.1016/j.jaridenv.2006.09.019>.
- Herrick, J.E., G.E. Schuman, and A. Rango. 2006. Monitoring ecological processes for restoration projects. *Journal for Nature Conservation* 14: 161–171.
- Horn, K.J., and B.R.S.B. McMillanSt.Clair. 2012. Expansive fire in Mojave desert shrubland reduces abundance and species diversity of small mammals. *Journal of Arid Environments* 77: 54–58. <https://doi.org/10.1016/j.jaridenv.2011.10.003>.
- Horn, K.J., and T.S.B. BishopSt.Clair. 2017. Precipitation timing and soil heterogeneity regulate the invasion potential of red brome. *Biological Invasions* 19: 1339–1350.
- HornSt.Clair, K.J.S.B. 2017. Wildfire and exotic grass invasion alter plant productivity in response to climate variability in the Mojave Desert. *Landscape Ecology* 32: 635–646.
- Hunter R (1991) *Bromus* invasions on the Nevada Test Site: present status of *B. rubens* and *B. tectorum* with notes on their relationship to disturbance and altitude. *The Great Basin Naturalist* 52(2): 176–182
- JMP® Pro. 1989–2021. Version 15.0.0. SAS Institute Inc., Cary, North Carolina. <https://community.jmp.com/t5/JMP-Knowledge-Base/How-should-I-cite-JMP-software-in-a-publication/ta-p/575185>.
- Jones, R., J.C. Chambers, D.W. Johnson, R.R. Blank, and D.I. Board. 2015. Effect of repeated burning on plant and soil carbon and nitrogen in cheatgrass (*Bromus tectorum*) dominated ecosystems. *Plant and Soil* 386: 47–64.
- Keeley, J.E., and T.J. Brennan. 2012. Fire-driven alien invasion in a fire-adapted ecosystem. *Oecologia* 169: 1043–1052.
- Kerns, B.K., and M.A. Day. 2017. The importance of disturbance by fire and other abiotic and biotic factors in driving cheatgrass invasion varies based on invasion stage. *Biological Invasions* 19: 1853–1862.
- Klinger, R., and M. Brooks. 2017. Alternative pathways to landscape transformation: Invasive grasses, burn severity and fire frequency in arid ecosystems. *Journal of Ecology* 105: 1521–1533.
- Korfmacher, J.L., J.C. Chambers, R.J. Tausch, B.A. Roundy, S.E. Meyer, and S. Kitchen. 2003. a technique for conducting small-plot burn treatments. *Rangeland Ecology & Management/journal of Range Management Archives* 56: 251–254.
- Lenth, R.V. 2021. emmeans: Estimated marginal means, aka least-squares means. *R Package Version* 1 (6): 1.

- Levine, J.M., P.B. Adler, and S.G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* 7: 975–989.
- Levine, J.M., M. Vila, C.M. D'Antonio, J.S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Biological Sciences* 270: 775–781. <https://doi.org/10.1098/rspb.2003.2327>.
- Mack, R.N. 1981. Invasion of *Bromus tectorum* L. into the Western North America: An ecological chronicle. *Agroecological Ecosystems* 7: 145–165.
- Mahood, A.L., and J.K. Balch. 2019. Repeated fires reduce plant diversity in low-elevation Wyoming big sagebrush ecosystems (1984–2014). *Ecosphere* 10 (2): 1–19.
- NOAA (2023) Salt Lake City Climate Book 2021. *National Ocean Service Website* <https://www.weather.gov/slc/climatebook#>. Accessed 10 Oct 2023.
- Ojima, D.S., D. Schimel, W. Parton, and C. Owensby. 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry* 24: 67–84.
- Pilliod, D.S., J.L. Welty, and R.S. Arkle. 2017. Refining the cheatgrass–fire cycle in the Great Basin: Precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution* 7 (19): 8126–8151.
- Ponzetti, J.M., B. McCune, and D.A. Pyke. 2007. Biotic soil crusts in relation to topography, cheatgrass and fire in the Columbia Basin, Washington. *The Bryologist* 110: 706–722. [https://doi.org/10.1639/0007-2745\(2007\)110\[706:bscirt\]2.0.co;2](https://doi.org/10.1639/0007-2745(2007)110[706:bscirt]2.0.co;2).
- Pyke, D.A. (1986) Demographic responses of *Bromus tectorum* and seedlings of *Agropyron spicatum* to grazing by small mammals: occurrence and severity of grazing. *The Journal of Ecology* 74(3): 739–754
- R Core Team. 2018. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rejmánek, M., and D.M. Richardson. 1996. What attributes make some plant species more invasive? *Ecology* 77: 1655–1661.
- Salguero-Gomez, R., W. Siewert, B.B. Casper, and K. Tielbörger. 2012. A demographic approach to study effects of climate change in desert plants. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367: 3100–3114.
- Salo, L.F. 2004. Population dynamics of red brome (*Bromus rubens*): Times for concern, opportunities for management. *Journal of Arid Environments* 57: 291–296.
- Salo, L.F. 2005. Red brome (*Bromus rubens*) in North America: Possible modes for early introductions, subsequent spread. *Biological Invasions* 7: 165–180.
- Seabloom, E.W., J.W. Williams, D. Slayback, D.M. Stoms, J.H. Viers, and A.P. Dobson. 2006. Human impacts, plant invasion, and imperiled plant species in California. *Ecological Applications* 16: 1338–1350.
- Sharp Bowman, T.R., B.R. McMillan, and S.B. St. Clair. 2017. Rodent herbivory and fire differentially affect plant species recruitment based on variability in life history traits. *Ecosphere* 8 (12): e02016.
- Sharp Bowman, T.R., B.R. McMillan, and S.B. St. Clair. 2017. A comparison of the effects of fire on rodent abundance and diversity in the Great Basin and Mojave deserts. *PLoS ONE* 12 (11): e0187740.
- Sharp Bowman, T.R., and B.R.S.B. McMillan St. Clair. 2017c. Rodent herbivory differentially affects mortality rates of 14 native plant species with contrasting life history and growth form traits. *Oecologia* 185: 465. <https://doi.org/10.1007/s00442-017-3944-y>.
- Soulard, C.E. 2012. *Central Basin and Range Ecoregion: Chapter 20 in Status and trends of land change in the Western United States--1973 to 2000*. US Geological Survey.
- St. Clair, S.B., and T.B. Bishop. 2019. Loss of biotic resistance and high propagule pressure promote invasive grass–fire cycles. *Journal of Ecology* 107: 1995–2005.
- St. Clair, S.B., R. O'Connor, R. Gill, and B. McMillan. 2016. Biotic resistance and disturbance: rodent consumers regulate post-fire plant invasions and increase plant community diversity. *Ecology* 97: 1700–1711.
- Underwood, E.C., R.C. Klinger, and M.L. Brooks. 2019. Effects of invasive plants on fire regimes and postfire vegetation diversity in an arid ecosystem. *Ecology and Evolution* 9: 12421–12435.
- Wells, P.V. 1979. An equable glaciopluvial in the West: Pleniglacial evidence of increased precipitation on a gradient from the Great Basin to the Sonoran and Chihuahuan deserts. *Quaternary Research* 12: 311–325.
- Whisenant, S.G. 1989. *Changing fire frequencies on Idaho's Snake River plains: Ecological and management implications symposium on cheatgrass invasion, shrub dieoff and other aspects of shrub biology and management*, 4–10. Las Vegas, NV: U.S. Department of Agriculture.
- Young, J.A., R.A. Evans, and J. Major. 1972. Alien plants in the Great Basin. *Rangeland Ecology & Management/Journal of Range Management Archives* 25: 194–201.
- Zuur, A.F., E.N. Ieno, and C.S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1: 3–14.

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